# LONGITUDINAL STUDIES OF PLAY IN *RATTUS NORVEGICUS*

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Thesis submitted for the Degree of Doctor of Philosophy

University College London

September 1986

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ACKNOWLEDGEMENTS:

This is the first page of the thesis; the last to be written; and the most important one as far as I'm concerned, since this is the one chance I get to record for posterity the names of some of the people who've helped me get this far. During the xxx years it's taken me to write this thing, I've often thought of the witty or profound things I'd put on this page. Unfortunately, now it's finally time to do it, I can't think of any of them - something that's particularly frustrating since this is the one chance I get to express my opinions and prejudices without having to back them up with proof, or qualify them in some way !

So, at the risk of sounding like some aged American actor receiving an Oscar with tear-brimmed eyes, I'd like to express my deepest thanks to the following people, without whom all of this would not have been possible:

First and foremost, thanks to Sandra. She has supported me both spiritually and financially, and given up a great deal merely for me to have a stab at doing what I wanted to do. This thesis has taken priority over her for longer than I care to remember.

Secondly, thanks to my supervisor and mentor, Henry Plotkin. Henry has looked after my interests and inspired me intellectually for a long time; I truly could not have wished for a better supervisor.

Thanks to my parents, both for providing me with an adequate genetic endowment and for nurturing it during the first eighteen years.

Finally, but not least, thanks to all those of my friends who encouraged me when I got despondent - Amita, Sue, Lynda, and especially Andy, whose advice to "get it out the door" I finally followed. And although it might seem out of place to thank her, given that she's going to examine this thesis, I would nevertheless like to express my gratitude to Dorothy Einon, who has looked after my academic interests in the same way as Henry.

Oh yes, and thanks to all the little rats and their mummies, and the inventors of commercial video equipment...

## ABSTRACT:

This thesis describes experiments and observational studies of social play in *Rattus norvegicus*, focussing on two aspects of play which have received relatively little attention: the relationship of play to other behaviours during development, and the immediate causation of play.

Chapter two looks at play in relation to other social and non-social behaviours. Social play showed a distinctive inverted "U"-shaped ontogenetic trend (as did exploration), and was the major form of social interaction for young rats. However, social behaviours accounted for little of the developing animal's overall time-budget.

No evidence was found for a relationship between play and the agonistic behaviours it is traditionally supposed to resemble. Experiments two and three provide further data on this point.

Chapter three looks at temporal and contextual aspects of play - features which have been studied very little. Most play-bouts were found to be very short, and to show little reciprocity between interactants. Play occurred in a context of exploration, play, and activity, and was not associated with sedentary or agonistic behaviours.

Experiments on play's immediate causation highlight the importance of environmental factors in determining whether play will occur. Experiment one shows that the "rebound" effect (increased play induced by prior short-term social deprivation) is not ameliorated by non-playful social contact. Experiment two looks at the effects on play of environmental change. Experiment three shows that food-deprivation selectively suppresses play.

These results suggest that play's "costs" may have been overestimated; that play may have immediate benefits (exercise and allo-grooming); and that of the plethora of benefits which play could provide for this particular species, practice of agonistic activities seems the least plausible.

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# CHAPTER ONE: INTRODUCTION:

## 1.1: GENERAL INTRODUCTION:

### 1.1.1: Reasons for studying social play in rats:

This thesis concerns itself with studies of social play in laboratory-housed *Rattus norvegicus*. Why study social play, and why investigate it in the laboratory rat?

The answer to the first question is that over the past thirty years or so, the potential importance of play in development has increasingly come to be appreciated. From being regarded as a "frivolous" or "trivial" epiphenomenon, play is now regarded as the source of any benefits imaginable - a view sometimes taken to absurd extremes (eg, Athey, 1984). While the true significance of play for normal development probably falls somewhere in between these two viewpoints - being neither "trivial" nor "vital" - nevertheless it is now clear that play is a major aspect of development, and yet one which is still poorly understood. By studying play, one is investigating early development.

Another reason for being interested in play is because of the way in which it highlights many of the most serious problems in contemporary behavioural biology. In particular, when one looks at play, one is forced to grapple with problems of definition (the difficulties of dissecting the continuous stream of behaviour into meaningful units, and distinguishing between units which appear to be morphologically similar but motivationally

different from each other), and of function (play's apparent lack of function posing a challenge for adaptationist assumptions that all behaviour must have survival value of some kind). Social play, as opposed to other more solitary forms of play, also raises problems for the study of communication, altruism and co-adaptation. One of the most important reasons for studying play is because of the way in which it brings to the fore difficulties such as these, problems which are less apparent (though ultimately no less real) in other areas of behavioural inquiry.

A number of factors influenced the decision to use the laboratory rat as a species in which to study social play. The rat's prime advantage is its convenience: rats have a relatively short period of development, within which there is a fairly circumscribed period of social play (Einon and Morgan 1977). Rats are of course also easy to breed and maintain in captivity.

These are all important considerations if one wishes to study a developmental phenomenon. However, there are other reasons which have less to do with matters of practicality: Rodentia are the largest group of mammals, and yet relatively little is known about the development of their social behaviour, even in a species as otherwise well-studied as the rat. This is especially true in the case of play; as will be evident from the reviews to follow, research on play in infra-human species has been heavily dominated by studies on primates.

While these have provided a great deal of information on play, it is important to see to what extent conclusions drawn from them can be applied to other playing species, if one is interested in trying to formulate cross-species generalities about play.

A final point is that progress in our understanding of play is most likely to come about by relating play to other aspects of a species' biology and behaviour (in both immature and adult individuals), rather than by looking at play in isolation (Fagen, 1981). If this is so, then the rat must be a prime candidate for use as a species in which to study play, since there already exists such a wealth of information (on the rat's adult social and non-social behaviour, cognitive abilities, physiology, and non-playful development) to which data on play can be related.

1.1.2: Areas of inquiry to be reviewed:

The primary aim of the studies described in this thesis was to obtain observational data on social play in the rat, since it is the writer's conviction that objective and detailed observations are an essential preliminary to all further research.

Obviously, however, observations are influenced by the observer's theoretical preconceptions about the phenomena to be studied. This section thus has four aims.

The first objective is to define the subject-matter - particularly important with "play", where reliance on mutual intuitive understanding has substituted for

precision of definition.

Secondly, there will be a brief summary of the principal theoretical orientations towards play (those dealing with the issue of its possible functions), since they have largely determined what features of play have been examined to date, and hence how play is perceived.

Thirdly, reviews will be made of two areas of play research which have been unduly neglected, considering their importance to our understanding of what is essentially a developmental process: the issues of play's immedate causation, and its ontogenetic development.

Finally, there will be a brief discussion of the strengths and weaknesses of the surprisingly few studies that have been made of the development of social behaviour in the rat.

In all of these reviews, it will be noticed that scant attention will be paid to the most playful of species, Homo sapiens. While the writer is familiar with the literature on human play, a conscious decision was made to restrict the following discussions (with a few exceptions) solely to infra-human species. The main reason for this is because much of human play appears to be qualitatively different from animal play, in that the former often involves elements of fantasy and employs language. With the possible exception of the higher primates, it is doubtful whether such elements have any counterpart in animal play. As will be discussed below, it is difficult enough to make valid comparisons

between different infra-human species, without involving humans as well. This is not to deny, however, that there may be many points of similarity between humans and animals in their play, especially in the case of the particular kind of play to be studied in this thesis, rough and tumble social play-wrestling (Blurton-Jones 1967; Smith and Connolly, 1972; Aldis 1975; Humphreys and Smith 1984).

## 1.2: THE DEFINITION OF PLAY:

### 1.2.1: The Problem of Definition:

Many writers on play have noted that there is no widely-accepted definition of play, but have nevertheless then proceeded to give details of their work on this same topic, claiming that "play, though difficult to define, is behaviour which can easily be recognised" (Poole and Fish 1975). Lorenz (1956) sums up the typical attitude towards defining play: "There is a good excuse for naively using a word of common parlance even if one cannot give an exact definition of the concept corresponding to it: very usually there is a real natural unit corresponding to a concept for which the natural growth of common language has developed a word".

It is true that human observers can often show high agreement on their judgments of whether or not a behaviour is "play", both in humans (Matthews and Matthews 1982; Smith and Lewis 1985) and in animals (Humphreys 1982). In the case of social play, since we ourselves are social, playing animals, we may often be responding to the same cues that inform the animals themselves that play is occurring. However, reliance on intuitive recognition is hardly sound science, and attitudes such as that of Lorenz are probably the source of most of the confusion in the literature on play.

Some attempt at explicit definition should be made every time play is discussed, for at least two reasons.

Firstly, whether or not he commits himself to a formal definition, any researcher nevertheless holds an implicit definition of play which is affecting his observations. Secondly, the lack of common definitions in the field of play research makes it extremely difficult to integrate information on play from different studies.

The one term "play" has actually been applied to a wide variety of behavioural phenomena. It has most commonly been used to describe "social play", interactions between two or more animals that resemble agonistic behaviours such as wrestling, chasing, pawing, clawing and biting, but without the expected damaging consequences of "serious" aggression.

"Play", however, is a term also used to describe "object play", a category comprised of two overlapping kinds of behaviour. The first of these, "predatory object-play", involves a predator repeatedly chasing, pawing, pouncing upon and otherwise manipulating a prey animal in a vigorous manner, thereby (in the opinion of an observer) deferring the processes of killing and eating it. The second type of "object play" covers various examples of extensive object manipulation which is apparently "functionless" or which seems to be engaged in "for its own sake".

Yet a third category of playful behaviour consists of "locomotor play", gambolling, frisking and other energetic locomotor behaviours displayed by young animals without apparent environmental cause- for example, running which

resembles fleeing from a predator, except that there is no predator. The term "locomotor play" is also used to describe "play-chasing" and "approach-withdrawal" play, behaviours which apparently occur in close relation to bouts of playful wrestling.

With problems like this is mind, the terminology to be used in the following discussion will be made clear at the outset: throughout chapter one, the term "play" will henceforth be used as a generic term, as a shorthand way of writing "social, locomotor and object-play". Where something is felt to be relevant only to one particular type of play, then terms such as "social play" or "object play" will be used. For the rest of the thesis, the term "play" should be taken as meaning "social play", unless otherwise stated.

As will be discussed below, these three broad categories of playful behaviours may be quite distinct, and the usefulness of distinguishing between them is becoming increasingly accepted (eg. Bekoff and Byers 1981; Smith 1982; Burghardt 1984). However, failure to define exactly what is meant by play whenever the term is used, has led to them being indiscriminately lumped together with each other, and with other juvenile social and exploratory behaviours. The term has been used as a "wastebasket" category into which have been placed any behaviours for whih no obvious "function" can be detected, and this in turn has further clouded the issue of definition (Muller-Schwarze, 1978).

1.2.2: Definitions of Play:

Attempts at defining play can be classified in various ways. "Functional" definitions have attempted to classify behaviours together on the basis of common function, while "structural" definitions have grouped behaviours according to perceived similarities in the morphology of the behavoiur patterns themselves. Most definitions consist of a mixture of these two approaches (Martin 1984).

"One-line" definitions of play have generally been less informative than attempts to define play by presenting lists of characteristics, which try to capture the "essence" of play by describing a group of features which, although none of them by itself is unique to play, when taken together demarcate play from other behaviours - an "injunctive definition" (Lorenz 1965, after Hassenstein 1945).

The set of characteristics which has received most attention has been that devised by Loizos (1966), but numerous other attributes of play have been suggested before and since. These will therefore be considered at the same time.

1.2.2.1: Play is "pleasurable":

It has been suggested that play is "pleasurable" (Beach 1945; Bekoff 1974, 1978; Mears 1978) or "self-rewarding activity" (Morris 1962). This may be so,

but motivational or emotional states are difficult enough to identify in humans, let alone in animals. Play, however, can be used as a reinforcer (Humphreys and Einon, 1981).

1.2.2.2: Play is predominantly a juvenile activity:

(Beach 1945; Bekoff 1978). This is so for all species so far studied in which play occurs. Adults may play, especially in captivity, where animals are freed from pressures of foraging and predation and are often placed in abnormal social situations (Redican and Mitchell 1974). Even in the wild, adults of some species may play frequently (eg, adult male bonnet macaques, Kaufmann 1967; adult male rhesus macaques, Simonds 1965). However, adult play is mainly social play wth young animals, in response to the latters' solicitations: relatively rarely have adults been reported to initiate social play, play wth other adults, or engage in locomotor or object play. Even in species in which individuals remain highly playful in adulthood, such as the chimpanzee (van Lawick-Goodall, 1968), play is always most frequent in the young.

1.2.2.3: Play has no immediate biologial function:

A common failing has been to define play by functional exclusion. Schaller (1963), for example, defines play as "any relatively unstereotyped behaviour in which an animal was involved in vigorous actions seemingly without definite purpose"; Hinde (1970) considers play to be a "general term for activities which seem to the observer to make no immediate contribution to survival";

and Rasa (1971) calls play "behaviour with no immediate reward other than its peformance". This is an approach which is indefensible on logical grounds (Beach 1945), since not only is it very difficult to show that a given behaviour has no function, but also play then by definition has to be functionless behaviour - an untenable position.

1.2.2.4: Play-patterns have a distinctive sequencing:

(Loizos, 1966). The sequencing of actions in play is held to differ from the sequencing of the "serious" behaviour patterns that play patterns are claimed to resemble.

1.2.2.4.1: Temporal reorganisation:

There may be temporal reorganisation of "serious" patterns when they are performed in play (Loizos, 1966). Such evidence as there is on this point seems somewhat equivocal. Muller-Schwarze (1971) studied the temporal features of bouts of social play in the black-tailed deer, and found that the "irregular" appearance of the bout was due to alternation of sequences of playful and "serious" patterns; but within each category, motor patterns of both the serious and playful sequences had the typical "serious" order. In contrast to this, Bekoff (1977a) found that temporal sequences in canid social play differed significantly from those in non-play situations.

1.2.2.4.2: Unpredictable sequencing:

It has been claimed (Loizos, 1966; Bekoff, 1974) that

the sequencing of patterns in play is less predictable than in "serious" behaviour. If "unpredictability" is equated with "high variability", then there is some evidence that this is so. Muller-Schwarze (1975), in the black-tailed deer, and Bekoff (1976a) in canids, found that social play-sequences were less ordered than those in non-play behaviour. However, Poole and Fish (1975) found that social play in young rats did have definite sequences, though these were not the same as those observed in adult aggression, which employs apparently similar behaviour patterns.

1.2.2.4.3: Sequence fragmentation by "irrelevant" acts:

There may be fragmentation of a behaviour pattern that resembles a "serious" pattern, by the introduction of "irrelevant" acts (Loizos, 1966). Muller-Schwarze (1971) claims that this is a feature of both deer and rat play. However, as Bekoff (1976a) points out, in the absence of detailed behavioural analyses it is hard to say whether any behaviour is "relevant" or "irrelevant".

1.2.2.4.4: Exaggeration and repetition of patterns:

Play patterns may show exaggeration and repetition compared to their non-play counterparts (Loizos 1966; Bekoff 1974; Henry and Herrero 1974). Wilson and Kleiman (1974) defined exaggeration in terms of the amplitude of the movement and the rapidity with which it was executed, designating movements of this kind "locomotor-rotational

movements". Although Wilson and Kleiman themselves used this description for behaviour patterns which few would agree were truly playful (Hole and Einon 1984), Bekoff (1974) for three species of canid, and Poole (1966) for the polecat, did find an increase in the amplitude of behaviour patterns in social play, resulting in a "loose", "bouncy" gait. With respect to duration, however, although there are reports of play-fighting being performed more slowly than adult aggression in the rhesus monkey (Symons 1974) and the Northern elephant seal (Rasa 1971), Henry and Herrero (1974) found exaggeration in terms of duration for only one of six motor patterns in the play of black bear cubs, and Hill and Bekoff (1977) found no increases in duration in coyote social play. Henry and Herrero (1974) did find greater repetition of motor-patterns in play, which was not attributable simply to play sequences lasting longer than adult aggressive behaviour patterns. Increased repetition compared to non-play behaviours has also been reported for the orang-utan (Horr 1978), the wolf, dog and coyote (Bekoff 1974), the rhesus macaque (Symons 1974) and the badger (Eibl-Eibesfeldt 1950).

Loizos (1966) suggests that play seems "uneconomical" and "inefficient" in appearance; inasmuch as these phrases have any meaning, such features probably relate to exaggeration and repetition in play.

1.2.2.4.5: Incompleteness of sequences:

There may be incompleteness (again, with respect to non-play behaviour of similar appearance), and repetition

of this incomplete sequence (Loizos, 1966). This could be taken to represent the way in which play lacks the "consummatory acts" characteristic of non-play behaviour. For example, predatory play does not lead to eating or the killing bite (eg, African dwarf mongoose, Rasa 1973), and play-fighting does not lead to physical damage of one interactant by the other nor to their dispersl (Loizos 1969). There does seem good evidence that certain adult behaviour-patterns are absent in play, especially threat postures and alarm vocalizations. This is so for deer (Muller-Schwarze 1971); black bear cubs (Henry and Herrero 1974); polecats (Poole 1966); baboons (Cheney 1978); rhesus macaques (Symons 1974); patas monkeys (Hall 1965); coyotes (Bekoff 1974); and Steller's sea-lions (Farentinos 1971). Rat social play lacks "those behavioural elements indicative of high levels of attack or fear" (Poole and Fish 1975). In the badger and the black bear, incomplete piloerection occurs and there are few vocalizations. Biting is generally inhibited in social play, as shown for example in the polecat (Poole 1966), badger (Eibl-Eibesfeldt 1950), Columbian ground-squirrel (Steiner 1971) and Steller's sea-lion (Farentinos 1971).

1.2.2.5: Patterns unique to play: "Play Signals":

There may be certain motor patterns which are observed only in play (Loizos 1966). Such patterns seem to be mainly "play signals", acts or postures which serve a "metacommunicative" function, informing the partner that "this is play" (Bateson 1955). Numerous examples have been

reported, mainly in the context of social play. Perhaps the best example is the "play face" (van Hooff 1967) which occurs in the social play of many primates (eg, chimpanzee, Goodall 1968; rhesus macaque, Symons 1974; stumptail macaque, Chevalier-Skolnikoff 1973) and is also found in the polecat (Poole 1966, 1978), coyote (Bekoff 1974) and black bear (Henry and Herrero 1974). Play signals are used both to solicit social play, and to maintain an ongoing play interaction. The latter signals may be quite sophisticated; for example, Bekoff and Jamieson (cited in Bekoff 1974) found that canids perform very subtle eye and head movements throughout the the course of a play-bout, which inform the partner that the behaviour has a playful intent.

Loizos (1969) considers the existence of play signals to be one of the major features distinguishing play from other activities such as aggression. Logically they must be an essential accompaniment of social play, since otherwise players would continually run the risk of having their behaviour misinterpreted. (One might expect them also to be essential in locomotor play, since otherwise playful "escape from a predator" might elicit "serious" predator-avoidance behviour from every other conspecific in the vicinity!) Yet despite the many and varied play signals which have been reported, and the fact that some animals spend a considerable amount of their playing time in such behaviours (48% in polecats, according to Poole 1978), the emphasis in play research has generally been on

those behviour patterns which superficially resemble behaviour from other motivational categories.

1.2.2.6: Suspension of rules:

Dolnihow and Bishop (1970) suggest that in human play, at least, there is "suspension of rules" that otherwise would be in force. This might correspond to claims that prominent features of animal social play are role-reversal (animals in turn dominating and being subordinate, chasing and being chased), and "self-handicapping" of stronger animals when playing with weaker ones (Bekoff 1978). Role reversal occurs frequently in canids (Bekoff 1974), baboons (Cheney 1978; Owens 1975a, 1975b) and the Columbian ground squirrel (Steiner 1971), whereas rhesus macaque social play is characterised by both partners adopting dominant roles for the duration of the interaction (Symons 1974). Poole (1978) and Poole and Fish (1975) found no evidence of role reversal in polecats and rats respectively, but attributed this to their small sample sizes in each case.

This is not to say that there are no rules in force during social play: role-reversal and self-handicapping may be seen as alternative rules to those normally in operation during the agonistic encounters which social play is held to resemble. Together with the "rule" that play must not be rougher or more physically damaging than the weakest interactant will tolerate, these rules serve to ensure that neither partner "cheats" by obtaining the benefits of play experiences at the expense of the other,

and that the interaction does not break down prematurely. (This is not of course to suggest in any way that the "rules" of play are adhered to with any degree of "consciousness" or "awareness").

1.2.2.7: Evaluation of definition by enumeration of characteristics:

There are three major problems with these kinds of definitions, at least as they are originally conceived.

1.2.2.7.1: The level of analysis of definition:

It is often unclear at exactly what level of analysis, behaviourally, play behaviours are being discussed. For example, if "exaggeration" is claimed to be a general feature of play, then it needs to be made very clear exactly what is being exaggerated. Also, since "exaggeration" is a comparative term, one should specify what behaviour one has in mind as an "unexaggerated" baseline for comparison (Moran 1985). "Exaggeration" might conceivably occur on a number of different planes of description, from the level of the individual behaviour patterns comprising play (ie, a pounce in play being physically higher than one in the context of aggression) to much grosser levels of analysis (ie, the whole playful behaviour sequence being exaggerated in terms of length or some other feature). Failure to clarify exactly what level of analysis is under consideration when a characteristic of play is being considered may render that feature too imprecise to be used validly in cross-species comparisons

of play. More precise descriptions are required of just what kinds of features are common attributes of play.

1.2.2.7.2: Over-inclusiveness of definitions:

It is often not made sufficiently clear just what type of play is being defined. The assumption that social, locomotor, and object play represent a unitary phenomenon is often taken for granted. However, if these behaviours are distinct, as seems more likely, then such definitions are doomed to failure.

Loizos' (1966) list of characteristics, for example, was originally conceived in relation to social rough and tumble play, and may not apply so well to predatory play. Many of these attributes of play seem to cover all instances of play equally well: for example, there is no consummatory act apparent in predatory play (where the prey is not killed or eaten), in social play (where there is no infliction of damage to the partner), or in locomotor play (where there is no escape from a predator because the predator does not exist).

Other features of play appear to be less universal; for example, explicit play-signals seem to be more a feature of social play than of locomotor or object play (although the exaggerated motion of locomotor play might be considered a play signal, and even in "serious" object-play a play-face may sometimes be shown - Goodall, 1968). Role-reversal is obviously exclusive to social play. In short, every attempt at defining play should make clear the limits of the phenomena it is attempting to

cover.

1.2.2.7.3: Inappropriate comparisons in definition:

The preceding discussion shows that a prominent feature of most attempts at defining play is the tendency to do so by comparing play behaviours to their "functional" counterparts, behaviours to which they bear some supposed morphological resemblance. Most usually, these comparisons are between "play" and "serious" adult behaviours. For example, Aldis (1975) writes: "the serious counterparts of [chasing and playfighting in young animals] may be broadly classified as agonistic behaviours- predation, aggression, and flight. In play, these behaviours are usually accompanied by play signals and are modified in certain ways (lower intensity, relaxed muscle tone) from their serious counterparts. In addition, some serious behaviours may be omitted, new behaviours may be added, and the order may be changed..." Wilson (1971b) asserts that "in mammals, play is comprised largely of rehearsals performed in a non-functional context of the serious activities of searching, fighting, courtship, hunting and copulation". It is as though play behaviours have somehow been "borrowed" from other contexts, rather than being behaviour patterns in their own right. The concept of "borrowing" still persists in recent definitions of play (eg, Bekoff and Byers 1981; Martin 1984; Meaney, Stewart and Beatty 1985).

This practice of defining play by comparison is

understandable and often almost unavoidable. The very terms employed to discuss play force one into such trains of thought: "play-fighting, "play-chasing". So too does the way in which play is often defined in practice, eg by noting that the context in which the behaviour in question occurs, is not what would be expected if the behaviour represented agonistic behaviour. To cloud the issue further, there are documented cases of intergradation of "playful" and "agonistic" behaviours: a single play bout may turn into "serious" fighting, and play itself may become rougher or more aggressive with increasing age (Fagen 1981).

Consequently, given this apparent lack of clear structural differentiation of play from other behaviour patterns, an assessment must be made of the extent to which the various kinds of play may validly be considered motivationally distinct from their non-play analogues. At least in the case of social play, there is a wide range of evidence in favour of regarding play as a discrete category of behaviour, motivationally as well as structurally.

### 1.2.3: Play in Relation to Other Behaviours:

Play has been confused with a wide variety of other kinds of behaviour. Ethologists have attempted to re-classify play patterns (especially locomotor and predatory object-play) as either "vacuum", substitute or displacement activities, while psychologists have

confounded object play and exploration. The other main confusiom has been between play and "serious" activities - researchers either trying to interpret play as adult activities misinterpreted in some way, or looking at play simply in terms of its similarities and differences to adult "functional" behaviour patterns.

1.2.3.1: Play and Displacement Activities:

As shown by Meyer-Holzapfel (1956) and Ewer (1968), although there are superficial similarities between play, and displacement and vacuum activities, on closer inspection they are quite distinct. Vacuum and substitute activities give the impression of being "driven", and their goal is to perform a consummatory act - the very act that is so often said to be lacking in play. The context in which displacement and vacuum activities occur is very different from that of play, the former behaviours generally occurring under conditions of stress, whereas all types of play are traditionally held to occur only in a "relaxed field" (Bally 1945). Other differences are that play is primarily a characteristic of young animals, whereas the other behaviours occur especially in adults; play signals exist which are unique to play and do not occur in the other categories; and a great deal of play is of a socially-interactive nature. Finally, something about the detailed morphology of play patterns gives human observers subjective impressions of "looseness" and "relaxedness" which are lacking in observations of the other activities (Ewer 1968).

1.2.3.2: Play and Exploration:

Play (in particular object and locomotor play) has often been confounded with exploration. Lorenz's (1971) conception of "play" is synonymous with "latent exploratory learning". Welker (1956abc), in describing some determinants of exploration and play in chimpanzees, treats them as being indistinguishable. Welker (1961), following Groos (1898), says that "play is the generic term, exporation being only one type of play". Thorpe (1963) considers that general exploration of the environment often takes the form of play, learning deriving from this process of play or exploration.

Attempts to define exploration precisely have been as unsuccessful as attempts to define play. One factor in this difficulty may be that, as with play, different types of behaviour have been subsumed under one heading. Berlyne (1960) contrasts "specific" exploration (directed at particular features of a novel object or environment, with the aim of specific information gain), to "diversive" exploration (which constitutes attempts at varying the stimulation gained from a familiar object or environment). Specific exploration seems quite distinct from social, locomotor or object play. Diversive exploration of the environment or a conspecific may be only an incidental element of locomotor and social play, but seems to be synonymous with object play.

The main confusion in the literature can thus be

traced to failure to distinguish playful object manipulation (diversive exploration) from exploratory manipulation (specific exploration). However, Hutt (1966) found that the two were clearly distinguishable on the basis of their differing time-courses. Specific exploration seems to be directly concerned with learning the properties of a novel object, since it is at a maximum level immediately after the object's initial presentation and shows a monotonic decline with increasing familiarity. Diversive exploration (object play) shows the opposite trend, reaching a peak only once the object is familiar. Learning of stimulus properties seems to be less in evidence in the latter behaviour. West (1974) found that domestic cats play more with familiar objects, and explore more with unfamiliar objects. Muller-Schwarze (1971) noted that in the black-tailed deer, there were clear differences in the daily cycles for exploration and play, play being largely restricted to two activity periods each day, whereas exploration tended to occur throughout the day.

In addition to these short-term differences in temporal patterning, there are also differences in the ontogenetic distribution of the two kinds of manipulation: play is generally confined to a more or less discrete period between infancy and adulthood, whereas specific exploration generally both precedes play and persists beyond it, into adulthood (at least in many species). Thus in the rat, social play disappears at about 70 days, but

the rate of exploration does not decrease (Muller-Schwarze, 1966).

1.2.3.3: Play and "serious" behaviours:

As already mentioned, an overriding concern has been to differentiate play from similar non-playful behaviours, and there is considerable evidence to suggest that social play is not "immature aggression".

Within a species, social play is recognised as distinct from "serious" aggression by both adults and peers. Acts can be performed in social play which would not be tolerated in "serious" contexts - for example, domination of an animal by a partner who is otherwise subordinate to him. This differentiation of play from other behaviours is due largely to the presence of "play signals"; the existence of play signals, which the partner recognises and in the absence of which actual aggression may occur, is strong evidence that the players themselves view play as something which is separate from other behaviours.

Furthermore, social play at least, is also recognised across species. There is high inter-observer reliability for deciding that something called "play" is occurring. This is not only so for humans: there are a number of reports of social play occurring between members of different species (eg, badger and dog, Eibl-Eibesfeldt 1950; howler monkeys and chimps, cited in Fagen 1981) which suggest that the two species concerned are able to

recognise certain attributes of the other species' behaviour as play behaviour and respond to them appropriately.

The factor which is most important in determining whether play should be regarded as a behaviour category in its own right, is whether there exists a separate motivation for play. Some critics of the concept of play have claimed that play is somehow "not motivated", that play is a non-directed activity attributable to some factor such as a random discharge of neural energy or a lack of inhibitory mechanisms (Altmann, Brunner and Bayer 1973). Others have suggested that play does not have a motivational basis distinct from that of other "serious" behaviours, play being either the result of inadequate motivation of "normal" behaviour sequences of feeding, aggression, sex, etc, or the consequence of the animal being too immature for the effective performance of a behaviour pattern- for example, "play-mounting" would be "real" mounting if the animal were sufficiently developed to be able to mount and achieve effective intromission. There now exists, however, some evidence that much of play does have its own motivation.

Deprivation of play or social contact during the time in ontogeny at which animals would otherwise play, leads to a subsequent increase in play which is quite distinct from increases in other behaviours (eg, Einon, Morgan and Kibbler 1978; Panksepp and Beatty 1980). Humphreys and Einon (1981) have shown that play is a reinforcer; young

rats will learn a T-maze in order to obtain an opportunity for social play. Play behaviours are performed regardless of whether or not they result in more traditional reinforcers being obtained (Bruner 1974), and indeed conventional reinforcers may actually decrease the occurrence of play in certain circumstances (Schiller 1949). Play may even be engaged in despite considerable negative reinforcement (Bernstein 1976). Further evidence for considering play as a distinctive behavioural category comes from observations that food deprivation often reduces the frequency of play more than it reduces the frequency of other behaviours (eg, Baldwin 1976; Muller-Schwarze et al, 1982).

Play occurs at a distinct time in life, generally in quite species-specific ways. The work of Einon and her associates (eg, Einon and Morgan, 1977; Einon, Morgan and Kibbler 1978) suggests that in the rat, at least, there is a "sensitive period" for play in ontogeny, within which paired isolates show social play, and outside of which play does not occur. There are a number of studies claiming that play and agonistic behaviour occur at quite separate stages in development. For example, in the polecat, social play occurs at 7-21 weeks whereas fighting occurs at 7-8 months (Poole 1978). In coyotes (Fox and Clark 1971; Bekoff 1977), severe fighting occurs before the development of social play. If play shared motivation with other behaviours, such a distinctive distribution in ontogeny would not be expected to occur.

1.2.4: Why is Definition of Play Difficult ? :

There is thus some evidence that play is a discrete behavioural category; at times it may intergrade into other behaviors, but this is a feature of any definitional category. Difficulties in defining play arise not from its lack of validity as a category of behaviour, but from other factors.

1.2.4.1: No consummatory act in play:

In other areas of behaviour, a behaviour is defined by looking at its consummatory act, its endpoint or immediate "function" (Ewer 1968). Play, however, has no immediately discernible function; there is no consummatory act. Since our methods of defining behaviour categories have been developed to cope with categories where there are immediate observable results (or where, as in the case of learning and memory, techniques have been devised by which to produce immediate observable consequences), difficulties arise when it comes to coping with play.

1.2.4.2: Apparent similarity of "playful" and "serious" behaviours:

Most motivational states are identified by means of their own relatively distinct behaviour patterns, but this is not so in the case of play. Play patterns are said to resemble the behaviour patterns of other motivational states, but to differ from them in some subtle, elusive and indefinable manner. In effect, attempts to define play by listing the qualities by which it differs from (usually adult) "serious" activities, really represent attempts to

identify exactly what feature of play is being used intuitively to distinguish it from other behaviours. This quality of play has been termed "exuberance" (Ewer 1968, Einon 1980) or "appearing pleasurable" and generally left at that.

However, exuberance must represent some feature of the animals' behaviour which is potentially amenable to objective measurement. This quality effectively makes the behaviour patterns seen in play, behaviours in their own right, rather than being "borrowed" from some other context.

Because play patterns superficially resemble those of other behaviours, researchers on play have concentrated on attempting to distinguish between what they regard as the same patterns under different motivational systems. Thus play behaviours are seen as "reordered", "exaggerated", etc, but always with respect to how they might be expected to be seen in some other context. This approach is too unsubtle in its determination of what constitutes a "separate" behaviour pattern; it is better to regard playful and "serious" behaviours as superficially similar but essentially different behaviours, each in its own right. The continual contrasting of play and adult aggression, which was originally a useful simile for highlighting certain features of play, has become a misleading constraint on our conception of play.

In short, analysis of play requires a finer level of

analysis than the gross behavioural comparisons to date. This is not to say that play behaviours do not resemble "serious" behaviours; they may do so, but that must be a secondary consideration. It would seem profitable to take a different orientation towards defining play.

Play should be defined in structural terms: in an area where function is poorly understood, it seems futile to use functional criteria in definition. In any case, such use of functional terms has generally been in a negative sense - ie, play has "no function", play is "goalless", etc. Only by detailed definitions in terms of the morphological patterns involved in play might researchers assess effectively whether or not they share the same opnnions as to whether or not a given behaviour is "play". Such definitions should also, by their very nature, force workers into identifying exactly what factor of the behaviour they are studying, is "playful".

This should not be accomplished primarily in terms of contrasts between "play" and "non-play" behaviours, and especially not between play and adult behaviours, since rigid dichotomising of this kind encourages a static view of play, and obscures the fact that behaviours intergrade and develop in ontogeny. Muller-Schwarze (1978) emphasises that play may develop as much as any other behaviour and is part of an ontogenetic continuum of behavioural development. Lazar and Beckhorn (1974) were making a valid point when they claimed that the present concept of play is a hindrance because it obscures investigation of

behavioural development.

1.2.5: An Attempt at Definition:

The above discussion suggests a number of conclusions.

Firstly, in the light of our present knowledge, it seems futile to attempt to include under one all-embracing definition, all of the phenomena which have been described as "playful". It is an open question whether all of the different types of play that have been described differ only in the object to which they are directed (so that play is a unitary phenomenon, expressed in different ways), or whether quite different processes have been lumped together because we lack an adequate vocabulary to differentiate between them. In the absence of certain knowledge that they are distinct, it would seem safer to consider social, locomotor and object play separately.

Secondly, emphasis should be placed on the uniqueness of play behaviour-patterns, both motivationally and morphologically. At the sane time, it is futile to try to construct a definition of play which distinguishes it in an absolute sense from all other behaviours. Probably the best approach is something like Fagen's (1981) concept of "focal points" of categories, which are "typical" examples of the category in that they show all of the characteristics claimed of that category, and around which are grouped less definite examples. Chalmers (1980, 1984) has adopted a similar approach, dividing play patterns

into "play markers" (behaviours which we are highly confident in calling "playful", eg play-signals which are unique to play) and "components" (behaviour patterns which we are more or less confident in terming playful, depending on the context within which they occur). This concept of "confidence" in the definition of play could equally well be applied on the level of categories or in terms of the individual behaviour patterns within a category.

A working definition on the basis of these points thus posesses the following features. Only social play will be considered in this thesis. Behaviour will be regarded as social play if it possesses the following characteristics, placed in decreasing order of value in identifying play behaviour:

1: There are play signals, patterns unique to the play context; for social play, these are the crucial "focal points" of the category. Play signals probably pervade the whole of the encounter, giving rise to play's "exuberant" appearance, and ultimately objectively analysable in terms of the characteristics enumerated by Loizos (1966) and others. However, until features such as "exaggeration" and "unpredictability" are better defined, quantified and considered away from inappropriate comparisons with adult behaviours, then use of play signals in a working definition of social play must be restricted to the more obvious ones - such as, in the rat, the high pounce which almost invariably precedes

play-wrestling.

2: There is an absence of threat signals, biting and general infliction of damage to the other animal.

3: The encounter is interactive in nature, with each animals' behaviour being a stimulus for the other, and each animal attending to the other.

4: There is a high degree of physical contact between interactants.

5: The behaviour occurs in an apparently non-competitive context: ie, there is no apparent contest for resources such as food. Defining play by its lack of apparent immediate consequences (eg, Bekoff and Byers 1981; Martin 1984; Hole and Einon 1984) is logically distinct from saying that play can be defined by its actual lack of an immediate function. Nevertheless this is an admittedly very weak criterion, as there is always the possibility that there is a competitive element in an interaction which is not being recognised by the observer, and it also logically implies definition by exclusion.

These criteria are a preliminary basis for deciding what is play in the animals observed, with as little recourse as possible to interpretations of motivation, function or relationship to adult behaviour. Such a definition permits an analysis of play in relation to other juvenile social behaviours such as grooming or aggression, these latter categories possessing some but not all of the features of play. For example, grooming has the social and contextual criteria of play, but lacks the

morphological features (ie. play signals); whereas aggression differs on all these points except perhaps for some gross morphological similarities (but certainly not in the sense of showing play-signals).

## 1.3: THE FUNCTION OF PLAY:

### 1.3.1: Introduction:

Fagen (1981) suggests that theories on play's functions have guided data collection as much as have definitions of play. This section will therefore examine the question of play's function, in order to make explicit the present writer's own views on this issue (and hence reveal any possible biases in the studies to be described in this thesis).

Play has been cited as the cause of virtually any benefit that might result from juvenile experience; Baldwin and Baldwin (1977) list thirty different postulated functions for play, and Symons (1978) describes eighteen different categories of function! It is easy to conceive of a large number of potential benefits that could be provided by play; but which of these actually do occur in natural conditions, and which are benefits uniquely obtained from the quality of the play experience, are questions which have never been satisfactorily answered.

Smith (1982) has reviewed the literature on animal play in an attempt to decide which interpretation of play's function best fits the existing data, citing findings from studies on diverse species that show features either apparently supporting or negating a particular theory. However, as Smith (1982) himself recognises, such an aproach must take account of the

considerable theoretical and practical difficulties inherent in any attempts to investigate play.

## 1.3.2: General Problems in Determining the Function of Play:

### 1.3.2.1: Inadequacy of the database:

Fagen's (1981) extensive review of play research revealed that "playful" behaviour has been reported in at least 400 species of mammal and 40 species of bird. However, in many of these studies, description of play was an incidental interest. We simply do not know the range and extent of play in the vast majority of species, nor do we have sufficiently detailed information on all but a minute proportion of those species which we know do play.

There has been a bias in research towards domestic, zoo and laboratory animals, and probably towards animals which show a high incidence of social play. However, we know little about how the nature of play might be affected by domesticity or captivity. Certainly animals should play much less frequently in the wild, where a young animal's time and energy are taken up with activities more obviously concerned with immediate survival, such as foraging for food (eg. Baldwin and Baldwin 1974; Loy 1970; Hall 1963; Southwick 1967). This may be especially true of object play (eg. Menzel 1965, Symons 1978), but has also been reported for social play

in a number of primates (eg. Schaller 1965; Fady 1969; Horr 1977). Play may thus have a lesser role in the development of animals in natural conditions than one might conclude from observations on captive subjects.

A practical difficulty with second-hand comparisons of play data is that the data are obtained from different observers, who are placing varying emphasis on particular aspects of behaviour and who often are observing under very different conditions. While this problem is common to all areas of behavioural research, it is particularly acute in the study of play, where difficulties of defining the subject-matter aggravate the situation. Also, as Fagen (1981) points out, extraneous factors may easily intrude into our assessment of something as apparently straightforward as the amount of time spent playing. As well as the influences of captivity on levels of play, there may merely be apparently less play in certain groups of animals (such as females or certain age-groups) because these groups are more easily stressed by the presence of a human observer and so play less for the time during which they are under scrutiny.

1.3.2.2: There may be many functions for play:

Prompted by the apparent diversity of the phenomena which have been labelled "play", and their widespread phylogenetic distribution in birds and mammals, many workers have suggested that there may be a multiplicity of functions for play (eg. Beach 1945; Berlyne 1960; Millar

1968; West 1974; Bekoff 1974; Owens 1975; Einon 1980; Fagen 1981; Smith 1982). There may well be different functions for social, locmotor and object play; each of these types of play may have different functions in different species; and even within a particular species, there is no reason why play should not provide more than one benefit. Nevertheless, there still lurks an implicit and untested assumption in much of the literature on play that "play" is basically a unitary phenomenon with more or less universal characteristics across species.

When discussing the possible functions for play, most researchers probably have in mind the benefits of play for the particular species that they have studied; however, the qualifying phrase "in this particular species" is lost along the way. Poole (1978) makes a similar point, claiming that for example, failure to distinguish between social play, manipulative object play, and play with inanimate but mobile objects (described earlier in this thesis as "predatory object-play") has led to confusion about the functions of play. Workers oriented towards object play stress its possible role in the acquisition of skills, while researchers into social play emphasise socialization functions. Thus different writers may disagree over the function of "play" when in fact they are using the same term to describe different phenomena. Once again, confusion due to inadequate definition is in evidence.

1.3.2.3: Play may not provide unique benefits:

Any benefits provided by play may equally well be provided by alternative forms of behaviour; play may represent a particularly effective means of obtaining certain benefits, but it may not be the sole means of acquiring them (Baldwin and Baldwin 1977; Fagen 1982). It might be possible during development to compensate for a lack of play by falling back on other behaviours, including other types of play. Bekoff (1974) for example, on the basis of observations on canids, suggests that self-directed (solitary) play may substitute for social play, if the latter is unavailable due to the unreceptiveness or absence of partners. This may be an example of "equifinality" in development (Bateson 1979, 1981; Martin 1984); a given end-point may be reached in more than one way.

The practical implication of this is that theories which postulate a particular benefit for play should not be dismissed on the grounds that it is possible to find cases where the benefit is obtained without the use of play. Similarly, if a behaviour can develop without play occurring (ie, in experimental isolates) this does not necessarily prove that play is not important in that behaviour's normal course of development.

1.3.2.4: Play may provide benefits normally provided by other behaviours:

An even worse difficulty for experimental

investigations of play's functions, is that play could, in certain circumstances, provide benefits normally provided by other behaviours. Examples of this might be the work of Harlow and his associates on the effects of early isolation on the later social behaviour of rhesus monkeys (eg, Harlow and Harlow 1966; Suomi and Harlow 1971); and the work of Einon and her associates on isolation-induced cognitive deficits in the rat (eg, Einon, Morgan and Kibbler 1978).

While peer-play may ameliorate many of the deleterious consequences of social isolation, this does not prove that play is the normal means by which socialization occurs; the abnormal rearing conditions may instead have encouraged the utilisation of play in atypical ways. Play, for example, might have therapeutic effects not in itself, but because it merely happens to result in close contact between immatures so that some other socialization proesses can occur.

### 1.3.2.5: The Problems of Analysing Play in Terms of Design:

In the preceding discussion, the terms "function" and "benefit" have been used loosely and interchangeably. Strictly speaking, however, they are not synonymous.

Williams (1966) distinguishes between "function" and "effect" (or benefit) on the grounds that the latter are merely consequences of a behviour or structure, whereas a

function is that effect for which the behaviour or structure shows evidence of having been specifically designed by natural selection. Hinde (1975, 1982) makes a similar distinction between function in the "weak" sense of a beneficial consequence, and in the "strong" sense of a beneficial consequence that is maintained in the population by natural selection.

This distinction has led a number of researchers (eg, Fagen 1976a, 1981; Symons 1974, 1978b; Smith 1982) to claim that by looking at the "design features" of play, we can get an idea of what function it serves - the argument being that play should show evidence of having been specifically designed by natural selection to produce that function for which it has been selected, and should not show evidence of being designed to produce its "incidental" or "secondary" benefits. It is the present writer's contention, however, that this approach in terms of an "engineering analysis" (Lewontin 1978), is unlikely to throw much light on the function of play, for a number of reasons.

1.3.2.5.1: There may be alternative explanations for the same design features:

A given set of play characteristics may be interpretable in many different ways. For example, the length of a play bout may be the outcome of selection to provide the optimum duration of physical training for muscle development; or it may be the result of selection to produce the optimum duration of sensory stimulation to

maintain arousal levels.

In theory, sufficiently deep knowledge of play's design features would incline the investigator towards or away from a particular interpretation of function. In practice, however, play is sufficiently vaguely demarcated from other behaviours, and there are a sufficiently large number of "playing" species from which to take examples, that the technique can be used to support any particular theory desired.

In the absence of any objective criteria by which to evaluate the extent to which a given set of play's characteristics reflect selection for a particular function, the design features approach runs the risk of succumbing to evaluation on the grounds of plausibility and advocacy.

1.3.2.5.2: Play may not be optimally designed for its function:

Lewontin (1978), and Gould and Lewontin (1979), point out the dangers ofthe "adaptationist fallacy" - the belief that every feature of an organism's structure and behaviour has a function, and is perfectly adapted to that function by natural selection. The design features approach represents an example of this kind of thinking, by assuming that play must have a function, to which it is perfectly adapted.

However, an analysis of play in terms of its design for a particular function ignores the fact that an organism is not a collection of discrete traits which can

be considered in isolation from the rest of its structure and behaviour. This approach takes no account of the potential operation of optimality principles, ie the need for compromise and trade-off between conflicting selection pressures operating on the animal.

Many of play's features may not be direct adaptations for its function, but rather may arise from other considerations - for example, the need for metacommunicative signals to inform conspecifics that play is occurring. Sade (1973), for example, points out that play movements in free-ranging rhesus monkeys are clearly antithetical to those of other "moods" (attack, submission, amicable and exploratory behaviours); this probably minimises the risk of play being misinterpreted by the interactants.

Play may not even be optimally adapted for its function; since play represents only part of an animal's "mean phenotypic fitness" (Williams 1966), it may be selected for or against not because of its particular virtues, but merely because it occurs in an otherwise-successful phenotype. In other words, play may represent an example of what Lewontin (1978) calls a "hitch-hiker" - a behaviour with no function in itself, but which is selected for because it is partly determined by the same genes as some other, functional, attribute. In such a way, play could have very small benefits, but be "allowed" to exist in animals which are not unduly disadvantaged by it.

Finally, even if play were functional and highly beneficial, it might still only be approaching optimality in terms of its function; or it might be prevented from reaching optimum levels of adaptation to its function (ie, its "adaptive peak") by conflicting selection pressures or some design constraints. The design features approach implies that play is perfectly adapted to its function; but it may not be, since animals are in the process of adapting, rather than being adapted. Evolution has no end-states, but is a continuous process occurring in the present, as well as the past.

1.3.2.6: Conclusion:

Many of the preceding problems in assessing play's functions are obvious, and they are common to all behavioural research. It is felt, however, that these issues need more emphasis than they have hitherto received in reviews on play. The basic point is that the two chief tools of reviewers attempting to gain insight into play at second-hand - ie, a design-features approach, and cross-species comparisons - are fraught with dangers. While they are fruitful sources of hypotheses about play, they should be used with more caution than they have been hitherto. Neither technique can be used reliably to identify the function of play, although they may be suggestive. Until the function of play is determined by other means (direct experimental and observational studies on particular species) the extent to which play can be said to fulfill a particular role will remain highly

debatable.

Nevertheless, there are still at least two ways in which a design-features approach can be used to investigate the function if play. Firstly, since we know something about the functional properties of communication, those features of play which show clear evidence of design for communicative processes can be "set aside" and assumed to be for the purpose of mediating the interaction rather than serving the ultimate function of the play itself. Secondly, it may be possible to rule out postulated functions for play on the grounds that there are no features of play which show evidence of being designed to fulfill that function; or, better still, thatthere are features present which are inconsistent with a design for the hypothesized function. A successful example of this latter approach is Symon's (1974) critique of the theory that social play practices social communicative skills, on the grounds that play's design is inappropriate for such a function.

Even if play is assumed to have basic common features across species, a naive comparative approach is faced with severe difficulties. The principal problems - such as observer reactivity effects - should be recognised and accounted for, in any detailed cross-species comparisons; but the main problem, poor definition of those behaviours which we term "playful", makes precise cross-species comparisons of play effectively impossible at present. Yet such a detailed comparison is an essential preliminary to

attempts such as that of Smith (1982) to identify the functions of play by looking across species for supportive data. At present it is only too easy to fall prey to the dangers of advocacy and special pleading, too easy to find facts to fit ad hoc "predictions" on the nature of play and to explain away "awkward" observations or use them to "disprove" other workers' theories.

In any case, even if cross-species comparisons could be reliably made, they could tell us little about the function of play. In biology, homology of structure tells us nothing about function, but merely informs us of common descent. Cross-species comparisons are interesting, and the differences between species may be informative; but just as knowledge of forelimb structure in the rat gives no clue as to the function of the same structure in the dolphin, so knowledge that the rat uses play, say, for socialisation purposes, throws little light on the dolphin's uses for play. Even worse, in the case of a forelimb, there are definite objective criteria demarcating that limb from the rest of the body; in the case of play, the problems of definition compound with those of comparison itself. Cross-species comparisons of play should be made with more emphasis on determining how species differ, and to how particular species use play, rather than in attempting premature and superficial generalisations across all or most playing species.

## 1.3.3: A review of hypothesised functions of play:

With the problems discussed in the previous sections in mind, an extensive review of play's functions will not be undertaken here. In any case, the reviews by Fagen (1981) and Smith (1982) are still a reasonably up to date survey of our knowledge of play.

The issue of function cannot be totally disregarded, however, for two reasons: firstly, as mentioned earlier, since data collection must always to some extent reflect the theoretical preconceptions of the observer, there should be some awareness of what these preconceptions are. Secondly, the hypothesised functions of play often reveal inappropriate and "unbiological" conceptions of play and the developing animal, on the part of the workers propounding them. Consequently, a brief - and very incomplete - survey of the principal theoretical conceptions of play's significance will be given. Although numerous different theories have been put forward to account for play, most (but by no means all) of them amount to variants of two broad conceptions of play, distinguishable in terms of the kind of benefits that they envisage play might provide. These are as follows:

1. Play represents direct and specific practice of adult activities.

2. Play has general, relatively non-specific effects on the development and/or maintenance of various

physiological systems.

There are other theories that do not fit into either of these categories, for example that play "modulates arousal levels" (eg, Baldwin and Baldwin 1977) or that play promotes "social cohesion" (eg, Ewer 1968; West 1974), but these will not be considered in the following discussion. These hypotheses are interesting, but they make no firm statements about what kind of play might be expected to be performed. In contrast, the two overall conceptions of play mentioned above both make firm, testable predictions about the nature of play. Their chief importance, however is that they have largely shaped the way in which researchers have actually looked at play.

Before evaluation of hypotheses about play's function, it is necessary to discuss another conception of play which has had considerable influence: the idea that play has no "function", but is merely a means of releaing surplus energy.

1.3.3.1: Theories that play has no function:

Many theories about play suggest that it has no appparent immediate function; but the kind of theory to be discussed in this section goes further than this, and proposes that play has no deferred functions either. Spencer (1878) suggested that play is merely the expression of "surplus energy"; "higher" animals, by virtue of being skilled, have to spend less time in

activities which promote survival, and so have time and energy which are surplus to their immediate requirements. Play has no function other than to release this pent-up energy.

1.3.3.1.1: Arguments against this hypothesis:

Firstly, there is no known physiological basis for the idea of "surplus energy"; it could equally well be claimed that adults should play more than juveniles, because it is the former who have energy to spare whereas the latter could better divert their energy into growth and development. Also, in captivity, where there are no demands to hunt for food or avoid predators, one would expect adults and young to have equal amounts of surplus energy and therefore to play to much the same extent. While it is true that captive animals do play more than in their natural habitats, play still occurs rarely in adults and frequently in the young (eg, many primates, Dolnihow 1971, Poirier 1970, Symons 1978b; the polecat, Poole 1966; the meerkat, Ewer 1963; various canids, Bekoff 1978; and the rat, Baenninger 1967). The assumptions made concerning adaptation and phylogeny are also erroneous since they imply that "lower" animals (whatever that means) are less well-adapted to their environment than "higher" animals.

Secondly, "surplus energy" theories fail to explain fundamental details concerning the nature of play: for example, why play is usually directed towards certain aspects of the environment (a conspecific in social play or an inanimate object in manipulative play) in an

oriented way. It is not clear why play behaviour patterns should result from the discharge of the excess energy, rather than other behaviours. (It could be argued, however, that their function is to inform conspecifics that "energy-discharge" (play) is occurring, rather than "serious" behaviour, so as to avoid the risk of misinterpretation). The structural characteristics of play in general could be accounted for by Muller-Schwarze et al's (1982) suggestion that play occurs as vigorous activities in order to release as much energy as possible, and in brief, intense bouts in order to expose the animal to less risk of predation than would result from being active at a lower level for most of the day.

"Surplus energy" theories offer no explanation of why there are different types of play (ie, social, locomotor and object play), and why some species play while other closely-related species do not appear to do so: for example, amongst murids the rat play-fights while the mouse does not, even if reared with rats (Poole and Fish 1975); and amongst marmots play is seen in the Olympic marmot but not the woodchuck (Barash 1973).

The most fundamental inadequacy of "surplus" energy theories is that they imply that a young animal is not adapted to its environment, and that it is somehow an imperfect precursor of an adult form which represents the endpoint of selection. However, selection must occur throughout ontogeny, not merely on adult forms; "the

nature and uses of immaturity are themselves subject to evolution" (Bruner 1972).

The assumption underlying all other theories of play is that play must be functional. If play has significant "costs" to the developing animal in terms of time, energy resources and increased vulnerability to predation or injury, then it must have some significant compensatory advantages in order to have been selected for (Dolnihow 1971, Fagen 1981, Smith 1982).

1.3.3.1.2: The costs of play:

This "costs imply function" argument is so vital to all theories that postulate a function for play, that it is worth considering what the costs of play actually are. Fagen (1981) stresses how costly play can be to a young animal, in terms of both direct costs (increased risk of injury and predation while playing) and indirect costs (expenditure of energy in play which could be invested in growth or in knowledge-gaining processes such as exploration of the environment).

However, while the potential costs of play may be very high (ie, death), the actual costs of playing for the majority of animals are probably quite low, and this would be enough for play to have been selected for. In any case, there is evidence that certain features of play serve to minimise its costs. Firstly, animals do not expose themselves unnecessarily to risks of injury during play; for example chimpanzees and rhesus macaques play only in

the lower branches of trees, which reduces their risk of injuries from falling (Goodall 1968; Symons 1978). Secondly, play is easily disruptible; it occurs near social groups (if it is a social species) or near the litter (if it is a solitary species), often within the care of adults who terminate play if it might lead to danger or predation. Direct estimates of the energy-costs of play suggest that they may actually be quite low for animals under conditions of food abundance (MArtin 1982, 1984); and the effects of food-deprivation on levels of play (Baldwin and Baldwin 1974; Muller-Schwarze et al, 1982) show that play is readily dropped from the behavioural repertoire if its energetic costs cannot be easily accommodated.

1.3.3.1.3: Conclusion:

Fagen's (1981) claims for play's costliness are probably over-stated, although we know so little about the exact costs of play in any species under natural conditions, that the issue remains largely a matter of opinion at present. While the "costs imply function" argument is debatable, however, it is likely to be nearer the mark than "surplus energy" explanations since the latter effectvely render play positively maladaptive on two counts: firstly, because there should be "safer" ways of dissipating energy than by playing; and secondly, because obtaining energy only to squander it subsequently would imply that animals make grossly inefficient use of

their time/energy budgets, whereas what we know about such budgets suggests that animals are often very finely "tuned in" to their environmental constraints and make sensitively balanced trade-offs between costs and benefits (McFarland 1980).

A final point is that although high costs for play would imply that play has significant compensatory benefits, the opposite - that play has low costs, therefore play is unimportant - is not necessarily the case, as Martin and Caro (1985) seem to assume.

Play may not be functional; but for it to be actually maladaptive in the way implied by surplus energy theories would surely have caused it to be selected against in the course of evolution. Yet we find play developed to a high degree in species which we know are in many other respects closely adapted to their environments. The argument that play has signficant costs is unproven, and by itself insufficient basis for claiming that play must have some function; but in view of the implications of suggesting that play has no benefits, the idea that play has some function makes a better working hypothesis.

"Surplus energy" theories have been criticised at some length because such concepts have persisted to the present day, despite their obvious inadequacies. (Valid objections were made as long ago as 1898, by Groos). Altmann, Brunner and Bayer (1973), for example, propose that play merely represents an immaturity of central

inhibitory mechanisms, behaviour being released spontaneously in the absence of appropriate stimuli until such inhibitory mechanisms are formed.

More recently, Muller-Schwarze (1968, 1982) has hypothesised that play is "behavioural fat", a built-in "waste" of energy which in favourable conditions, is taken in surplus to the developing animal's requirements. In times of scarcity and stress, play can be dropped and the resultant energy used for maintenance actiities. Burghardt (1984) endorses Muller-Schwarze's suggestion, but clothes it in an "evolutionary" guise by adding that behavioural flexibility and other hypothesised benefits of play may have evolved secondarily.

If a concept as unsatisfactory as that of "surplus energy" can survive for over a century, then it is hardly surprising that other, less implausible theories on play have proved just as durable.

1.3.3.2: Theories postulating direct and specific functions for play:

The most popular theory concerning play is that it serves to practice and perfect skills which are needed in later life. First suggested by Groos (1898), and more recently advocated by Aldis (1975), Symons (1978b) and Smith (1982), this idea derives largely from the observation that play behaviours seem to resemble adult behaviour patterns that are "functional", eg aggression, predation, predator avoidance and sex. Theories differ

according to what exactly is considered to be practiced in play.

1.3.3.2.1: Social play as practice for adult intraspecific aggression:

Symons (1978b) suggests that much social play consists of practice of the ability to fight "seriously" with conspecifics later in life. Much of the evidence for this claim rests on the reported similarity between social "rough and tumble" play, and adult fighting patterns (eg, rhesus macaques, Symons 1978b; Steller's sea-lion, Gentry 1974; Northern elephant seal, Rasa 1971; olive baboons, Owens 1975a; Olympic marmots, Barash 1973b).

This theory's major weakness is its over-reliance on intuitive recognition of "similarity" between juvenile and adult behaviour patterns, bolstered by post hoc correlation between some aspect of play (for example, the presence of sex differences) and some aspect of adult behaviour (for example, social organisation). The dangers of cross-species comparisons like these have already been discussed; ad-hoc searching of the literature can equally well find examples of play to "support" or to "contradict" any hypothesis.

As Einon (1980,1982) points out, while it is true that only social rodents have so far been found to play, there is a poor correlation in rodents between play-fighting and adult intraspecific competition: *Rattus rattus* and *Rattus norvegicus* are highly playful when young, but show little intraspecific

* For example, Bertrand (1969) claims that "sparring" and "king of the castle" games in stumptail macaque play, do not occur in adult fighting in this species. Wrestling is a prominent feature of social play in lions, but not in adult aggression (Schaller 1972). Henry and Herrero (1974) report that rearing and pawing occur in the social play of black bears but not in their adult fighting behaviour (although these authors do say that the rest of bear play-fighting resembles serious fighting).

aggression as adults, whereas mice, voles and hamsters do not playfight when young but fight as adults. Also, social rodent species do not necessarily play-fight (eg, gerbils, guinea-pigs and Octodon degus), so that play-fighting is not universally associated with social living.

As far as the similarities between play and adult aggression are concerned, they may often be quite superficial. There are examples of "agonistic" behaviours which are observed in play and yet have no counterpart in adult aggressive encounters.* Poole (1966, 1978) has pointed out that in the polecat, differences between social play and "serious" fighting may be just as important as the similarities.

Poole (1966) also found no evidence that play led to an improvement in adult behaviour patterns similar to those shown in play. In contests between differently-sized animals it was usually the larger animal that took the dominant role - physique was important, not experience. The young of some species, moreover, show skilled fighting at the same age as they show social play, or earlier (eg, coyotes, Fox 1969, Bekoff 1974; baboons, Miller 1973, Owens 1978b).

Finally, some of the "design features" of play do not square with this hypothesis. It is difficult to imagine how specific skills could be learnt effectively from interaction with conspecific peers who are as equally ignorant of those skills. Also, in play-fighting, stronger animals often "handicap" themselves in order to play with

weaker ones (Poole 1966, Bertrand 1969). If play were specific practice, weaker animals would thus not learn that in "serious" fighting, stronger animals would beat them and that "serious" fighting of such superior animals would have damaging consequences.

1.3.3.2.2: Other specific practice hypotheses:

The hypothesis that play is specific practice for intraspecific aggression has been dealt with at length because it is relevant to the prime concern of this thesis, social rough and tumble play. There have been a number of other applications of the "play as specific practice" concept, however. For example, Symons (1978) has suggested that some types of locomotor play may represent "emergency locomotor behaviour" for avoiding predators or conspecific aggressors.

The apparent similarities between predatory object play (as exemplified by the play with prey displayed by domestic cats) and actual predation (West 1974; Egan 1976) have prompted a number of workers to investigate the hypothesis that this type of object play is practice for adult predation. While direct tests of this hypothesis (Caro 1980b, Thomas and Schaller 1954) have so far failed to find any effects of playful experience of object manipulation on adult predatory skills, there is the practical difficulty that in the wild, very small differences in skills might have very marked consequences. If play does have practice effects, although

they might be important, they might also be slight and thus difficult to detect (Bekoff 1974, Symons 1978). (This argument also applies to the hypothesis that social play practices intraspecific aggression).

1.3.3.2.3: Play as learning of intraspecific communication skills:

Play has been hypothesised to result in learning of social communication skills (Mason 1963, Dolnihow 1971, Poirier 1971, Poirier and Smith 1974). While there is evidence that social experience is important for the normal development of these abilities (at least in rhesus macaques: eg, Sackett 1965a, Miller et al 1967) there is no evidence that these effects are attributable specifically to play deprivation.

Symons (1974) makes two criticisms of this hypothesis, which represent a good example how the "design features" should be used - to attack a theory, by showing that it is incompatible with certain features of play, rather than to support it.

Firstly, on an empirical level, rhesus monkeys observed by Symons did not learn, refine or practice agonistic signals in play-fighting; these signals appear, unlearned, in isolate rhesus monkeys, and although they require social experience in order to be used effectively, this experience is not obtained in play. Threat signals are a major part of agonistic communication in adults, but they have not been observed in the vast majority of

reports of social play (Symons 1974).

Secondly, the very structure of play-fighting makes it unsuitable as a means by which to learn agonistic signals; due to the jumbled, variable nature of play behaviour sequences, a young animal could never learn a signal's effect by noting the play partner's response to it.

Such theories also fail to consider that young animals must already have highly developed communicative skills in order to distinguish effectively between play and non-play, and that play occurs within a social framework of which the participants are aware (Dolnihow 1971, Meier and Devanney 1974). A player has to know who to play with, whether play is appropriate or not, and, even more fundamentally, he must be able to recognise whether or not another animal's behaviour is playful; to do this he must be able to understand other animals' social signals including threat signals and the metacommunicative signals informing him that the other animal is playing. For these reasons, Smith (1982) is incorrect in saying that animals learn play-signals in play; play-signals must be understood before play ever occurs.

Baldwin and Baldwin (1976) suggest that social play might be important for "more complex, varied social interaction patterns", over and above a basal level of social skills that could develop without play. This is essentially a weaker version of the argument above, with

the added difficulty that "complex social skills" are not clearly defined, so that the hypothesis is effectively untestable.

1.3.3.2.4: Play as learning of social rank:

Poirier and Smith (1974) and Panksepp (1981) have suggested, for primates and rats respectively, that "animals find their place in the existent social order" through social play. By means of rough and tumble social play, animals could discover their strengths and weaknesses compared to their conspecifics (Cheney 1978). Steiner (1971) proposes that play settles or shapes dominance relationships, on the basis of observations on juvenile Columbian ground squirrels, in which there seems to be increasingly less exchange of aggressor and defender roles wth age.

Once again, the "design" of social play does not support this hypothesis. Play bouts do not usually end in a "winner" and "loser", aggression is inhibited in play, and stronger individuals may "handicap" themselves in interactions with weaker animals - all factors which would seem to hinder rather than facilitate the learning of social rank through play (Smith 1982).

There is also good evidence that rank order is often learned through actual fights, before social play occurs (eg, coyotes, Bekoff 1974; domestic pigs, Sus scrofula, McBride 1963, McBride and James 1964). Apart from direct fighting, there are other means of determining

rank; in many primate species, the mother's status is more important than play in determining a young primate's social rank (Schwartz and Rosenblum 1981). Chivers (1984), on the basis of a review of the literature on dominance in rodents, concludes that there is no good evidence for the existence of linear dominance hierarchies in Rattus norvegicus, and yet young rats are highly playful. In contrast, guinea-pigs show marked dominance hierarchies, but no social play.

1.3.3.3: Theories postulating non-specific effects of play on physiological systems:

The difference between these hypotheses and those described in the previous section, is in the perceived relationship between play behaviours and adult abilities. The previous set of hypotheses envisage a close mapping between specific "serious" behaviours, and what are seen as their incompetent, unperfected "play" counterparts. The hypotheses to be described in this section also see play behaviours as a means to obtain certain benefits, but in terms of obtaining more general benefits rather than in terms of perfecting behaviours resembling those in play.

1.3.3.3.1: Play as "physical training":

This theory suggests that play provides some form of "physical training" or "exercise" for the developing animal. Play is held to provide exercise of muscle groups or sequences of muscular contractions used in

"serious" behaviours such as escape from predators, and intraspecific fighting, muscles which would otherwise not be used until needed in their "functional" context in adulthood. Play is additionally supposed to have more diffuse physical benefits, developing endurance and general physiological well-being. Such ideas have frequently been put forward as incidental benefits of play (eg, Spencer 1878, Ewer 1968, West 1974), but Brownlee (1954) seems to have been the first to suggest that exercise is a primary function of play. Fagen (1976a, 1978, 1981) remains the chief exponent of this theory, adducing a great deal of modern physiological evidence in its support.

The basic thesis is that animals exercise when young because this is when their physiology is at its most plastic; exercise at this time will have the maximum effect and hence ultimately be less costly to the animal in terms of energy expenditure. There are some physiological responses which cannot be developed once growth has ceased; and even when a training-response is not age-specific, the physical capacity of an animal which has trained from a very early age will at least temporarily exceed that of an age-mate who begins training in adulthood, simply as a function of the former having trained for longer.

Exercise is supposed to be obtained in play rather than in "serious" activities because the latter would be too costly to the animal in terms of energy expenditure

and risk of injury, and because if social play consisted of "serious" agonistic encounters the partner would be adapted to fight back and hence minimise a bout's efectiveness.

Once an animal reaches a certain level of fitness, it is claimed that this can be maintained in the adult by less vigorous and less frequent activity in functional contexts, so that play is rendered superfluous.

Play's structural characteristics are claimed to reflect the fact that play is designed to provide optimal exercise "programs". According to Fagen (1981) play is interrupted and repetitive because this gives the most effective pattern for physical training. Different types of play provide different physiological benefits.

As Fagen (1976a) himself points out, the exercise theory copes best with locomotor play, and is a less convincing explanation for other types of play, especially social play and manipulative object play. This is only a problem if one believes that play is a unitary phenomenon witb a single universal function, and there is no reason to believe that this is so. Even for locomotor play, however, there is the problem that the theory does not explain why some species play but not others, given that exercise might be thought to be advantageous for any mammalian species.

1.3.3.3.2: Play promotes neural growth:

Fagen (1978, 1982) has attempted to explain social

play by an extension of the exercise theory, suggesting that social play may promote "neural growth". He argues that the "behavioural flexibility" of players (eg Einon, Morgan and Kibbler 1978) may have a physiological basis in the work of Rosenzweig's group on the effects of environmental experience on aspects of neural development.

This argument is a good example of the operation of advocacy in theorising about play's function. Firstly, Fagen confuses different types of "play". He cites the work of Ferchmin and Eterovic (eg, Ferchmin and Eterovic 1977) in support of his case, but they used the term "play" to describe exploratory object-manipulations, not social play.

Anything more than a cursory reading of Rosenzweig et al's papers reveals that many of the details of the enriched-environment research are incompatible with the hypothesis that social play is the basis for the results of the enriched environment studies. For example, the effects are reversible (Rosenzweig et al, 1967); they can be produced in isolates (Rosenzweig and Bennett, 1977); and they can be obtained outside of the period in development when rats show social play (Riege 1971; Malkasian and Diamond 1971). In contrast, isolation-induced behavioural inflexibility is apparently irreversible and induced by isolation within a specific period in ontogeny (Einon and Morgan 1976; Einon, Morgan and Kibbler 1978).

1.3.3.3.3: Play and "behavioural flexibility":

The work of Einon and Morgan and their associates is one of the few programs of research to directly investigate the role of social play in behavioural development. Morgan (1973) identified an "isolation syndrome" induced in rats by social isolation from weaning until sexual maturity. Some aspects of this syndrome are produced by isolation at any age, are reversible by subsequent social housing, (Morgan 1973, Einon and Morgan 1976), and may be due to emotional factors (Einon and Tye 1977); but other effects seem to be attributable to the isolates' lack of social experience at the age at which rats normally play, appear to be more cognitive in nature, and are not reversible by social housing (Einon and Morgan 1977).

The most striking feature of the second category is the slowness of isolates to reverse a previously-learned response, although they are not impaired in their initial acquisition of the task (Morgan 1973; Morgan, Einon and Nicholas, 1975). Einon, Morgan and Kibbler's (1978) results provide strong indirect evidence that social play is the important factor in these effects.

Other workers report similar behavioural inflexibility in rats isolated between weaning and puberty (eg, Ough et al 1972; Rosenzweig 1971), and there are descriptions of similar deficits in isolated beagles (Fuller 1966) and chimpanzees (Davenport et al 1973).

The possibility remains that in these experiments,

social play is performing a therapeutic function, compensating for the lack of other social experiences which in the normal course of development would produce normal behavioural development; this would, however, be a very difficult notion to test, and Einon et al's work remains the strongest experimental evidence we have in support of any hypothesised function of social play to date.

1.3.3.4: Conclusions:

This brief survey of functions for social play shows that, out of the wealth of hypotheses advanced to account for play, only one has so far received any empirical support: the idea that social play in the rat produces behavioural flexibility in adult learning tasks. However, faith in many of the other hypotheses - notably the "surplus energy" concept - has been remarkably persistent, considering the virtually total lack of evidence in their favour. This in itself is no bad thing; if there is no good evidence to decide between various possible functions for play, then there is conversely no good reason to dismiss any of them out of hand. However, the "play as practice" hypothesis has dominated not only thinking about play's function, but also the very ways in which play has been perceived, defined and described.

It was mentioned earlier that this review of theories of play's function was undertaken in an attempt to make explicit the present writer's preconceptions about play.

On the basis of the evidence described in this review, it is felt that while the concept of play as immature preparation for adult activities is attractive in many ways, at present it exerts a damagingly restrictive influence on play research, blinkering students of play to other possible functions for this behaviour. A conscious attempt not to view play merely as tutelage for adult behaviour was therefore adopted on the part of the present author, during the collection of data for this thesis.

A possibility which has not so far been discussed is that play might have immediate, specific benefits rather than ones deferred until some later point in ontogeny. Martin and Caro (1985) have suggested that predatory object play in cats may have facilitative benefits for practice with prey. The possibility exists that social play in the rat might represent a means by which the young rat could damage its partners in subtle ways, or secure provisional "rights" to territory, resources, etc. Alternatively, play could be used for immmediate amicable purposes, such as olfactory investigation and allo-grooming. The apparently "playful" air may be blinding us to play's immediate utilities. One concern in the studies to be described in this thesis will therefore be to examine play with a view to identifying any features which might have immediate benefits to either of the participants.

## 1.4: THE DEVELOPMENT OF PLAY:

### 1.4.1: Introduction:

Despite the fact that play is essentially a developmental phenomenon, there are comparatively few studies of the ontogenetic development of play, and of play's relationship to other behaviours performed by the immature animal.

Those studies that have examined the development of play have generally used a cross-sectional design, "representative" individuals being chosen from different age-groups of a population to illustrate any developmental trends in play. The reasons for this are understandable: longitudinal studies of play in the wild would often be impracticably time-consuming, especially in the case of the higher primates, where play may occur over a period of years. (Although paradoxically, the richest source of data on developmental aspects of play comes from studies of primates. As Muller-Schwarze (1984) points out, the literature on play is heavily dominated by studies on primates, and much of the following discussion will be based largely on such accounts).

While the data from such investigations are very valuable, repeated observation of the same individuals throughout their ontogeny might provide a deeper insight into any fine-grained changes in play which might occur.

Most of our knowledge of play's development concerns its onset and termination, rather less being known about

any detailed changes that might occur between these two points. These three topics - onset, development and termination - will be reviewed in turn.

### 1.4.2: The Onset of Play in Ontogeny :

It is extremely difficult to make detailed cross-species comparisons (or even comparisons within a species) because of the problems in defining exactly what is meant by the term "onset". This could be taken to represent the first occurrence of a complete sequence of play behaviours, or the first appearance of any one of that species' play patterns, or the first appearance of a behaviour which could somehow be regarded as a precursor of a play pattern. Nevertheless, some broad trends can be identified in the extant literature.

#### 1.4.2.1: Factors determining when play begins:

Fagen (1976) points out that animals would be expected to play as soon as they are able; simply as a consequence of having played for longer, an animal who starts playing early in life will receive more of play's benefits by the time he reaches maturity than will an animal that starts to play at a later age. However, as Meier and Devanney (1974) have noted, in practice the onset of play seems to be affected by an interaction of at least two factors, the relative contribtions of which differ between species. One factor is the degree of maturation of the young animal, in terms of whether it has

sufficient sensorimotor development to be able to perform the vigorous and rapid behaviour patterns of play. The other factor is to what extent the environment provides opportunities for play to occur. For example, deferring the onset of play may be advantageous in environments which are not conducive to play; in environments which place at a selective disadvantage players who are below a certain level of physical ability; or in environments containing social organisations which restrict opportunities for play.

One consideration that will obviously affect the relative influence of these two factors is the degree to which the playing animal is precocial or altricial. Play should occur at an earlier age in precocial animals simply because they are already sufficiently well-developed physically in order to be able to perform play patterns; therefore, barring any social or ecological constraints on play, precocial species should play virtually from birth. This is indeed so for the reindeer (Espmark 1971), which engages in solitary locomotor play (running and frisking) from the first day of life. In contrast, in the altricial polecat (Poole 1966), the onset of play seems to be governed by maturational factors; play begins at about 6 weeks of age, the age at which the kits' eyes open. Animals below this age did not respond to play solicitations by older animals.

The onset of play may have to be deferred until essential preliminaries have occurred, for example the

establishment of dominance rankings (eg, the coyote: Bekoff 1972, 1974, 1978b) or nipple preferences (the mountain lion, Pfeiffer 1980).

In many species, however, factors in the social environment which are in a sense independent of the young animals themselves, may be most significant in determining the onset of play. Many animals do not commence playing as soon as they appear physically capable of doing so, and this delay can be traced to features of the social organisation of the species. For example, the Northern elephant seal (Rasa 1971) is quite precocial, but social play does not begin until the environment provides the opportunity for it to do so - until after the pups have been pushed into contact with each other, due to their being deserted by their mothers.

A similar but less drastic facilitation of social play due to maternal rejection fostering peer-contact, appears to occur in a number of species which characteristically produce small litters - for example, many of the primates. In the rhesus macaque, this seems to be an important factor in normal development; without the impetus of the mother's rejection at weaning, infants maintain immature clinging patterns which prevent the peer interaction that is conducive to social play, and thus delay the onset of play (Harlow 1969; Suomi and Harlow 1977; Chamove et al, 1973). Thus, by diverting the immature animal's focus of attention away from its mother and towards its peers, weaning may effectively provide

more opportunities for play to occur.

This relation of the onset of play to weaning seems to be a common phenomenon in social species. At first sight, it seems odd that young animals should begin to play at the very age at which they have to start fending for themselves. This means that play, a relatively low-priority behaviour, begins just at the time when other behaviours with higher direct survival value (such as foraging) are coming to be placed at a premium in the young animal's time and energy budgets.

The process just discussed - that the onset of social play occurs because young animals are thrown together by the mother's rejection - helps to explain why social play peaks after weaning, in species in which single progeny are the norm. But in species which typically produce large litters, play presumably has ample opportunity to occur before weaning takes place, and the significance of play's timing is unclear - especially since weaning may herald the dispersal of the litter and the loss of play-opportunities.

In primates, the onset of play seems generally to depend largely on the social environment, given a certain minimum level of physical development. This probably partly explains why play typically seems to commence at an earlier age in captive animals (eg, Baldwin and Baldwin 1974): the facilitatory effects on play of captivity (freedom from predation and abundant provision of resources) may primarily affect the adults of the group,

including mothers, who in turn affect the behaviour of their young.

1.4.2.2: Relationship between different types of play in terms of onset:

An interesting question is whether or not different types of play commence at the same time in ontogeny. If play were a unitary phenomenon, then one might expect social, locomotor and object play to begin at the same age. Unfortunately, there is relatively little detailed information on this issue. In captive rhesus macaques, Meier and Devanney (1974) claim that object, social and locmotor play all first appear at the same time, at two weeks of age; but in many primates, social play occurs before locomotor play simply as a function of locomotor maturation. A readily available partner for social play (the mother) happens to be present before the young aninal is sufficiently motile to be able to engage in locomotor play. In the domestic cat, object and social play seem to have fairly distinct developmental courses; while social play begins at 4 weeks of age, object play markedly increases at about 7-8 weeks, at which age social play begins to decline (Barrett and Bateson 1978; Caro 1980).

1.4.3: Developmental Trends in Play:

A number of trends have been reported in the development of play, in various species.

1.4.3.1: Increasing complexity:

With increasing age, play often seems to increase in its complexity. "Increasing complexity" is a somewhat vague term which may be interpreted in a number of different ways.

In the polecat (Poole 1966), social play becomes more complex in the sense that an increasing number of behaviour patterns are incorporated into the playful repertoire as the animal matures. He claims that each playful behaviour pattern resembles an adult agressive behaviour, and occurs in a seemingly complete form on its first appearance. Poole (1966) suggests that most of these playful behaviour patterns develop as and when the animal has the requisite agility and coordination to be able to execute them. Poole (1978) similarly found increased complexity in polecat social play, in that older animals showed a greater number of different behaviour patterns than younger animals, and also performed these patterns more rapidly.

Muller-Schwarze (1968), in observations on the development of social play in the black-tailed deer, and West (1974) for the domestic cat, report similar increases in complexity in terms of age-related increases in the number of behaviour patterns shown.

Simpson (1976) claims that the ontogeny of locomotor play in the rhesus macaque shows similar trends. Sequences of leaps, climbs and runs are repeated, and become increasingly more complex. In this way, Simpson suggests,

the young macaque directs his attention to the environment in a circumscribed, and thus more comprehensible, way. The increased complexity comes from the way in which simpler movements, once perfected, become incorporated into more complex "projects" which in turn are practised until perfected and then subsumed into even more complex movements.

1.4.3.2: Increased amount of play:

Play in many species seems to show a trend of increasing from its onset up to a pre-pubertal peak, and then decreasing during subadulthood. (eg, polecat, Poole 1966, 1978; rhesus macaque, Meier and Devanney 1974; chimpanzee, Goodall 1968; domestic cat, West 1974).

In some species, play seems to follow a more complex developmental course than this. In male *Papio anubis*, for example, Owens (1975b) found an age-related frequency-distribution of social play that showed two peaks, separated by a trough and followed by a steady decrease, until by five years of age little play was seen. With increasing age, there were fewer bouts, but they were longer. In females, this pattern did not occur; there were wide individual variations, and play apparently remained at a uniform level from one to three years of age. Cheney (1978) reports broadly similar results.

Such complex developmental trends are not limited to primates. Sachs and Harris (1978) found two peaks in the ontogenetic distribution of play in domestic lambs. They

make an interesting (but, considering the scantiness of their data, highly speculative) suggestion that this pattern relates to the ecology of wild mountain sheep. These are born in the mountains; migrate down to the nursery bands near these cliffs (which is held to account for the first peak in play); and then migrate from the wintering to the summering grounds three to four weeks later (the migration supposedly causing the "trough", and the arrival at the summering grounds coinciding with the second peak in play).

Different play-patterns may show different developmental courses (see below). Muller-Schwarze (1968), however, found that all play-patterns in black-tailed deer increased in frequency with age, especially running; as they matured, fawns ran more, and ran further away from their mothers. Espmark (1971) reports similar findings for the locomotor play of reindeer.

1.4.3.3: Increased "roughness" and "vigour":

Increases in the "roughness" and "vigour" with which play patterns are performed are commonly reported. However, exactly what is meant by these terms is seldom defined precisely. Increased "roughness" is used in the context of social rough and tumble play; the "rougher" the play, the more difficult it is to distinguish it from "serious" agonistic behaviour patterns, and the more it tends to "escalate" into uninhibited aggression and/or terminate prematurely due to one or other of the

interactants being hurt, or at least, finding the intensity of the play bout aversive. Objective measures of roughness might include increased frequency of pain and distress vocalisations, increased danaging biting and clawing, and an increasing tendency for play-bouts to end abruptly with the dispersal of the participants. Inasmuch as the "vigour" of play can be differentiated from "roughness", greater vigour presumably implies more rapid alternation between the component behaviour patterns of play, and greater amplitude of patterns (eg, higher leaps and pounces, more abrupt turns, wilder swings and pawings). Increased vigour could as equally well accompany locomotor and predatory object play, as it could social play. However, as with the term "play" itself, terms such as "vigour" and "roughness" need explicit and precise definitions, rather than relying on mutual intuitive understanding as they do at present.

A typical example of developmental trends in these aspects of play comes from Poole's (1966) report that polecat social play becomes more "active" (vigorous) and rougher with age. Crying and hissing, proably related to this increased roughness, become more common in play as the animals get older. The proportion of "active" play also increases with age in the closely-related mink, Mustela vison (Poole 1978). Rasa (1971) notes similar developmental trends in the Northern elephant seal. The most active and coordinated behaviours (rearing up and slamming the body against the opponent) do not occur in

very young animals, but are frequent components of social play in older ones.

Increased roughness and vigour of social play are also commonly reported in primates (eg, baboons: Hall and DeVore, 1965; rhesus macaques: Hinde and Spencer-Booth 1967, Suomi and Harlow 1969, Meier and Devanney 1974; chimpanzees: Goodall, 1968).

1.4.3.4: Sex differences in roughness:

Sex differences are commonly found in the roughness of social play, with males playing more roughly than females. With age, this difference seems to increase, so that males become markedly more active players. Such differences have been reported in a wide range of species, including rats (Poole and Fish 1976), black bears (Henry and Herrero 1974), Steller's sea-lion (Gentry 1974), squirrel monkeys (Baldwin 1969), langurs (Jay 1965), vervets (Lancaster 1971), rhesus macaques (Goy and Phoenix 1971; Harlow 1965; Hinde and Spencer-Booth 1967), baboons (Owens 1975a,b) and cercopithecoid apes in general (Wolfheim 1978). In Toggenberg goats (Chepko 1971), "mock battles" including butting and mounting become more frequent with age in males, but decrease in frequency in females.

Such differences are not confined to social play; Redican and Mitchell (1974) found that solitary locmotor play in male rhesus macaques was more "intense" than that of females. Not all species show sex differencs in the

roughness of their play, however; Bekoff (1974) and Hill and Bekoff (1977) found no differences in roughness of social play in the coyote, nor were there any apparent sex differences in the wolf or beagle (Bekoff 1974). In domestic cats, sex differences appear to emerge only in the closing stages of social play (Caro 1980).

Sex-differences in play may be present from a very early age. In the Northern elephant seal (Rasa 1971), sexual dimorphism in play patterns (mirroring that of adult agonistic behavior patterns) is evident in infants, and in rhesus macaques sex differences in the rate of play may be due to perinatal differences in hormone levels. Sex differences in the roughness and vigour of social play do not appear to be due simply to the larger size and greater strength of males, at least not in baboons, where there clear differences in play despite males and females under five years of age being similarly sized (Owens 1975b).

In primates, there may be sex- and age-differences in the relative importance within social play of contact and non-contact elements (Suomi and Harlow 1971; Hinde and Spencer-Booth 1967; Chalmers 1980). The overall picture given by these studies is that in baboons and rhesus macaques, rough and tumble components of social play ("wrestling", "mauling" and "sparring") are more characteristic of males than of females, and that this becomes increasingly so with advancing maturity. Females either "drop out" of play altogether because it is too

rough for them, and/or increasingly prefer non-contact, "gentler", forms of social play such as approach/withdrawal behaviour.

1.4.3.5: Consequences of play's increased roughness with age:

Maturational differences in the roughness of play may have numerous implications for the developmental course of play.

1.4.3.5.1: Preference for peers:

Increased roughness of play with age may be a factor in the commonly-reported finding that young animals prefer to play with their peers, rather than with animals much older or younger than themselves. This is true for baboons (Hall 1962; Kummer 1968; Owens 1975b; Cheney 1978); Japanese macaques (Itani 1954); crab-eating, rhesus and bonnet macaques (Fady 1969; Altmann 1962; Simonds 1965); langurs (Jay 1963); squirrel monkeys (Baldwin 1969); and chimpanzees (Van Lawick-Goodall 1968). Altmann (1962) and Fady (1969) suggest that when animals choose partners of similar strength and weight, play is less likely to break down, since both partners have the chance to direct or dominate the play. When the age-difference between the two players is too great, the smaller animal soon gets caught in a chase, or cannot catch up if he is the chaser, or drops out of rough and tumble because it is too rough for him.

"Equally-matched" play-partners are generally peers;

but where peers are not equivalent in abilities, animals prefer to play with partners of similar physical strength to themselves. For example, in baboons, females prefer infants as play-partners, rather than males of their own age; although an attraction to infants per se is a factor in this, the females' preferences are also affected by the fact that their male peers play more often and more roughly than they do themselves. This effectively makes the infants the females' most comparable play partners (Owens 1975b; Cheney 1978). In other words, animals may prefer to play with an appropriate partner, rather than with a peer merely for the sake of it being the same age.

Of course, for preference of equally-matched rather than equal-aged partners to occur, the choice must be available. In many species, play will occur between peers regardless of differences in size and disparities in roughness, simply because peers are the only available animals with which to play. For example, at 14-18 weeks, male and female polecats of the same litter play together even though the males weight one and a half times as much as the females (Poole 1966). "Handicapping" of the stronger partner may go some way towards reducing the inequality of the interaction, with males attenuating the roughness and vigour of their play when playing with females. However, a significant factor in the common finding that females stop playing at an earlier age than males, may be that females find their male peers' play too rough, but lack alternative partners and so give up

playing altogether.

1.4.3.5.2: Preference for same-sexed partners:

Related to the previous point, the sex-differences in roughness may also be a factor in the preference of players for partners of their own sex (eg, hamadryas baboons, Kummer 1968; *Papio anubis*, Owens 1975b, Cheney 1978; langurs, Dolnihow and Bishop 1970). This is probably so for the reason just discussed, that players prefer equally-matched opponents. It may also represent a secondary consequence of play typically ceasing earlier in females than in males, thus forcing males to play more with other males simply because there are no other options available.

1.4.3.5.3: Initiation of play:

The greater roughness of older animals in play may affect their ability to initiate play successfully. For example, in play between male baboons (Owens 1975b), the older animal was found to initiate the bout unless the difference in age was very great, in which case the younger animal tended to initiate play. In play between males and females, males initiated most of the bouts with females of similar age to themselves; but if the age difference was greater, there was a tendency for the females to initiate bouts. Presumably attempts by older and stronger animals to initiate play are less successful because their greater vigour intimidates their intended partners. Similarly, in rhesus macaques (Harlow 1965) and talapoins (Wolfheim 1978), males often initiate rough and

tumble play with either sex, whereas females rarely initiate such games with males. Apparently, this is because the females find the males' greater roughness in play somewhat aversive.

1.4.3.5.4: Increased metacommunication in play:

The increase with age in the roughness of play presumably makes social play harder to differentiate from "serious" aggression not only for human observers but also for the animals concerned. Together with the fact that, as the interactants mature, they are potentially able to damage each other more effectively, this means that it is increasingly important for players to ensure that their playful intentions are not misconstrued by the partners to which they are directed. The metacommunicative aspects of the play interaction may thus become clearer as the animals get older. This is so in the polecat; Poole (1966) notes that the open-mouth play-face is slightly more frequent in older animals, and that from 15 weeks of age onwards, it becomes a more distinct element which is not necessarily associated with biting, as it is earlier in ontogeny. Similarly, coyotes, which are more aggressive than wolves or beagles, show a strong tendency to use the most successful play initiation signals most often. This both ensures a better chance of soliciting play, and reduces the "risk" to the initiator that his signals will be misinterpreted. Wolves and beagles can afford to have a more "casual" approach to initiating play (Bekoff 1974). In the domestic cat, West (1974) considers that play

patterns are quite constant in form and are performed at a "typical intensity" (Morris 1957).

1.4.3.5.5: Developmental relationships between different types of play:

An interesting issue is the nature of the relationship between the developmental courses of different kinds of play. One possibility is that object, social and locomotor play either represent or occur in different developmental stages; another is that the different types of play follow separate and parallel lines of development. Researchers tend to emphasise one or other of these views, according to whther they conceive of play as a unitary phenomenon or as a diversity of behaviour categories lumped together by chance. In any case, there may well be differences between species in these relationships, if only in the sense that not all species show all types of play.

What data we have on this issue, tend to support the view that different types of play follow different time-courses in development. The main comparisons seem to have been made between social rough and tumble play, and approach-withdrawal play (social locomotor play). Poole (1978), for example, found that locomotor play in the polecat tended to increase with age, while rough and tumble declined. This is also the case in baboons (Owens 1975b).

The development of approach-withdrawal play seems to

be related to the development of the animals' locomotor abilities; in both feral baboons (Owens 1975b) and captive rhesus macaques (Hinde and Spencer-Booth 1967) such play develops later in ontogeny than does rough and tumble.

There are fewer accounts of the relative developmental trends of different types of play in non-primate mammals. Probably the best-documented are those of the domestic cat.

West (1974) reported that cats show a progression from solitary performance of individual play patterns to solitary and then social performance of sequences containing several patterns. Social play was found to increase from 4 to 12 weeks and then decline, so that by 16 weeks there was little social interaction between siblings. In conjunction with this decline, predatory object play increased from 8 weeks onwards (although predation itself actually commenced at about 5 weeks of age).

The investigations of Barrett and Bateson (1978), Bateson and Young (1981) and Caro (1980, 1981) confirmed and extended this work. In the domestic cat there appears to be a marked reorganisation of behaviour at about 7-8 weeks of age. At this time, earlier correlations between social play patterns begin to break down, with some patterns showing little change in frequency while others continue to increase. Object contacts become markedly more frequent from this time on. The net result is a shift in attemtion from siblings to prey. It would seem that

different play patterns come increasingly under the control of different motivational systems (Barrett and Bateson 1978), some play patterns apparently showing greater association with agonistic behaviour, and some showing little change due to being connected to some extent with both agonistic and predatory systems.

These complexities in the relationship between social play, object play and predation are a good example of what can be revealed by the use of longitudinal, rather than cross-sectional, developmental studies.

### 1.4.4: The termination of play:

This section will discuss the proximate influences on when play ceases in development, as opposed to the ultimate causes for this. Ultimately play presumably ceases once whatever benefits it provides have been obtained (so that the ultimate cause of termination will depend on whatever theory of play's fuction is ascribed to) or once the disadvantages of play begin to outweigh its advantages. A number of proximate influences on levels of play, however, may both reflect the operation of these ultimate factors, and also modify their effects.

In some species, playfulness is maintained into adulthood, though at a reduced level compared to that shown by immature animals. This is true for the chimpanzee (Van Lawick-Goodall 1968), and the bonnet macaque (Simonds 1965). In other species, there is a fairly distinct period in ontogeny during which play occurs and after which it

does so rarely. This is the case for baboons (Owens 1975b) and rats (eg. Einon 1980).

As with the onset of play, the age at which play ceases to be prominent in a species' behvioural repertoire seems to be the outcome of an interaction between endogenous and environmental factors. But although the social organisation and ecological situation of a species may be important influences in determining exactly when play will cease, even under optimum conditions for play to occur (such as captivity, where all biological needs are catered for), adults typically play less than their conspecific young (eg. polecats, Poole 1966; meerkats, Ewer 1963).

The influence of a number of factors can be identified in leading to the cessation of play in mature animals. They can all be summarised as representing behaviours which are incompatible with the existence of the amicable relations essential for play to occur.

1.4.4.1: Dispersal of litters:

In solitary species living under natural conditions, social play may cease to occur when littermates disperse, thus removing opportunities for social contact, including play. This seems to be one factor in the termination of play in the polecat (Poole 1978) and in the domestic cat (West 1974), although, as the latter author points out, it cannot be the only explanation since play also becomes less frequent in captive cats which remain together.

1.4.4.2: Competition wih other behaviours:

In mature anials, play has to compete with other behaviours more directly concerned with biological survival, such as eating, drinking, avoiding predation and reproducing. These may simply leave no time for play activities to occur. From Farentinos' (1971) descriptions of behaviour in different age-groups of Steller's sea-lion, this seems to be the case for this species; all other sex and age-groups play except for adult bulls, whose energies are solely taken up with mating. West (1974) suggests that in the domestic cat, the development of sexual behaviour appears to alter the formerly friendly relations between males and females. In the chimpanzee, play is increasingly supplanted by more obviously "functional" amicable behaviours such as grooming. Goodall (1968) suggests that the decrease in play is approximately proportionate to the increase in the intensity and length of grooming sessions.

1.4.4.3: Development of aggression:

Play may be prevented by the development of intraspecific aggression. The way in which the increasing roughness of play becomes a factor in terminating play in females has already been mentioned. In a number of species, social play increasingly comes to resemble aggression and perhaps intergrades with it (eg. the Columbian ground squirrel, Steiner 1971; and the rat, Meaney and Stewart 1981). In rats, Meaney and Stewart (1981) found that not only did dominance behaviours become

more frequent in rat play, but also there was an increase with age in the frequency of "boxing" and "lateral display", behaviour patterns representing direct confrontation.

Other aspects of adult aggressiveness may militate against play occurring in mature animals, apart from play itself becoming aversively rough or aggressive. Poirier and Smith (1974) suggest that social play may be potentially dangerous for adult players; misinterpretations may have hazardous consequences in the form of uninhibited and damaging retaliation. They also make the point that adults of many species enforce a "personal space" within which they will not tolerate intruders, and that this is not conducive to the close physical contact involved in the initiation of social play. Dolnihow (1971) points out that adults may find it too difficult to indicate their playful intentions; signals of playfulness may be insufficient to counteract the strength and potential for damage that other group members have learned to associate with that adult.

### 1.4.5: Conclusions:

Despite the study of the development of play having been incidental to most researchers' interests, a considerable body of data has been accumulated on the topic. However, considering that play is a developmental process, not nearly enough research has been carried out. There is a need for more detailed longitudinal studies in

which changes inthe component patterns of play are traced throughout development, from the time of their first appearance (Welker 1971). Those studies that have been performed, generally suffer from a number of weaknesses.

Firstly, the role of environmental factors in the development of play has been largely ignored; there is a persistence of the old view that the environment merely "supports" the unfolding of the animal's genetic potential, rather than that the animal interacts with its environment during development. It is interesting, however, to note that whereas the behavioural sciences have traditionlly emphasised the passive and reactive nature of the developing animal towards environmental stimulation, play researchers have (at least implicitly) stressed the active nature of the young animal in determining aspects of its own development.

Secondly, the development of behaviour has traditionally been thought of in terms of dichotomies (Hinde 1970; Wilson 1975), and this is also true of play. Our understanding of development has been obscured by a preoccupation with a simple-minded dichotomy between the contributions to normal development of "play" and "other experience".

A third problem with studies of play's development is that they tend to view the developing animal as "immature", "inefficient" and "ineffectual", and the adult animal as representing the "end point" of developmental analysis (Galef 1981). There has been too much emphasis on

the emergence of "adult" behaviour patterns, rather than on the transition of early responses into later patterns (Lazar and Beckhorn 1974). This has occurred in play research because of attempts to distinguish "play" from "serious", "adult" behaviours.

From consideration of these points, it would seem worthwhile to attempt to look at development including play - rather than looking at play or other juvenile behaviours in isolation from each other. Again, this is an area of play research which has suffered from researchers' obsessions with defining play and discovering its function; but a developmental approach to play could provide insight into both of these issues. For example, the work of Bateson and Caro on the domestic cat, cited earlier, and the longitudinal studies of marmoset social behaviour by Chalmers and Locke-Haydon (1984) show how close inspection of the developmental course of behaviour can throw light on such questions as whether or not the different types of play represent a unitary phenomenon.

A dynamic view of play as a set of behaviours which shows development and change throughout ontogeny, and which must be examined in the light of other changes occurring in the young animal's life (such as weaning) is likely to prove much more informative than a static concept of play which is concerned only with differentiating play from everything else that goes on in development.

It was with the former conceptualisation in mind that

the present research was undertaken. One of the aims of the studies to be described in this thesis was to examine the development of play in relation to the other behaviours present in the young rat's behavioural repertoire, within a developmental framework. Some of the age-changes in play described by the research described in this section will be examined in the light of longitudinal data obtained on the rat.

## 1.5: THE IMMEDIATE CAUSES OF PLAY:

### 1.5.1: Introduction:

Identification of the immediate causes of play behaviour is important on both theoretical and practical grounds: theoretical, becuase a causal analysis of play emphasises the adaptive and integrated way in which play fits in with the rest of the immature animal's behaviour; and practical, because play is a phenomenon which has to be studied as and when it occurs, and a good understanding of play's causation will lead to cost-effectiveness in observation time.

The analysis of those factors precipitating play has been incidental to most studies of play, but nevertheless there is a fairly extensive body of data on the topic. For the purposes of discussion, the factors eliciting play may be divided into two types:

1. External factors in the causation of play.

(a) Elements of the physical environment which affect the occurrence of play.

(b) Aspects of the social environment which affect the occurrence of play.

2. Internal factors in the causation of play.

These two factors will be dealt with in turn, but obviously they could interact in complex ways to produce a net effect on the occurrence of play which may be of a very subtle kind.

1.5.2: External factors in the causation of play:

As far as external (environmental) factors involved in play are concerned, more is known about those factors which inhibit the appearance of play than of those which facilitate its appearance.

1.5.2.1: Elements of the physical environment which affect the occurrence of play:

It seems well established that all types of play are most likely to occur in a "relaxed field" (Bally 1945), an environment that does not contain any features causing physical discomfort or stress to the animal. In fact this statement probably has the most generality of any claim that can be made about play. The effects on play of a number of environmental factors has been assessed.

1.2.1.1: Weather:

A number of workers have described inhibitory effects of poor weather on play (eg, domestic lambs: Sachs and Harris, 1978; Toggenberg goats: Chepko, 1971; chimpanzees: Goodall, 1968). Generally, extremes of weather and temperature seem to depress activity in animals, and hence also depress play.

The weather may also affect play indirectly, for example by affecting food availability (see below) or, in the case of reindeer, by encouraging the growth of flies which continually irritate the young and so disrupt their behaviour (Espmark 1971).

1.5.2.1.2: Food availability:

There are numerous accounts of the effect of food availability on social play, generally concluding that food deprivation markedly reduces the incidence of play. Hall (1963) found that play was non-existent in several troops of chacma baboons living under starvation conditions on an island. Loy (1970) recorded a 94% drop in the frequency of play in a rhesus macaque population which had endured severe starvation for 22 days.

Experimental manipulation of food availability produces similar effects. Muller-Schwarze (1982) found that reducing the milk intake of unweaned female white-tailed deer fawns (*Odocoileus virginianus*) decreased locmomotor play (running) by 33%, and general activity by 9%. Southwick (1967) produced a "complete drop-out of play" in a captive group of rhesus monkeys by reducing their food supply by 50% for five days. Rosenblum et al (1967) found that two days' food deprivation produced a decrease in play in pigtail macaques (*Macaca nemestrina*) but led to a slight increase in play in bonnet macaques (*M. radiata*). Manipulating the quality of food provided, rather than its quantity, produces similar effects (Zimmerman et al, 1976); rearing rhesus macaques on a protein-deficient diet affected activity levels selectively, with all non-food-oriented behaviours (including play and social behaviours generally) occurring at very low levels.

Quite apart from physiological debilitation caused by

lack of nourishment, food deprivation may reduce play by forcing the animals to spend more time in foraging for food; the extra foraging time is obtained at the expense of play behaviours. For example, at the same time that locomotor play decreased by 33%, Muller-Schwarze et al (1982) observed a 62% increase in grazing which resulted in virtually complete energetic compensation for food deprivation.

The replacement of play by extra foraging also appears to be the case at Barqueta in S.W. Panama, where Baldwin and Baldwin's (1974) failure to observe any instance of play in a ten-week study of squirrel monkeys (Saimiri sciureus) was apparently due to food scarcity forcing the animals to forage for 95% of their waking hours. An experimental analogue of this situation simulated the effects of enforced foraging and feeding in the laboratory, by restricting the animals' access to powdered food and comparing their play-levels to those of animals fed the same amount of food in a more readily accessible form (Baldwin and Baldwin, 1976). Enforced foraging in this manner caused the frequency of play to drop to as little as 1% of that shown by the controls.

As Baldwin and Baldwin (1976) point out, although the incidence of play may be severely reduced by food deprivation, play seldom disappears entirely from the behavioural repertoire. In Loy's (1970) study, conditions were so severe that 6 out of 69 animals starved to death, and yet a minimal amount of play still occurred. The

Baldwins attribute the total lack of play at Barqueta to the fact that food shortage there had been prolonged, so that young animals had no prior play experience at all: where there has been play previously but it has been disrupted by a period of starvation, play may persist in some small measure due to its previously-acquired history of reinforcement.

One type of play not apparently affected by food deprivation, is predatory object play in the domestic cat (Egan 1976). She concludes that inasmuch as this is also a characteristic of "serious" predatory behaviour, predatory object play may be a juvenile substitute for predatory behviour rather than truly "playful" in nature. It would be interesting to know what effects food shortage has on other species which engage in predatory object play, but these observations do suggest that such types of play are motivationally distinct from social amd locomotor play.

1.5.2.1.3: Novelty:

A novel environment, or the presence of novel objects within a familiar environment, has often been reported to inhibit play. That this should be so is probably highly adaptive, in that it ensures that play does not occur until attributes of the environment which might have important consequences for the animal (eg, predators) have been attended to and their significance assessed.

This is not so just for prey species: Poole (1966) noted that fear-inducing stimuli and an unfamiliar

environment are factors which inhibit play in the polecat, Mustela putorius. Even if a polecat was introduced into an environment which was unfamiliar to him but was familiar to a polecat already in it, he would explore the environment before responding to the resident's play solicitations. Poole (1978) found that in a complex testing environment (one containing objects), more object exploration occurred and less social play, than in a less complex setting.

Although novelty initially inhibits play, once an environment or object have been explored they may serve to enhance play (Poole 1966). Most of the studies investigating these effects have focussed on object play rather than social play.

West (1977) distinguished exploration, "play-exploration" (leaping over and around an object while investigating it) and "play" (manipulation of an object), and found that exploration and play-exploration were used for longer durations with unfamiliar objects, whereas play was used for longer durations with familiar objects. Small size and mobility were important factors for play to occur, but no object property was important for exploration except novelty.

The Northern elephant seal is similarly most attracted to small moving objects, to which it directs playful movements perhaps resembling predatory behaviour appropriate to fish; social play is directed towards larger, more stationary objects, which presumably serve as

substitutes for social partners. Rasa (1971) suggests that the releaser for social play in this species is not "small conspecific", but merely a stimulus complex with the features "medium size, slow and heavy". Henry and Herrero (1974) claim that for black bears, object play was most likely to occur with an object that was new, chewable but inedible. They report that objects also served as a focus for social play, one cub seizing the object from another and investigating it, and then the other cub seizing it back again. Biben (1982) reports similar behaviour in the African Cape hunting dog.

Novel environmental features may trigger off new forms of play, or at least, new uses for established play patterns. Eibl-Eibefeldt (1950) describes how his pet badger learnt to slide on an icy path, and thereafter performed endless repetitions of this new behaviour pattern.

In general, the effects of environmental novelty on levels of play appear to be summed up by Millar's (1968) conclusion that one of the most universal events preceding play is some change in the environment. Redican and Mitchell (1974) confirm this, claiming that the particular environmental changes which precede play are those which seem to raise, moderately, the animal's arousal level.

1.5.2.2: Elements of the social environment which affect the occurrence of play:

The fact that the social environment affects the

occurrence of play suggests that the immature animal is not socially naive, but from an early age is part of a social group to which it responds. However, at least initially, social interactions may be significantly influenced and controlled by the mother. There seems to be potential for complex interaction between the social forces acting upon and around the infant, especially in primates, for whom the richest data on social behaviour have been obtained. Again, for the sake of convenience in discussion, the principal agents in influencing play will be considered separately; but in practice, they obviously interact to differing degrees, not only between species but between indivduals within a population.

1.5.2.2.1: The mother:

An immature animal's mother may have a profound effect on his social interactions, including play.

Especially when the young animal is an infant, the mother may have a predominantly inhibitory effect on play; she often seems to act as a preliminary "censor" of playmates, screening them for suitability and terminating social play if it becomes too rough (Bekoff 1977). Owens (1975b) describes how Papio anubis mothers determine the choice of play partners for their young infants and often terminate social play by picking up the infant and walking away.

In some species, the mere presence of the mother apparently inhibits play. Meier and Devanney (1974) for example, note that play-wrestling occurred between young

captive rhesus macaques only when they were out of their mothers' reach. The occurrence of play in domestic lambs (Sachs and Harris 1978) and in reindeer (Espmark 1971) coincides with the mothers going off to feed. Farentinos (1971) reports that in Steller's sea-lion the occurrence of play is largely correlated with the daily activity-cycle of the adult females; unattended pups congregate, and this provides the main opportunity for social play. In the Northern elephant seal (Rasa 1971), pups are forcibly weaned at about one month of age, by the mother leaving for the sea; weaners between 2 to 3 months are thus effectively pushed into interaction with each other, and so commence playing. While the mother is present, she prevents social play from occurring by refusing access of other young to her own.

The mother's inhibitory effect on play may vary according to her own responses to the social environment in which she and her offspring find themselves. Individual differences in such factors as the mother's rank, cautiousness and timidity may affect the infant's play (Meier and Devanney 1974; Nicholson 1977).

Relationships between adult females may decide the play-partners of their offspring by determining with whom they come into contact. (eg. Papio ursinus: Cheney, 1978; rhesus macaques: Fady, 1969). Findings such as these show that the mother's influence on play is not totally inhibitory, but may act to facilitate play in certain respects - for example, by bringing the infant

into contact with conspecifics to whom it would not normally have easy access. As well as acting as a "barrier" between her young and other conspecifics, in many species the mother also serves as a source of reassurance, a safe base from which the young animal ventures out into his environment. The mother may also facilitate play by reducing environmental demands on the immature animal, especially if play starts before weaning. In species which are solitary as adults, the mother may act as a focus of resources which serves to keep the young in close proximity and so encourages social play (West 1974).

Mothers may also act as play-partners for their young. Such interaction may amount to a considerable proportion of a young animal's total play (eg, mountain lions: Pfeiffer, 1980; orang-utans: Horr, 1977). In all reported cases of mother-infant play (and adult-infant play generally) it seems to be the infant who has to do the soliciting. This may be so for three reasons: firstly, because the mother or adult is less willing to participate in play, but does so if "requested"; secondly, because the adult's play solicitations would frighten or intimidate the infant, due to the adult's greater size and strength, so that the adult cannot successfully solicit play; and thirdly, because infants are more playful than adults, so that even if both solicit play equally readily, nevertheless the infant will solicit play more often simply because it plays more often.

1.5.2.2.2: Availability of playmates:

Perhaps the most important social factor affecting play is the availability of conspecifics with which to play. Poole (1966) states that the most powerful elicitor of play in the polecat is another polecat; the presence of a strange polecat will elicit play from a group of polecats which were not previously playing. The importance of playmates is obviously important for social play to occur, by definition; but there is also evidence for social facilitation effects in other types of play. In reindeer, running in one calf seems to release running in others (Espmark 1971). In predatory object play, the presence of peers leads to social facilitation in coyotes (Vincent and Bekoff 1978) and domestic cats (Leyhausen 1965, Egan 1976).

The availability of playmates may determine the apparent playfulness of some species: for example, Ellefson (cited in Dolnihow and Bishop 1970) suggests that the lack of play in young gibbons may be due to the absence of partners of similar size and strength in the family unit. Similarly, in the orang-utan, the relative lack of interactive contact play seen in the wild may be related to the fact that the main social unit is the adult female and her young. Infants have only their mother or juvenile siblings to play with, and juveniles rarely have playmates due to older siblings moving away (Horr 1977).

Availability of potential partners for play may vary

within a species or population over time. This may affect both the quantity and quality of the play observed. In the case of squirrel monkeys, Baldwin and Baldwin (1974) found that the larger the forest, the more play was observed. This was presumably because a larger forest could support a larger troop, and thus provided an infant with more peers with which to play. An example of how the availability of partners may affect play qualitatively, is shown by Baldwin's (1969) observation that infant squirrel monkeys born towards the end of the breeding season show play that seems less physically coordinated than that of their older peers, perhaps because they are able to play only with infants.

Cheney (1978) remarks on how the play of infant Papio ursinus appears to be affected by the number and ages of potential play partners. She points out that immature animals have preferred age and sex classes with which to play, but that if these are not available they will play with the next best alternative. Play among individuals of difeent ages and sex therefore seems most likely to occur when the social group is small; as the number of potential play partners increases (and hence there is an increased choice of who to play with) so the observer gets a greater idea of actual playmate preferences. Such factors obviously have implications for any studies claiming to show the "species-typical" or "normal" distribution of play in a species.

Cheney (1978) points out that the sex/age composition

of a group at the time of an infant's birth might have important effects on his choice of play partners. Immatures in those species in which females give birth during a short, distinct birth season (eg, most macaques) might be expected to be brought into close contact predominantly with closely-related individuals. In those species in which individuals live in relatively small groups (eg, vervets) or give birth at random intervals throughout the year (eg, baboons), there might be wide scope for play among different ages, sexes and ranks.

Availability of play partners may be a factor in the numerous observations claiming that young animals play more with their siblings than with non-siblings of equivalent age and sex (eg, rhesus macaques, Southwick, Beg and Siddiqui 1965; crab-eating macaques, Fady 1969; vervets, Fedigan 1972; baboons, Owens 1975b, Cheney 1978; and chimpanzees, Goodall 1968). This preference for siblings may be due simply to the fact that siblings are more readily available for play: in social species, they are closer and easier to get access to, and in solitary species they may be the only avaibale playmates.

1.5.2.2.3: Other conspecifics:

There is wide variation between species in the responses shown towards immature players by conspecific adults other than the players' mothers. At one extreme is Steller's sea-lion, in which adult females who are not the mothers of either of two players will abruptly stop play by growling if they come too near, and in which adult

bulls wil trample pups if they get in their way. At the other extreme, many adult primates are quite playful (eg, the chimpanzee, Goodall 1968).

Adult conspecifics may affect play merely by their presence. Meier and Devanney (1974) noted that social play did not occur in their group of rhesus macaques except when the group were peaceful. Rosenblum and Plimpton (1979) found that the mere presence of adults was sufficient to restrict activity in immature rhesus macaques, with unfamiliar adults providing the most constraint.

Adults may also take a more active role in regulating play. Owens (1975b) reports that adult male Papio anubis frequently intervened if an infant was hurt and caused to scream during play. Such behaviour on the part of adults may effectively act as a precaution against "cheating" in play, punishing immature animals who attempt to damage their opponents under the guise of play.

Toleration of players by adults, and responsiveness of adults to play solicitations directed at them by immature animals, may depend on the opportunities for interaction presented to them by the social structure of their species. Redican and Mitchell (1974) found that adult rhesus males, which in the wild are generally indifferent and sometimes aggressive towards infants, could under appropriate conditions show a great potential for affiliative behaviour towards them, including play.

In short, it seems that the presence of adults may

have a major and as yet comparatively unappreciated effect in determining the structure and patterning of playful interactions both across and within species.

1.5.2.2.4: Play and social deprivation:

A number of experimental studies have attempted to selectively deprive subjects of play experience for limited periods, examining the effects of this manipulation on play levels when opportunity for play is reinstated, in expectation of finding a subsequent compensatory increase in play - a "rebound" effect.

There have been a number of studies investigating the effects of short-term deprivation on the amount of play subsequently shown; most of them are unfortunately flawed in some respect.

Muller-Schwarze (1968) deprived one male and one female black-tailed deer (Odocoileus hemionus) of play, but not of other opportunities for exercise, by distracting them with milk whenever they gave the head-jerk which characteristically initiates a play-bout in this species. He did this for 24 hours, on alternate days, and measured the amount of play on the days following the deprivation days. No significant differences between deprivation and non-deprivation days were found in the frequency of leaping, running or other play movements. The only effect was an increase in running speed in the female, after deprivation. If the entire period between two play-bouts was considered, there were no significant

differences due to deprivation;but if the amount of locomotion in the first five hours after deprivation was compared to the corresponding five hours of a "normal" day, the animals were found to move much more than usual. However, defects in this study include the small number of subjects used; the use of hand-reared animals, which in itself may have produced aberrant social behaviour; and the use of milk as a distractor from play, thus potentially reinforcing play intention movements or even perhaps reinforcing the deer for not playing. Also, as Chepko (1971) points out, since Muller-Schwarze's deer only played for two eight- to fifteen-minute sessions per day, deprivation of only one of these sessions might not have caused a significant increase in play in the following session.

Chepko's own experiment used Toggenberg goats (Capra hircus) in three groups: an undisrupted control group, to provide a baseline against which to compare the two experimental groups; experimental group one, which were prevented from playing for 24 hours by yelling or physical restraint, confined for a further 24 hours due to heavy rain, and then observed for 24 hours; and experimental group two, which were confined for 24 hours and then observed for the next 24 hours. Chepko found an increase in the frequency and duration of both play and "activity periods" on post-deprivation days. However, she too used few subjects (one pair of goats per group); took no account of the weather and temperature, both of which

can markedly affect play; and one subject had already been used in an experiment on the effects of one hour's maternal separation at birth. In a personal communication to Bekoff (cited in Bekoff, 1976) she reported that a follow-up study controlling for some of these factors failed to replicate her original findings.

In contrast, Panksepp's work (Panksepp and Beatty 1980; Panksepp 1981) used better experimental designs and large numbers of subjects (rats), but was deficient in that whereas Chepko (1971) and Muller-Schwarze (1968) observed their animals for 24 hours following experimental manipulation, Panksepp looked at his subjects for as little as 5-10 minutes. Also, Panksepp deprived his animals not just of play but of social contact in general. Observing 20 pairs of like-sexed littermates at day 21 for 5 minutes each, he found that 10 pairs which had been housed in family groups until day 18 and then socially-isolated from then on, usually played for the whole of the observation period. In contrast, animals raised in family groups until day 18 and then housed in pairs thereafter, engaged in vigorous social interaction for less than one third of the observation period. Isolation in this manner increased pinning by 1000%, social solicitations by 367%, following by 265%, and the amount of time spent together by 300%, compared to the socially-housed animals.

In a second experiment (Panksepp and Beatty 1980), rats aged 25-30 days were tested twice, once after 24

hours of social isolation and once after social housing. In both conditions, the pairs had had no social contact with each other since weaning at 21 days. During 10 minutes' observation time, male rats spent a mean time of 146 seconds in rough and tumble play after isolation, and a mean 26 seconds in play after social housing. Female rats showed very similar results. The effects of isolation were much greater at 28 than at 18 days.

Using this reliable "rebound" effect, Panksepp (1981) tested socially-housed rats and isolates for 5 minutes each, on days 18, 20 and evey four days thereafter until day 64 of age. In this way, he was able to chart the development of play, albeit "amplified" from the low levels exhibited by undisturbed animals. He found that the effect of play deprivation on subsequent levels of play to be maximal at 32-40 days, the point at which play is normally at its height in the rat.

Perhaps the best-designed experiment in this field so far, is that by Smith and Hagan (1980). Using young children in the familiar setting of their nursery school, Smith and Hagan manipulated the amount of confinement within their subjects' normal daily routine, rather than simply its presence or absence. A longer confinement period indoors (one and a half hours) was correlated with considerably more outdoors exercise play subsequently than was a shorter (half-hour) confinement period. In this experiment, confounding of play deprivation with other variables was kept to a minimum,

adequate numbers of subjects were used, and the observation periods were sufficient to obtain a reasonable smaple of behaviour. Perhaps the main criticism of Smith and Hagan's study is that confinement indoors deprives children not only of exercise play but also of unrestricted social access in other respects.

In addition to these experimental studies, there are also a number of field observations of "rebound" effects. For example, the behaviour of winter-hibernating animals on awakening is a good "natural" experiment of this kind: Krott and Krott (1963) describe vigorous approach-withdrawal play in young free-living brown bears (Ursus arctos) in March following several months of winter inactivity.

Baldwin and Baldwin (1974) observed almost no play in two groups of squirrel monkeys (Saimirii spp.) in 261 hours of observation distributed over ten weeks. This was correlated with these animals having to spend an unusually large amount of time in foraging and travelling, due to food scarcity. In the laboratory, Baldwin and Baldwin (1976) experimentally manipulated the ease of access to food (while keeping constant the quantity supplied), so that the monkeys had to spend a great deal of time simply in obtaining food. In this way, the amount of time spent in play could be reduced - presumably because the monkeys had less "free" time in which to play. When these restrictions on access to food were lifted, a rebound effect occurred, with the frequency of play increasing to

a level up to 50% higher than the average baseline level, before returning to normal levels.

On balance, the "rebound" effect thus seems to be a prominent feature of social play. These studies have been described at length because of their importance in demonstrating firstly that play has a distinctive motivational basis, and secondly how levels of play can be affected by environmental factors. They imply that levels of play are internally regulated, in a way that is able to compensate for deficits in the amount of play performed. One of the aims of this thesis will be to to specify more precisely what factors are involved in this phenomenon, in particular investigating whether or not other social experiences can compensate for the lack of opportunity for social play.

### 1.5.3: Internal factors in the causation of play:

#### 1.5.3.1: Activity cycles and play:

The relationship of the occurrence of play to diurnal activity cycles is an interesting topic to which relatively little attention has been paid. Few studies have involved the continuous 24-hour surveillance which would be necessary to make firm conclusions about the relation of play to diurnal activity levels, or have made time-sampling or spot-checks over a fraction of that period. The problem is that such continuous observation may often be impracticably difficult in field studies, especially of marine or forest-dwelling species

(Aldrich-Blake 1970); and although unlimited observation of captive animals is posible, they may show abnormal daily activity-rhythms.

Many studies on play have involved placing together otherwise-isolated animals solely for the purpose of observing them play (eg, Bekoff 1974; Poole 1966, 1978; Panksepp 1980; Panksepp and Beatty 1981). This can tell us very little about daily play cycles, since under these conditions levels of play are typically enhanced (eg, Chepko 1971; Einon, Morgan and Kibbler 1978; Panksepp 1980). Even where captive animals are housed together under conditions which enable them to form virtually normal social groupings, there is the problem that play levels may be indirectly influenced by factors such as at what time of day the animals are fed or have their bedding changed.

What information we have suggests that play does not occur at random intervals throughout the day, but has a daily pattern which is probably the result of an interaction between internal factors (the activity level of the animal) and social factors (such as when the rest of the group are resting, peaceful and generally amenable either to play themselves or to tolerate play).

Play-bouts often seem to be concentrated in the early morning and/or in the late evening. For example, Muller-Schwarze (1968) found that black-tailed deer engaged in locomotor play twice a day, once in the morning and once in the evening. This seemed to be an endogenous

cycle, since no other conspecifics were available to influence the animals' behaviour. However, this daily pattern was not clearly established for the first two months of life, during which the deer would play during the daytime as well. A similar daily pattern was found for social play in the Northern elephant seal (Rasa 1971), although the onset and duration of play were affected by the weather.

Chepko (1971) also found, in Toggenberg goats, that social play occurred mainly in the morning and evening; however, there were also bouts in between these peaks, and the general impression was one of variability in the daily pattern. In Steller's sea-lion (Farentinos 1971), although sporadic bouts of social play may occur at any time of day, most infant play-fighting occurs when the pups congregate into peer-groups, due to being left alone at the end of the day. Sub-adult male play-fighting however, is distributed throughout the day.

In some species, play seems to be concentrated at just one time of the day. In the reindeer (Espmark 1971), locomotor play was found to be strongly concentrated into a period between 18.00 and 21.00 hours. Lumia (1972) says that in the buffalo, play bouts are most frequent in the late afternoon and early evening, after the herd has eaten. Muller-Schwarze (1982) observed just one daily play-bout in white-tailed deer fawns, between 07.30 and 08.30 hours.

In general, play seems to occur at times of greatest

activity, as might be expected for a vigorous and energetic activity; this is known to be the case for the rat (Poole and Fish 1975) and the racoon (Welker 1959). In view of these findings, the studies to be described in this thesis all involved observation of subjects at around "dusk" or "dawn".

1.5.3.2: Sex differences in play:

Sex differences in play (males typically playing more frequently, roughly and vigorously than females) have been frequently reported, although they are by no means universally found (Stevenson and Poole, 1982; see Meaney, Stewart and Beatty, 1985, for an extensive review of this topic). Description of the kinds of sex differences found in play have been given in the section on development. The concern here is with what causes such differences.

It appears that, at least in rats and monkeys, sex differences in social play are the result of hormonal differences between the sexes. Phoenix (1974) found that prenatal administration of testosterone influenced play behaviour in female rhesus monkeys; and Olioff and Stewart (1978) found that post-natal injection of testosterone caused female rats to show levels of social play comparable to those of males when tested pre-pubertally (ie, before 30 days), although these effects were not apparent when testing occurred at 40 days of age.

Meaney, Stewart and Beatty (1985) suggest that

androgens exert an organisational, rather than an activational effect: administration of testosterone affects female behaviour only during a sensitive period of neurological development, and not at the time when the play behaviours are actually expressed. These effects may interact with the social behaviours performed towards the young animals by other conspecifics (especially the mother), further accentuating the sex differences in behaviour.

There may be sex-differences in some types of play but not in others; for example, in the domestic cat, sex differences appear in the frequency of object-contacts from 8 to 12 weeks of age onwards, but not in the frequency of certain elements of social play (Barrett and Bateson 1978).

The existence of sex differences in play has been cited as evidence for play having a specific practice function (eg, Aldis 1975; Symons 1978; Meaney, Stewart and Beatty 1985). However, it is an open question whether the hormonal differences influence the amount and type of play shown, which in turn then affects later adult behaviour; or whether the hormonal differences between the sexes affect both play and other behaviours, differences in playfulness thus not producing differences in other behaviour patterns, but rather both reflecting a common, more fundamental, difference between the sexes.

There may be extensive interaction between these two possibilities, with hormonal differences affecting both

play and other behaviours, but with experiences during play enhancing or counteracting the effects of sex differences in other behaviours. An illustration of a possible interaction between hormonal and experiential factors may be found in the play behaviour of female domestic kittens; female kittens raised in litters containing at least one male show levels of object play comparable to those shown by males, whereas females from all-female litters typically show less object contact than males (Barrett and Bateson 1978; Bateson and Young 1979). Caro (1981) similarly reports significantly more contact behaviour in males from all-male litters than in females from all-female litters, and that females' rates of play increase as the number of male companions increases. These litter-effects on play are not due to males providing their female littermates with higher levels of playful stimulation, for example by patting objects around (Bateson and Young 1979).

### 1.5.4: Conclusions:

Considering its potential importance, the study of the factors responsible for the immediate causation of play seems to have been somewhat neglected, except perhaps in primates where the role of social factors in determining levels of play has been most appreciated. Once again, as with other aspects of the study of play, there is a need to look at play in relation to other behaviours and to the social milieu of the young animal. A

causal analysis emphasises how play fits in with other behaviours.

Although play is an easily disrupted behaviour with a low priority compared to behaviours more obviously concerned with survival, nevertheless under natural conditions its chances of occurring regularly are maximised due to a number of factors which act almost as "failsafes" , ensuring that play will occur. These include encouragement and protection from members of the player's social group, with adults often being prepared to play if no other, more suitable partners are available; and the fact that some kinds of play can apparently substitute for one another, so that, for example, if social play is not possible a certain amount of locomotor play can occur.

A causal analysis also emphasises to what extent the nature of play may be influenced by extraneous factors, especially those related to the social structure within which play occurs. These external influences may markedly affect observed types and rates of play, quite independently of any endogenous tendencies to playfulness, or in complex interactions with them. For example, a "relaxed" social system may facilitate play by allowing young animals unrestricted access to peers and toleration of free movement by adults; and endogenous sex differences in play may be intensified or attenuated according to the external environment within which play occurs.

The study of causation is also of practical importance, as it enables researchers to know exactly when

their observations are most likely to coincide with times at which the animal is playing.

This whole area warrants further investigation, particularly in non-primate species, and will be given particular attention in the following studies.

## 1.6: STUDIES OF SOCIAL PLAY IN RATTUS NORVEGICUS:

### 1.6.1: Criticisms of previous studies on play in the rat:

The preceding sections discussed problems that are general to all play research; this section focusses on the limitations shown by research on rat development in particular.

Considering that rodents represent the largest single Order of mammals, there are surprisingly few detailed studies of their play. Of those studies that do exist, close inspection reveals that even fewer are reports of social interactions involving rough and tumble social play as defined in section 1.2, rather than merely immature aggressive behaviour or rudimentary locomotor play (Hole and Einon 1984). Of the readily-available laboratory-bred species of rodent, only Rattus norvegicus appears to show social play of the kind described in this introduction (Einon, Humphreys, Chivers, Field and Naylor, 1981).

There are already a number of excellent studies of early social behaviour in the rat (eg, Small 1899; Bolles and Woods 1964; Poole and Fish 1975, 1976; Meaney and Stewart 1981), although considering the popularity of the laboratory rat for behavioural research it is remarkable that there are not many more. Bolles and Woods' (1964) contention still stands, however, that "...there is, actually, surprisingly little basic information about the domesticated rat's normal behaviour. The need for

normative data is perhaps most urgent in the developmental area..." Furthermore, there are a number of ways in which the studies so far performed could be improved upon.

1.6.1.1: Amount of time spent in observation:

Previous observational studies of young rats either involved relatively few observations of the subjects' behaviour, or else did so on very few animals.

Baenninger (1967) for example, observed her rats five days a week from 3 to 92 days of age, but looked at only one target pup in each of her socially-raised litters, so that her conclusions are essentially based on the behaviour of ten male pups. Poole and Fish's (1975) observations are even less representative, being based on behaviour seen during six 30-minute observation periods on one litter at 21 days of age, and another litter at 35 days of age. The same authors' 1976 study, however, did observe four litters aged between 25 and 35 days, and four between 35 and 49 days, each litter being observed for a total of 12 hours.

Meaney and Stewart (1981) observed four litters (each of six pups) daily from 21 to 55 days of age, but they observed each pup for a total of only thirty 20-second observation sessions. The study by Bolles and Woods (1964) remains the most extensive investigation of early rat behaviour, with 19 litters observed at varying intervals; however most of their observations were terminated at 26 days of age, and so are limited in their

informativeness on play.

Clearly there is scope for greater sampling of early rat social behaviour, and that statements such as Poole and Fish's contention that "rats show only minor age-dependent changes in the composition of play..." are based on relatively scanty evidence. The aim of the present research is not necessarily to contradict such claims, but rather to see how they fare in the light of more extensive observational data.

1.6.1.2: Limitations of cross-sectional studies:

Although Panksepp (1981), Meaney and Stewart (1981), Baenninger (1967) and Bolles and Woods (1964) all used longitudinal studies (the latter three studies involving daily observations), the most influential reports on rat social play - those of Poole and Fish (1975, 1976) - employed a cross-sectional technique, looking at two different groups of rats at 25-35 and 35-49 days respectively.

While cross-sectional techniques are economical on time and effort, they produce inherently greater variability in the data obtained than do longitudinal studies; the latter, while returning comparatively little information for a great deal of time and effort, are nevertheless more sensitive to changes over time and thus especially appropriate in developmental studies. The two approaches, longitudinal and cross-sectional, are complementary; but given Poole and Fish's (1976)

suggestion that "very considerable individual differences in playfulness exist", and their claim mentioned above, that only minor changes occur in play with increasing age, it was felt that a longitudinal approach would be more likely to detect any subtle changes in play behaviour during development.

1.6.1.3: Intrusive techniques:

Some of these purportedly-"observational" studies of rat development have actually used intrusive and potentially disruptive techniques.

One such treatment has been excessive handling of the litter and/or the mother. Some studies have kept handling to a minimum: for example, Poole and Fish (1975) and Meaney and Stewart (1981) left their animals undisturbed in family units except for early culling and sexing. Other studies, however, have involved extensive handling throughout development. Panksepp's (1981) attempt to study the development of social play by charting age-changes in a single easily-quantifiable measure - "pinning" - are marred by the fact that his animals were housed either in isolation or in pairs, except for a limited opportunity for social interaction with an unfamiliar peer in a strange cage, once every four days from 20 to 64 days of age.

These rats were thus subjected to more disruption of development than Einon et al's (1978) "playing isolates" - and yet Panksepp (1981) claims that the developmental

course of play in his rats was "normal", in that it correlated well with the findings of Small (1899) (who handled his rats extensively, and subjected them to various extreme and aversive stimuli); Muller-Schwarze (1966) (who also merely paired rats each day in order to observe play); Poole and Fish (1975); and Baenninger (1967). But it is arguable whether this correlation is on anything more than a gross level - ie, in terms of the quantity of play at different ages, rather than in terms of that play's quality.

Another treatment widely and uncritically used, is early enforced weaning. Poole and Fish (1975, 1976) and Meaney and Stewart (1981) observed their animals in intact mother-litter units (except for early culling). While this is still an unnatural social grouping (especially for the mother, who would be interacting with other adults and pups during this time), it is roughly the equivalent of the unit found in wild rats for the first 60 days of life, according to Calhoun (1962). Generally, however, it has been the rule to wean pups at 18 to 21 days of age, at which time the mother is permanently removed (Panksepp 1981; Booles and Woods 1964; Baenninger 1966). Baenninger even removed the mother from the cage while observations of pup social behaviour were being made, and then replaced her afterwards!

Given that the effects of manipulations such as these are ill-understood, and may well have complex and far-ranging effects, the observational studies to be

reported in this thesis will keep handling and other experimenter interference to a minimum. The studies in chapter two involve leaving weaning to take its own course, as would happen in more natural conditions (although unfortunately this was not the case in the studies described in chapter three, in which litters were weaned at 21 days).

1.6.1.4: Lack of naturalism in observational environments:

More effort could be made to observe subjects in something approximating a "natural" habitat than has previously been the case.

Except for Meaney and Stewart's (1981) work, where litters were supplied with a nesting area measuring 20 x 20 x 20 cms and an adjacent area of 60 x 30 x 45 cms, most studies have used breeding-cages of similarly-cramped dimensions (eg, Poole and Fish 1975, 1976; Bolles and Woods 1964). Panksepp's (1981) observation chamber was not even familiar to the animals, since they were placed in it only once every four days.

It is difficult to know what would constitute a "natural" environment for an animal which has lived for so long in close association with man and his artifacts (Barnett 1975). Nevertheless it was felt that in the present work, the following features would go some way towards making the observation conditions less "unnatural". Firstly, a large enclosure (2 metres square)

was used, in order to provide sufficient room for animals to selectively associate with or avoid each other. Thus social interactions should be regulated by the animals themselves rather than being thrust upon them by enforced physical proximity. Secondly, more natural lighting conditions were provided than have been used in other laboratory studies. Though the lighting cycle was reversed for the experimenter's convenience, artifical "dawn" and "dusk" effects were provided, in order to provide the subjects with a more natural diurnal pattern than would otherwise be the case.

## 1.7: OUTLINE OF THE AIMS AND METHODS OF THE FOLLOWING CHAPTERS:

### 1.7.1: Overall Conclusions from reviews in this chapter:

The main conclusion from the discussions in this section is that the lack of precise definitions of play, and the over-riding obsession with play's function, have worked together to produce a confused situation. While there is a large mass of data on "play", its potential usefulness is limited, firstly because of the confusion engendered by lumping together diverse behavioural phenomena under one heading; and secondly, because surprisingly many of the extant details of play are bound to the particular theoretical orientation which inspired their collection - generally the conception of play as practice for adult activities. This has led to neglect of the study of play's causation and development; and yet many of the more interesting discoveries about the nature of play stem from the few studies in these two areas.

Examination of the data on the early social development of the rat reveals that, for once, there is relatively little information on what must be the most studied of all species.

### 1.7.2: Summary of the research to be described in this thesis:

The following studies attempt to deal with some of these omissions.

Running across all of these studies, there are two main themes:

1. The relationship of play to other behaviours, especially aggressive and amicable social behaviours.

2. The motivation of play; what are the immediate causal factors in rat play, and is there an endogenous, homeostatic mechanism ?

Chapters two and three have a common objective: to use longitudinal observational techniques to provide normative data on play, and to relate it to other behaviours occurring at the same time in ontogeny. They differ in the depth of analysis of the behaviour observed.

Chapter two looks at social rough and tumble play, attempting to relate it on a very general level to other behaviours, both social and non-social, with a view to describing ontogenetic changes and to answering such questions as whether individual differences in playfulness are related to individul differences in other social behaviours. Are the most aggressive animals also the most playful, as one might expect if the two behaviours are related ? What sort of relationships are there between animals in play ? Are some individuals consistently dominant ?

Chapter three focusses on the play-wrestling itself, examining its temporal characteristics, features such as role-reversal and spatial attributes, and the relationship of wrestling to the behaviours occurring immediately

before and after it - the immediate context within which play occurs. It will look at whether play changes with age in anything more than simple ways (frequency of playing). Does play occur within a context that would also be appropriate to aggression ? How "reciprocal" is play ? How long does play last, and what factors cause it to end ? Are the situations in which play occurs compatible with a "territoriality" explanation ?

Chapter Four switches to experimental methods, to investigate certain aspects of the immediate causation of social play.

Experiment one looks at whether deprivation of play is the important factor in rebound effects, or whether wholesale deprivation of social contact is the cause. Is there a homeostatic mechanism governing how much play occurs ? Can limited opportunities for social experience substitute for play ?

Experiment two has two aims. Its prime purpose is to see if changes in the environment (produced by placing a novel object in the cage) result in increased play. This study has its basis in certain findings of experiment one, and in the work (reviewed earlier) which suggests that environmental change may stimulate playing. A secondary aim was to investigate pinning levels between pairs of animals, to see if consistent relationships in terms of pinning are developed.

Finally, experiment three examines the effects of food-deprivation on play and other social behaviours, with

a view to replicating the findings on primates and deer that food-deprivation suppresses play. If play has costs, then increasing the relative costs (by food-deprivation) should reduce the amount of play seen. If there is a homeostatic mechanism, it should increase the amount of play performed subsequently to compensate for the deprivation.

A secondary consideration in experiment three is that if play is related to incipient territoriality or defence of resources, then when those resources become more valuable, a resident should defend them more vigorously against an intruder - by performing a greater percentage of the observed pinnings.

# CHAPTER TWO: LONGITUDINAL STUDIES OF EARLY SOCIAL BEHAVIOUR:

## 2.1: INTRODUCTION:

This chapter reports the results of longitudinal observational studies attempting to relate social play to other behaviours performed during the period from 21 to 60 days of age. "Play" in this chapter is considered in fairly gross terms simply as "rough and tumble wrestling", in contrast to the more fine-grain analysis of aspects of play itself which will be presented in subsequent chapters. The prime concern here is with how much play occurs, compared to other behaviours; and how play fits into the daily organisation and patterning of behaviour, both of social behaviour and of "maintenance" activities such as feeding and sleeping. The main aims of this section are firstly, to corroborate the observations of previous researchers of rat play behaviour, assessing to what extent their findings are supported by more extensive, longitudinal data; and secondly, to attempt to discover more about play itself by examining its relationships with other behaviours. If playful rats were also more aggressive individuals, for example, then this might provide us with clues as to the nature of play itself. In brief, the concern of this chapter is to look at early development, including play, rather than studying play in vacuo. Specifically, the following issues will be dealt with.

1: The overall frequencies of social and non-social behaviours:

This will provide information on approximately how much time is allocated to social behaviours compared to maintenance activities. Within the class of social behaviours per se, estimates will be made of the relative frequency of each kind of interaction - for example, comparing the frequency of play as a form of social interaction, to that of allo-grooming, olfactory investigation of partners, etc.

The work of Poole and Fish (1975, 1976) and Meaney and Stewart (1981) suggests that there are sex differences in the play of young rats, with males playing more than females. The present study will look for the existence of sex differences not just in play but in other social and non-social behaviours as well.

2: Age-changes in behaviour:

The data will be examined for age-changes in play corresponding to those reported by previous authors. Any age-changes in other behaviours will also be investigated, in order to place play into some sort of developmental context. The effects of weaning and the development of sexual maturity on the organisation of behaviour can only be meaningfully interpreted by looking at behaviour as a whole, rather than by studying play in isolation. Any age-related sex-differences in behaviour will also be described in this section.

3: Individual differences in social behaviour:

Individual differences in playfulness will be examined, and related to individual differences in other social behaviours. This section will address such issues as the degree to which particular subjects show consistent patterns of playfulness throughout their ontogeny; whether highly playful subjects are also disproportionately involved in other social interactions (for example, agonistic ones); and the extent to which playfulness correlates with high levels of activity and exploration, as measured by olfactory investigation of the environment.

4: The role of the mother in social behaviour:

Although both Poole and Fish (1975, 1976) and Meaney and Stewart (1981) studied intact litters, they make relatively little comment about what the mothers actually did, and how they related socially to their pups. The present study will focus more closely on the extent to which the mothers interacted with their pups, and what form these interactions took.

## 2.2: METHOD:

### 2.2.1: Subjects:

Three litters of PVG rats were used to obtain the data presented in this Section. Each litter consisted of four pups (two of each sex) and their mother.

## 2.2.2: Apparatus:

A large purpose-built observation cage was used, 2 metres long, 2 metres wide and with walls 50 cm. high. Fig. 2.1 shows a diagram of this. The front and side walls ("front" and "side" relative to the observer's location) and roof were made of perspex, and the floor was constructed of opaque plastic sheet. The lower two-thirds of the rear wall were perspex, while the upper third consisted of wire mesh, to provide ventilation for the inhabitants. Ventilation was further facilitated by a "Ventaxia" fan on the rear wall of the room, which blew air into the cage and regulated the cage temperature to 21-23 degrees Centigrade.

A food-hopper was located in the near-right corner of the cage; this could be filled from outside the cage. In the near-left corner were two water-bottles; again, these were located outside the cage, with just the spouts protruding into it, so that they could be refilled without unduly disturbing the occupants. Food (S.D.S rat and maintenance diet number 1, in expanded form) and water were available ad-lib throughout the experiment. Large bricks were placed in both of these corners, to enable the animals to reach the food and water more easily. The floor of the cage was covered with garden topsoil to an initial depth of approximately 10 cm. Nesting material (two handfuls of wood-wool) was initially provided.

This observation cage was housed in a windowless room, approximately one metre wider than the cage and

**FIG.2.1: DIAGRAM OF THE OBSERVATION CAGE USED FOR THE STUDIES DESCRIBED IN CHAPTERS TWO AND THREE:**

about a metre and a half longer than it, and containing a sink on its left-hand side. At the front of the cage was a small shelf and the observer's chair.

Illumination was provided by six 100-watt tungsten light-bulbs housed in anglepoises, one clamped to each of the four corners of the cage and one located mid-way along each side. Two 40-watt red lights, one clamped to each side of the cage, provided illumination during the dark phase of the animals' daily cycle. Subjects were maintained on a 12 hour light/ 12 hour dark cycle. There was a gradual transition between light and dark and vice versa, to produce simulations of "dawn" and "dusk". This was achieved by means of a dimmer switch linked to a small electric motor and time-switch, so that the white lights were progressively brightened and dimmed, over a period of about 2 hours for each transition - although to a human observer, "dawn" and "dusk" subjectively took about half an hour each.

### 2.2.3: Procedure:

Each litter was tested singly. The mother was placed in the test environment when she was definitely known to be pregnant, so that the pups were born into the observation conditions. The litter was culled to four pups as soon as sex could be reliably determined. This meant that the mother had adjusted to the room's light-cycle, and that the pups were born into it.

Observations were made daily (except for the

* Each of the three litters used in this experiment was observed at a different set of "real" (clock) times, so as to avoid unintentional synchronisation of observation periods with extraneous factors such as the times at which the building's heating or ventilation was switched on or off. The actual times of observation were as follows:-

| Litter 1:- | Litter 2: | Litter 3: |
|---|---|---|
| 7.00 - 7.15 A.M | 9.00 - 9.15 AM | 11.15 - 11.30 AM |
| 7.30 - 7.45 " | 9.30 - 9.45 " | 11.45 - 12.00 " |
| 8.00 - 8.15 " | 10.00 - 10.15 " | 12.30 - 12.45 PM |
| 8.30 - 8.45 " | 10.30 - 10.45 " | 1.15 - 1.30 " |
| 9.00 - 9.15 " | 11.00 - 11.15 " | 1.45 - 2.00 " |
| 9.30 - 9.45 " | 11.30 - 11.45 " | 2.15 - 2.30 " |
| 11.00 - 11.15 " | 12.00 - 12.15 " | 2.45 - 3.00 " |
| 11.30 - 11.45 " | 12.30 - 12.45 " | 3.15 - 3.30 " |

(and, in each case, at the same times for the P.M. observation session).

The room lights began to dim or brighten (depending on whether it was the a.m or p.m. session) about one hour into each observation session.

occasional missed session) between 21 and 60 days of age. There were two observation sessions per day, (each of 3 3/4 hours) one covering the beginning of the light phase, and the other its end (ie, around "dawn" and "dusk"). Each of these two sessions was subdivided into eight 15-minute periods separated by seven 15-minute breaks. This maximised the amount of the day that could be covered reliably by one observer working "live", without video. *

2.2.3.1: Time-sampling conventions:

A focal-animal time-sampling method was used. Each 15-minute observation period was divided into three rounds of looking at each animal in turn for one minute. Within this minute, the behaviour of the subject in question was recorded every 10 seconds. ("instantaneous" sampling) Thus a 15-minute session would consist of the following sequence being performed three times in all: six samples of the mother's behaviour would be taken (one every 10 seconds), followed by six samples of pup number one's activity, followed by pups two, three and four. The same sequence - M, P1, P2, P3, P4, repeated three times - was used for each 15-minute observation session. This gave a total of 144 observations (ie, spot-samples) per animal per day (a.m and p.m. session combined).

2.2.3.2: Behaviours scored:

On the basis of pilot observations, twelve main categories were used to record behaviour. These were defined as follows.

1: Locomotion:

This included climbing (on the wire mesh of the food-hopper or at the rear of the cage, or on the water-spouts); running (alone, rather than chasing or being chased); walking, without obviously sniffing the ground.

2: Play:

"Play" was scored when rough and tumble wrestling was observed. A note was made of whether the animal whose behaviour was being scored was on top or underneath or evenly-matched with its partner in the wrestling, at the instant being scored.

3: Sleep:

Laying motionless was scored as sleep, whether or not the eyes were actually closed. "Sleep" excluded laying with the mother, which was taken to be maternal behaviour.

4: Eating:

This was scored for any ingestion of solid matter, including nest material and coprophagy.

5: Drinking:

This was scored if the mouth was in contact with the end of a water-spout.

6: Maternal behaviour:

This was scored whenever the mother was laying with the pups, since in practice it proved almost impossible to detect whether or not suckling was actually occurring.

7: Grooming:

"Grooming" consisted of self-grooming, including

face- and paw-licking.

8: Allo-grooming:

This was any grooming of one subject by another, but excluding that which was obviously part of an on-going play interaction. A record was made of whether the target animal was grooming or being groomed.

9: Agonistic interactions:

Most of these would more accurately be described as potentially agonistic or potentially competitive situations. They constitute a fairly diverse set of behaviours. Included in this category, for example, were jostling with another animal for access to the food-hopper or water-spout, and competing for space on one of the bricks or for access to a particular spot in the cage for sniffing. Stealing food from another animal was also considered as a potentially agonistic activity. This category did also include definitely-aggressive interactions such as fighting and biting, and chasing.

10: Sexual behaviour:

"Mounting" and "being mounted" were used as blanket terms to cover attempted mounts, mounts with thrusts and intromissions.

11: Olfactory activity:

This was scored whenever the animal was obviously sniffing some part of its environment. "Olfaction" was divided into "environmental olfaction" (sniffing the inanimate environment), and "social olfaction" (sniffing

another animal). This may have been a somewhat arbitrary distinction at times, since many examples of environmental olfaction presumably involved investigation of the scents left behind by another animal, and thus had a "social" component. In practice, this category overlaps to some extent with that of "locomotion" since it was sometimes difficult to exclude the possibility that an animal scored as "locomoting" was not also sniffing its environment - after all, olfaction is the dominant sensory modality of the rat, and much of its behaviour would appear to involve olfaction to a greater or lesser degree.

12: Other behaviour:

This included all activities not included in the above categories - for example, falling off one of the bricks or the wire mesh at the back of the cage.

In the case of social interactions, wherever possible a record was made of who did what to whom, ie whether the target animal was performing the behaviour to another animal or whether he was the recipient of another animal's attentions. *

2.2.3.3: Methods of data analysis:

The theoretical total number of observations was 28,800 for each Litter, but some fifteen-minute observation periods were missed, so that the actual total numbers of observations were 28,260 for L1 (6 periods missed); 28,530 for L2 (3 periods missed); and 27,540 for

* For observer reliability checks on the time-sampling method used in this chapter (and on the measures used in chapter three also), see Appendix One.

L3 (14 periods missed - eight of which were because no observations were made at all on day 63).

The missed periods were distributed fairly randomly over the 40-day study period, but not so randomly within the days on which they occurred, since they tended to be at the beginning or end of a morning or evening session. Inspection of the data for observation-periods at the same times on other days, suggests that the missing periods were largely taken up with sedentary activities rather than social behaviours; the results described below thus slightly underestimate the relative frequencies of sleeping and maternal behaviour in particular. However, in view of the small number of observations missed compared to the number of observations actually made, this is not felt to be a significant source of systematic error in the data.

Three complementary approaches were taken towards the problem of assessing how much time subjects spent on various behaviours. The focal-animal time-sampling technique employed provided information on the frequency with which each individual was observed to perform particular activities while he was the animal under scrutiny. Dividing the number of observations of each behaviour by the total number of observations on the individual concerned, converted the former into relative frequencies, so that estimates could be made of the relative amounts of time an individual apportioned to each activity. Using this method enabled direct

comparisons to be made between the proportions of observations of social and non-social behaviours.

For social behaviours, dividing the number of observations of each behaviour by the total number of observations of social behaviour performed by the individual concerned, gave an estimate of the relative amount of time devoted to each social behaviour in comparison to all other social activities.

More accurate estimates of the relative frequencies with which social behaviours were performed by each animal in a litter, were obtained by relying on two facts: firstly, that for each spot sample of a social behaviour, the identities of both participants were known; and secondly, that within a litter, equal numbers of spot samples were made on all individuals. This means that, within each litter, all instances of a given social behaviour could be pooled and treated as a random sample of that behaviour's frequency within the litter as a whole, regardless of the identities of the individuals on whom the data were actually obtained.

## 2.3: RESULTS:

### 2.3.1: Overall frequency of behaviours:

Table 2.1 shows the mean relative frequencies (in terms of percentages of the total number of observations

TABLE 2.1: MEAN RELATIVE FREQUENCY OF OBSERVATION OF BEHAVIOUR CATEGORIES: OVERALL, 21-60 DAYS:

(Percentages are mean percentages of the total number of observations made per animal, and thus represent the mean frequency with which individuals were observed to be involved in each activity. Figures in brackets = standard deviations. Statistics = Mann-Whitney 'U' tests, comparing male and female pups for relative frequency of performance of each behaviour. N1=6, N2=6 for all comparisons; all tests are two-tailed. "Gms" = "grooms"; "gmed" = "groomed"; "olf" = "olfaction; "envtl" = "environmental"; "bvrs" = "behaviours").

| | MALE PUPS | | FEMALE PUPS | | 'U' | p. |
|---|---|---|---|---|---|---|
| Maternal bvr: | 24.8 | (13.5) | 23.3 | (9.8) | 17.5 | ns |
| Sleeping : | 29.1 | (11.2) | 25.8 | (9.7) | 11 | ns |
| Drinking: | 1.4 | (0.2) | 1.6 | (0.2) | - | |
| Eating: | 11.6 | (1.4) | 10.9 | (0.8) | 10 | ns |
| Self-gms: | 10.9 | (0.9) | 11.8 | (1.5) | 11 | ns |
| Social Olf: | 1.9 | (0.5) | 2.0 | (0.2) | 14 | ns |
| Allo-gms: | 0.5 | (0.2) | 0.7 | (0.3) | 9 | ns |
| Being allo-gmed: | 1.8 | (0.5) | 1.8 | (0.5) | 16 | ns |
| Social play: | 2.5 | (0.9) | 2.4 | (0.4) | 16.5 | ns |
| Agonistic bvrs: | 1.4 | (0.5) | 1.6 | (0.8) | 14 | ns |
| Sexual bvrs: | 0.1 | (0.1) | 0.1 | (0.1) | - | |
| Envtl olf: | 10.2 | (1.2) | 13.4 | (1.9) | 0 | 0.002 |
| Locomotion: | 3.9 | (0.6) | 4.9 | (0.7) | 0 | 0.002 |
| Other bvrs: | 0.2 | (0.1) | 0.1 | (0.1) | - | |

TABLE 2.2: MEAN RELATIVE FREQUENCY OF SOCIAL BEHAVIOUR, OVERALL: 21-60 DAYS:

(Percentages are mean percentages of the total number of observations of social behaviour per animal; standard deviations in brackets. Other codes are as for table 2.1)

| | MALE PUPS | | FEMALE PUPS | | 'U' | p. |
|---|---|---|---|---|---|---|
| Social Olf: | 23.5 | (4.4) | 23.9 | (4.0) | 17 | ns |
| Allo-gms: | 6.2 | (2.8) | 8.3 | (4.3) | 11.5 | ns |
| Being allo-gmed: | 22.4 | (5.3) | 20.4 | (3.3) | 14 | ns |
| Social play: | 30.7 | (5.8) | 28.8 | (3.4) | 11 | ns |
| Agonistic bvrs: | 16.9 | (3.0) | 18.1 | (6.0) | 17.5 | ns |
| Sexual bvrs: | 0.4 | (0.5) | 0.6 | (0.5) | - | |

per subject) with which male and female pups were observed to be involved in the various behaviours recorded, during the whole of the period studied (ie, 21-60 days) and combining the data from all three litters studied.

It is important to note that, for all non-social behaviours and those social behaviours for which the initiator could be identified (social olfaction, allo-grooming and being groomed), these frequencies correspond to the frequencies with which animals were observed to perform the behaviour in question; but in the case of certain of the social behaviours (play, sex and agonistic activities), they merely represent the frequency with which the animals were involved in that activity.

The observed relative frequencies of behaviours were highly consistent between litters. For convenience of discussion, the behaviour-categories employed can be broken down into three broad categories: non-social, "maintenance", behaviours; non-social, "activity"; and social behaviours. The relative frequency of the behaviours within each of these categories will be described in turn.

2.3.1.1: Relative frequency of maintenance activities:

Most observations were of sleeping and maternal behaviour, these two categories together accounting for approximately 54% of all observations of male subjects, and 49% of those of females. This is not surprising,

considering that the morning and evening observation periods were timed to coincide with the diurnal transition from inactivity to activity and vice versa.

A further 13% of observations were spent in eating and drinking, in both male and female pups. Grooming accounted for approximately 11%-12% of observations on males and females respectively.

2.3.1.2: Relative frequency of non-social activity:

Sex-differences in the overall relative frequency of behavioural observations were confined to these behaviours. Female pups showed a higher mean relative frequency of olfactory investigation of the environment (broadly interpretable as "exploration") than did their male peers; this behaviour accounted for a mean 13.4% of all observations on females compared to a mean 10.2% in males. Females similarly showed a small but consistent difference in the mean relative frequency with which they were observed to engage in locomotory activity: 4.9% of observations, as opposed to 3.9% in males. Both of these differences were statistically significant (Mann-Whitney 'U' = 0, N1=6, N2=6; p=0.002 in both cases).

2.3.1.3: Relative frequency of social behaviours, in comparison to all other behaviours:

Social behaviours, as a whole, accounted for only approximately 8% of all observations of behaviour, in either sex. There were no sex differences in the relative

frequencies of the various social behaviours, taken overall.

Social play was the most frequently-observed (2.5% of all observations), followed by social olfaction (approximately 2%), being groomed (1.8%) and agonistic behaviours (approximately 1.5%). Allo-grooming was seen comparatively infrequently, accounting for less than 1% of all observations in either sex; and sexual behaviour was observed least of all, accounting for less only 0.05% of observations on either sex.

The marked difference between the relative frequencies of allo-grooming and being allo-groomed, mainly arises from the fact that it was the mothers of the litters who performed most of the observed instances of allo-grooming, rather than the pups themselves.

2.3.1.4: The overall relative frequency of each social behaviour, in comparison to all other social behaviours:

The previous section compared the relative frequencies of social and non-social behaviours, to provide some conception of the way in which time is allocated to different behaviours, overall, during the time-periods studied. This section looks more closely at the relative frequencies of social behaviours compared to each other, thus attempting to assess for example, what proportion of an individual's total number of social interactions were agonistic, playful,

etc.

Table 2.2 shows the overall mean relative frequency of each social behaviour for each sex, expressed as a percentage of the total number of observations of social behaviour per subject.

There were no consistent sex-differences in the proportion of social interactions allocated to each type of behaviour.

2.3.1.4.1: Social play:

Of all social interactions, social play was the most frequently observed, accounting for about 30% of social behaviour in both male and female pups. These figures conceal some differences between the three litters studied. One litter (L2) showed the kind of sex-difference in play (with males playing more than females) that one might expect on the basis of previous studies (Poole and Fish, 1975, 1976; Meaney and Stewart 1981), whereas L1 showed no consistent sex differences, and L3 showed more play by females than males. However, as mentioned previously, note that these figures provide information only on how frequently each sex was involved in play, and not how often each sex initiated play.

2.3.1.4.2: Social olfaction, allo-grooming and agonistic behaviours:

Three other categories of social behaviour were observed with approximately equal frequency: social olfaction (which accounted for roughly 24% of all observations of social behaviour); being groomed

(20-22% of social behaviour); and agonistic interactions (17%-18% of social behaviour). The last category consists of diverse behaviours, (eg, competition for nipple access, food-stealing, and serious fighting) which are probably best considered individually, and this will be done in the next section. They do have in common the fact that they are all agonistic and potentially competitive interactions, however.

Allo-grooming accounted for a surprisingly small percentage of observations of social behaviour, especially in comparison to the frequency of being groomed. This at first sight paradoxical result stems from the fact that many of the instances of being groomed were performed by the mother; the incidences of allo-grooming and being allo-groomed between the pups themselves, were fairly similar.

2.3.1.4.3: Sexual behaviour:

Sexual behaviour accounted for a relatively small mean percentage of all observations of social behaviour, less than 1% of the interactions of either sex. Here again, however, there were substantial differences between the three litters, with sexual behaviour being observed on a total of 26 occasions in L1, but only 13 times in L2 and 4 times in L3.

2.3.1.5: Sex-differences in the overall frequencies of involvement in social behaviours, using pooled data:

This section examines the relative frequencies with

which male and female pups engaged in different social behaviours when data-points are pooled across subjects within a litter, as described in section 2.2.3.3. The frequencies here are thus based on the number of times (out of the total number of observations of social behaviour that were obtained, across all pups in a litter) that members of each sex were observed to perform a behaviour, regardless of which individual was actually under observation at the time. This enables more accurate estimates of any sex differences in involvement in social activities.

In calculating expected frequencies of interaction for any of the social behaviours, allowance had to be made for the fact that an individual of a given sex had two opposite-sexed partners with which to interact but only one sibling of the same sex. Purely by chance, one would expect more social interactions to occur between the former than the latter (approximately 33.3% between like-sexed subjects, as opposed to 66.7% between animals of the opposite sex). Consequently, adjustments were made to the expected frequencies for the Chi-squared tests performed, in order to take account of this.

2.3.1.5.1: Social play:

Table 2.3 shows the relative frequency with which males and females were involved in play, over the whole of the 21-60 day observation period. Note that this table shows only the extent to which males and females were seen to engage in play, since a record was made only of which

TABLE 2.3: OVERALL FREQUENCY OF INVOLVEMENT IN SOCIAL PLAY, USING DATA POOLED ACROSS ALL SUBJECTS (21-60 DAYS):

(All frequencies in this table, and in tables 2.4 to 2.6, represent the frequency with which individuals were observed to perform different behaviours, regardless of the identity of the individual under whose observation-time the data were actually obtained. This is in contrast to tables 2.1 and 2.2, where the data are based on the frequencies with which individuals were observed to perform behaviours while they themselves were the subject under observation).

(a) Overall frequency of involvement in social play:

(Figures represent the total observed number of instances of social play in which both of the subjects involved could be identified, expressed as percentages of the total number of observations of play between pups, but excluding from the total those in which either of the interactants was not identified, and omitting mother-pup play. Raw data are in brackets. Note that data provide information only on involvement, and not on who initiated the play. "L" = "litter"; "?" = observations in which one of the participants remained unidentified; "tot" = "total"; "exp." = expected frequency by chance).

| | category of participant: | | | | |
|---|---|---|---|---|---|
| | MM | FF | MF | ? | total |
| L1: | 25.8 (111) | 19.5 (84) | 54.8 (236) | 9 | 100.0 (431) |
| L2: | 24.3 (149) | 14.7 (90) | 61.1 (375) | 32 | 100.1 (614) |
| L3: | 14.9 (50) | 39.1 (131) | 46.0 (154) | 6 | 100.1 (335) |
| Tot: | 22.5 (310) | 22.1 (305) | 55.4 (765) | 47 | 100.0 (1380) |
| Exp: | 16.7 (230) | 16.7 (230) | 66.7 (920) | | |

Chi-squared, 2 df, = 78.55; $p<0.001$.

2.3(b): Overall frequency of being on-top during social play:

(Figures represent the total number of observations of social play in which one of the interactants was clearly on top of the other at the instant of sampling, expressed as percentages of the total number of observations of play between pups in that sex-category - as shown in table (a) above - but excluding those in which either of the interactants was not identified, and omitting mother-pup play. Note that the 'M on F' and 'F on M' categories below, are sub-categories of the single class of 'MF' in the previous table. Raw data are in brackets).

| | category of participant (on-top partner first) | | | |
|---|---|---|---|---|
| | M on M | F on F | M on F | F on M |
| L1: | 81.1 (90) | 78.6 (66) | 39.8 (94) | 25.8 (61) |
| L2: | 73.8 (110) | 70.0 (63) | 45.9 (172) | 21.3 (80) |
| L3: | 84.0 (42) | 83.2 (109) | 46.1 (71) | 31.2 (48) |
| Tot: | 78.1 (242) | 78.0 (238) | 64.1 (337) | 35.9 (189) |

two individuals were involved, rather than who initiated it. There were thus three possible categories of interaction: males playing with each other, females playing with each other, or play occurring between two opposite-sexed partners.

Part (a) of table 2.3 confirms that there were no differences between males and female pups in the frequency with which they were involved in play (a total of 985 instances in which at least one of the two interactants was male, compared to 970 observations in which one of the players was a female), but also reveals that there was a significant departure from the expected frequencies of within- and between-sex play, (Chi-squared = 78.55, 2df; $p<0.001$), with significantly more play between like-sexed pups than between opposite-sexed pups. By chance, one would expect two-thirds of observations of play to have been seen between opposite-sexed partners, but in practice only just over half of the instances of play fell into this category.

Part (b) of table 2.3 shows the relative frequency with which members of each sex were observed to be in an on-top position in play, pinning down their partner. In this case, there were four possible outcomes: observations of males pinning males, females pinning females, males pinning females, or females pinning males. The percentages shown are of the total number of observations of play for that particular sex-category; ie, of the total of 310 observations of male-male play made in this study,

242 (78% of them) involved one of the males being clearly on-top of the other. Similarly, of the total of 305 observations of female-female play, 238 (also 78%) involved one of the players being in the on-top position. There was thus no difference between males and females in the frequencies with which they were observed to be on top when they were playing with a member of their own sex.

In play between males and females however, males were observed to be on-top in 44% of the total number of observations of mixed-sex play (ie, 337 out of 765), whereas females were on-top for only 25% (189 out of 765). Put another way, of the 526 instances of mixed-sex play in which one animal was clearly on top (which amounted to 69% of all mixed-sex play), 64% involved a male being on top but in only 36% of instances was a female interactant on top. This pattern was consistent across all three litters, even though they differed markedly in the extent to which they played overall.

2.3.1.5.2: Allo-grooming:

Table 2.4 shows the relative frequency of observations of within- and between-sex grooming, over the 21-60 day period. (As for the on-top position in play, it was possible from these data to determine who was grooming whom, and so there are four categories: male grooming male, female grooming male, male grooming female, and female grooming male).

These data again show that, while there were no sex differences in the extent to which males and females were

TABLE 2.4: OVERALL FREQUENCY OF INVOLVEMENT IN ALLO-GROOMING, USING DATA POOLED ACROSS SUBJECTS (21-60 DAYS):

(Figures represent the total observed number of instances of allo-grooming in which both of the subjects involved could be identified, expressed as percentages of the total number of observations of allo-grooming between pups, excluding those in which either of the interactants was not identified, and omitting mother-pup allo-grooming. Raw data in brackets. Codes as for table 2.3).

| | category of participants (groomer, followed by recipient) | | | | | |
|---|---|---|---|---|---|---|
| | MM | FF | MF | FM | ? | total |
| L1: | 33.1 (47) | 27.5 (39) | 14.1 (20) | 25.3 (36) | 7 | 142 |
| L2: | 23.9 (28) | 31.6 (37) | 17.9 (21) | 26.5 (31) | 9 | 117 |
| L3: | 36.5 (38) | 23.1 (24) | 10.6 (11) | 29.8 (31) | 6 | 104 |
| Total: | 31.1 (113) | 27.5 (100) | 14.3 (52) | 27.0 (98) | 22 | 363 |
| Exp.: | 16.7 (60.5) | 16.7 (60.5) | 33.3 (121) | 33.3 (121) | | |

Chi-squared = 115.07, 3 df; $p<0.0001$.

observed to be involved in allo-grooming (263 observations involving males, 250 involving females), nevertheless there were differences from the expected frequencies of within- and between-sex grooming. There was much more within-sex, and much less between-sex, allo-grooming than would occur if grooming partners were randomly chosen (Chi-squared = 115.07, 3 df; $p<0.0001$). Females were observed to groom males twice as often as males groomed females (98 observations compared to 52, across litters). Again, this pattern was shown by all three litters.

2.3.1.5.3: Social olfaction:

The relative frequencies of within- and between-sex social olfactory investigation are shown in Table 2.5. Examination of these data suggests that within-sex olfactory investigation occurred at close to the expected levels, while males sniffed females more frequently, and females sniffed males less frequently, than would be expected by chance. Male-female olfactory investigation accounted for over 37% of all observations of social olfaction, and this pattern was consistent over all three litters. These differences just failed to reach statistical significance, however (Chi-squared = 7.66, 3 df; $0.10> p >0.05$).

2.3.1.5.4: Agonistic and competitive behaviours:

Table 2.6 shows the relative frequencies of six classes of agonistic/competitive behaviour: (a) competing for access to the mother's nipples; (b) competing for

TABLE 2.5: OVERALL FREQUENCY OF INVOLVEMENT IN SOCIAL OLFACTION, USING DATA POOLED ACROSS SUBJECTS (21-60 DAYS):

(Figures represent the total observed number of instances of social olfaction in which both of the subjects involved could be identified; figures in brackets represent these data as percentages of the total number of observations of social olfaction between pups, excluding those in which either of the interactants was not identified, and omitting mother-pup olfaction. Codes as for table 2.4).

| | category of participants (sniffer, followed by recipient) | | | | | |
|---|---|---|---|---|---|---|
| | MM | FF | MF | FM | ? | total |
| L1: | 17.9 (36) | 18.9 (38) | 35.8 (72) | 18.9 (55) | 9 | 201 |
| L2: | 17.2 (41) | 16.3 (39) | 41.4 (99) | 16.3 (60) | 24 | 239 |
| L3: | 14.6 (20) | 18.2 (25) | 36.5 (50) | 18.2 (42) | 8 | 137 |
| Total: | 16.8 (97) | 17.7 (102) | 38.3 (221) | 27.2 (157) | 41 | 577 |
| Exp.: | 16.7 (96.2) | 16.7 (96.2) | 33.3 (192.1) | 33.3 (192.1) | | |

Chi-squared = 11.12, 3 df; $p<0.02$.

TABLE 2.6: OVERALL FREQUENCY OF INVOLVEMENT IN AGONISTIC AND COMPETITIVE BEHAVIOURS, USING DATA POOLED ACROSS SUBJECTS (21-60 DAYS):

(Figures represent the total observed number of instances of agonistic behaviour in which both of the subjects involved could be identified, expressed as percentages of the total number of observations of agonistic behaviour between pups, excluding those in which either of the interactants was not identified, and omitting mother-pup interactions. Raw data in brackets. Codes as for table 2.5).

(a) Overall frequency of involvement in competition for access to mother's nipples:

| | category of participants | | |
|---|---|---|---|
| | Male | Female | total |
| Litter 1: | 69 (48.9) | 72 (51.1) | 141 |
| Litter 2: | 64 (56.6) | 49 (43.4) | 113 |
| Litter 3: | 95 (43.4) | 124 (56.6) | 219 |
| Total: | 228 (48.2) | 245 (51.8) | 473 |

(b) Overall frequency of involvement in competition for access to food-hopper:

| | category of participants | | | |
|---|---|---|---|---|
| | MM | FF | MF | total |
| L1: | 43.8 (7) | 0.0 (0) | 56.3 (9) | 16 |
| L2: | 12.8 (19) | 16.1 (24) | 71.1 (106) | 149 |
| L3: | 13.2 (5) | 18.4 (7) | 68.4 (26) | 38 |
| Total: | 15.3 (31) | 15.3 (31) | 69.5 (141) | 203 |
| Exp.: | 16.7 (34) | 16.7 (34) | 66.7 (135) | |

Chi-squared = 0.796, 2 df; n.s.

2.6(c) Overall frequency of involvement in competition for access to water-spouts:

| | category of participants | | | | |
|---|---|---|---|---|---|
| | MM | FF | MF | ? | total |
| L1: | 42.9 (6) | 0.0 (0) | 57.1 (8) | 6 | 14 |
| L2: | 0.0 (0) | 0.0 (0) | 100.0 (10) | 0 | 10 |
| L3: | 0.0 (0) | 16.7 (1) | 83.3 (5) | 0 | 6 |
| Tot: | 20.0 (6) | 3.3 (1) | 76.7 (23) | 6 | 30 |
| Exp: | 16.7 (5) | 16.7 (5) | 66.7 (20) | - | |

Chi-squared = 3.85, 2 df; n.s.

(d) Overall frequency of food-stealing:

| | category of participants (stealer, followed by recipient) | | | | | |
|---|---|---|---|---|---|---|
| | MM | FF | MF | FM | ? | total |
| L1: | 12.5 (1) | 25.0 (2) | 50.0 (4) | 12.5 (1) | 1 | 8 |
| L2: | 33.3 (1) | 0.0 (0) | 0.0 (0) | 66.7 (2) | 0 | 3 |
| L3: | 10.0 (1) | 10.0 (1) | 20.0 (2) | 60.0 (6) | 0 | 10 |
| Tot: | 14.3 (3) | 14.3 (3) | 28.6 (6) | 42.9 (9) | 1 | 21 |
| Exp.: | 16.7 (3.5) | 16.7 (3.5) | 33.3 (7.0) | 33.3 (7.0) | | |

(Chi-squared computation not possible, since 50% of expected frequencies are less than 5).

2.6(e): Overall frequency of chasing and being chased:

| | category of participants (chaser, followed by recipient) | | | | |
|---|---|---|---|---|---|
| | MM | FF | MF | FM | total |
| L1: | 13.0 (3) | 4.3 (1) | 69.6 (16) | 13.0 (3) | 23 |
| L2: | 14.1 (9) | 12.5 (8) | 34.4 (22) | 39.1 (25) | 64 |
| L3: | 9.5 (2) | 19.0 (4) | 42.9 (9) | 28.6 (6) | 21 |
| Tot: | 13.0 (14) | 12.0 (13) | 43.5 (47) | 31.5 (34) | 108 |
| Exp: | 16.7 (18) | 16.7 (18) | 33.3 (36) | 33.3 (36) | |

Chi-squared = 5.75, 3 df; n.s.

(f) Overall frequency of involvement in fighting:

| | category of participants | | | |
|---|---|---|---|---|
| | MM | FF | MF | total |
| L1: | 0 | 1 | 0 | 1 |
| L2: | 3 | 0 | 7 | 10 |
| L3: | 0 | 0 | 0 | 0 |
| Total: | 3 | 1 | 7 | 11 |
| Expected: | 2 | 2 | 7 | |

access to the food-hopper; (c) competing for access to a water-spout; (d) food-stealing; (e) chasing; and (f) fighting. (One agonistic behaviour has been omitted from table 2.6, competing for access to an area of the environment in order to sniff at it; this is because too few observations were made of this kind of behaviour for any conclusions to be drawn from them).

2.3.1.5.4.1: Competition for access to nipples:

Whereas for all other social behaviours it was possible at least to determine who was involved - even if it were not always possible to record the identity of the initiator - this was not feasible in the case of competition for nipple access, because the animals were usually not in clear view. This is unfortunate because jostling for nipple access was by far the most common agonistic behaviour, with a total of 473 observations across all three litters. There were no sex-differences in this behaviour (binomial test, converted to "z"-score for large N, = -0.736; P>0.05).

2.3.1.5.4.2: Competition for access to the food-hopper:

There were no significant differences between the relative frequencies with which pups competed for access to the food-hopper with pups of their own or opposite sex (Chi-squared = 0.796, 2 df, p>0.05), nor were there any consistent trends in these data across litters.

2.3.1.5.4.3: Competition for access to the water-spouts:

As with the previous behaviour, there were no consistent differences either between males and females in the frequency with which they were observed in this behaviour, or in the sex of the individual they were jostling with (Chi-squared = 3.85, 2 df; $p>0.05$).

2.3.1.5.4.4: Food-stealing from another pup:

This behaviour was actually recorded fairly rarely, only 21 observations occurring in all three litters. There were too few data for any statistics to be performed, but casual inspection suggests that the frequencies with which within- and between-sex food-stealing occurred conform closely to chance.

2.3.1.5.4.5: Chasing:

As mentioned earlier, "chasing" was actually a fairly-heterogenous category motivationally. Much of it, particularly in the later age-periods, may have had sexual associations; however, although chasing of females by males was the most frequently-observed category, this difference was not statistically significant (Chi-squared = 5.75, 3 df; $p>0.05$). There were no other sex-differences in chasing behaviour: males initiated 56.5% of all chases, and females 43.5%, over all three litters.

2.3.1.5.4.6: Fighting:

"Serious" fighting between pups was quite rare, with only eleven instances occurring in the whole of this study. With so few data, no firm conclusions can be drawn

about any sex-difference in aggressiveness, particularly since, as in the case of play, it was not possible to record who actually initiated the fight. Inspection of the data in table 2.6(f) suggests that the relative frequencies of fighting between and within sexes, do not differ from chance.

2.3.1.6: Summary of overall results:

When the relative frequencies of behaviours are looked at across the whole of the age-period studied, social behaviours are seen to have occupied a comparatively small part (less than 10%) of the pups' time. Maintenance activities (resting, either with or without the mother, eating and self-grooming) were most frequently observed, at least during the sections of the daily cycle sampled in this study. Of the other behaviours seen, olfactory exploration of the inanimate environment was the most frequent.

Play thus appears to occupy a relatively small amount of the young rat's time, on an overall basis. However, in comparison to other social behaviours, play emerges as a major form of social activity, accounting for approximately a third of all social interactions between 21-60 days of age. Allo-grooming accounts for another third, and olfactory investigation of conspecifics accounts for nearly a quarter, of the rest of the total number of social interactions observed. Agonistic interactions of all types comprised only 17% of all

instances of social behaviour. These data suggest that the social life of the rat during this period is comparatively amicable.

Few sex-differences were observed in the frequencies of any of these behaviours at an overall level of analysis; such differences as there were, appeared in the non-social activity measures (exploration and locomotion) rather than in any of the social behaviours. This study has a major limitation in that for most of the social behaviours, it was possible to determine only who was involved rather than who initiated the interaction; this means that the possibility of sex-differences in the initiation of play and other social behaviours cannot be ruled out. However, the evidence so far suggests that there were no differences in the present study between males and females in terms of their readiness to be involved in social interactions, including play.

There were a number of differences in the choice of social partner for interactions, however, even if the absolute levels of interaction were similar for males and females. PROPORTIONATELY Less social play occurred between males and females than occurred between like-sexed siblings.* A similar pattern was shown by partner-choices for allo-grooming, which was primarily confined to individuals of the same sex as the groomer. There were also sex-differences in the percentage of play observations in which one animal was clearly in the on-top position: in mixed-sex play, males pinned females more than females

* (Given the expected frequency with which mixed-sex play should have occurred).

pinned males. A tendency for males to olfactorily investigate females more than vice versa, was also significant. These findings are in contrast to the lack of sex-differences amongst the various types of agonistic and competitive behaviours.

### 2.3.2: Age-changes in behaviour:

This section addresses the questions of whether there were any age-changes in the relative frequencies of social and non-social behaviours; how behaviours were affected by events such as weaning and the development of sexual maturity; and whether there were any age-related sex-differences in behaviour, which did not emerge in the overall analysis of behaviour.

To investigate whether there were any age-changes in the relative frequency of each behaviour, the period over which observations were made (21-60 days) was subdivided into five-day blocks. For each subject in each block, there was a theoretical maximum total of 720 spot-samples of behaviour; however, as mentioned earlier, some observation periods were missed, so that some five-day totals amounted to less than 720 in practice.

Within each five-day block, the total number of observations of each of the scored behaviour-categories was recorded, for each subject. As with the overall analyses, these data were treated in two ways. The

five-day totals for all behaviours were divided by the total number of observations in the appropriate ageblock, to provide relative frequencies of each behaviour for each subject, compared to the total amount of behaviour recorded from that subject in that ageblock; and the frequency of each of the social behaviours was divided by the subject's total number of observations of social behaviour, to arrive at relative frequencies of each social behaviour in comparison to the subject's other social behaviours.

Figures 2.2 to 2.12 show age-changes in the mean relative frequencies of each behaviour, in comparison to the total amount of behaviour recorded, for males and females in all three litters. (Age-changes in drinking are not shown, since this behaviour occurred relatively infrequently and, as might be expected, showed no systematic age-changes).

Figures 2.13 to 2.17 show the age-changes in the mean relative frequencies of each of the social behaviours, expressed as percentages of the total number of observations of social behaviour.

2.3.2.1: Age-related sex-differences in behaviour:

In order to test for the existence of sex-differences, Mann-Whitney tests were performed for each behaviour at each age, comparing the scores of males to those of females, across litters (N1=6, N2=6) in a similar procedure to that used by Meaney and

Explanation of the conventions and codes used for the Figures in Chapter Two:

The code-numbers on the horizontal axes of figures 2.2 to 2.21 correspond to the following age-periods:

"1" = "21-25 days".
"2" = "26-30 days".
"3" = "31-35 days".
"4" = "36-40 days".
"5" = "41-45 days".
"6" = "46-50 days".
"7" = "51-55 days".
"8" = "56-60 days".

Vertical bars correspond to the mean plus or minus one standard deviation (only one error bar is shown for each point, for purposes of clarity of presentation).

FIG.2.2: AGE-CHANGES IN MEAN RELATIVE FREQUENCY OF MATERNAL BEHAVIOUR (AS % OF TOTAL BEHAVIOUR IN EACH AGE-PERIOD)

FIG.2.3: AGE-CHANGES IN MEAN RELATIVE FREQUENCY OF SLEEPING BEHAVIOUR (AS % OF TOTAL BEHAVIOUR IN EACH AGE-PERIOD)

FIG.2.4: AGE-CHANGES IN MEAN RELATIVE FREQUENCY OF EATING BEHAVIOUR (AS % OF TOTAL BEHAVIOUR IN EACH AGE-PERIOD)

FIG.2.5: AGE-CHANGES IN MEAN RELATIVE FREQUENCY OF SELF-GROOMING (AS % OF TOTAL BEHAVIOUR IN EACH AGE-PERIOD)

FIG.2.6: AGE-CHANGES IN MEAN RELATIVE FREQUENCY OF ENVIRON--MENTAL OLFACTION (AS % OF TOTAL BEHAVIOUR IN EACH AGE-PERIOD)

FIG.2.7: AGE-CHANGES IN MEAN RELATIVE FREQUENCY OF LOCOMOTION (AS % OF TOTAL BEHAVIOUR IN EACH AGE-PERIOD)

FIG.2.8: AGE-CHANGES IN MEAN RELATIVE FREQUENCY OF SOCIAL PLAY (AS % OF TOTAL BEHAVIOUR IN EACH AGE-PERIOD)

FIG.2.9: AGE-CHANGES IN MEAN RELATIVE FREQUENCY OF ALLO-GROOMING (AS % OF TOTAL BEHAVIOUR IN EACH AGE-PERIOD)

FIG.2.10: AGE-CHANGES IN MEAN RELATIVE FREQUENCY OF BEING GROOMED (AS % OF TOTAL BEHAVIOUR IN EACH AGE-PERIOD)

FIG.2.11: AGE-CHANGES IN MEAN RELATIVE FREQUENCY OF SOCIAL OLFACTION (AS % OF TOTAL BEHAVIOUR IN EACH AGE-PERIOD)

FIG.2.12: AGE-CHANGES IN MEAN RELATIVE FREQUENCY OF AGONISTIC BEHAVIOUR (AS % OF TOTAL BEHAVIOUR IN EACH AGE-PERIOD)

Stewart (1981). All tests were two-tailed.

For non-social behaviours, the scores used for statistical testing consisted of the frequency of a given behaviour, expressed as a percentage of the total number of observations made on each subject in the age-period in question. In the case of social behaviours, the data were analysed in this fashion, and also considered as percentages of the total amount of social behaviour shown by each individual in the relevant age-period.

One problem with this method of analysis is that by performing large numbers of tests, one runs the risk of obtaining statistically-significant results purely by chance. It would be possible to perform eighty individual tests on the data which follow, and at the 5% level of significance, four of these could appear significant when they were not in fact so. Consequently, to minimise the number of tests performed, the graphs were inspected beforehand, and tests carried out only for the age-period in which the sexes showed the maximum difference in their scores. If these were significant, the next largest divergence was tested, and so on.

Even so, the results of seven separate tests are reported in the following sections, some of which are significant only at the 0.05 level. Consequently, caution must be applied in interpreting these findings.

2.3.2.1.1: Maintenance activities:

No sex-differences were found at any age in sleeping, maternal behaviour, or self-grooming. The only behaviour

in this category which showed a significant sex-difference was that males were more frequently observed eating than were females, between 36-40 days ("U"=4, $p<0.05$).

2.3.2.1.2: Non-social activity:

As might be expected from the results of the tests reported in section 2.3.1, the main differences between male and female pups were in olfactory investigation of the inanimate environment, and locomotion. Females spent a greater proportion of their time in environmental olfaction than did males, between 36-40 days ("U"= 4, $p<0.05$) and 41-45 days ("U"= 3, $p<0.02$). Females also showed higher frequencies of locomotory activity between 46-50 days ("U"= 4, $p<0.05$) and 51-55 days ("U" = 3, $p<0.02$).

2.3.2.1.3: Social behaviours:

Whether social behaviours were considered as percentages of all behaviour or as percentages of the total amount of social behaviour, the only statistically-significant sex difference in social behaviour occurred in observations of social play.

Examination of figures 2.8 and 2.13 suggests that males showed a higher peak of social play activity, at 31-35 days, and a less marked decline in play during the final age-period. Only the latter difference proved statistically significant, whether play was considered as a percentage of total observed behaviour ("U"= 4, $p<0.05$) or as a percentage of observed social behaviour ("U"= 3,

$p<0.02$).

2.3.2.2: Age-related trends in behaviours (males and females combined):

Given the general lack of sex-differences in behaviour, and the fact that figs. 2.2 to 2.17 suggest that males and females showed similar age-related trends even where there were sex-differences, age-changes in the performance of each behaviour were investigated in the following manner. The frequency data for both sexes and all three litters were combined and subjected to a non-parametric trend analysis, based on Kendall's "S" statistic (Ferguson, 1965). This was used to determine whether there were statistically significant monotonic (linear), bitonic (equivalent to quadratic), tritonic (equivalent to cubic) or fourth-order polytonic (equivalent to quartic) trends present in the data for each behaviour.

For convenience, each behaviour will be discussed separately in the following sections, although the frequencies are of course interrelated.

2.3.2.2.1: Age-changes in maintenance activities:

All of the relative frequencies described in this section represent mean percentages of the total number of behavioural observations per five-day age-block, taken over all subjects.

2.3.2.2.1.1: Maternal behaviour and sleeping:

Figures 2.2 and 2.3 show the mean relative frequencies of maternal behaviour and sleeping, for each of the five-day periods from 21 to 60 days. These graphs show that the frequency with which the pups slept with the mother steadily declined with age, from an overall mean of approximately 36% at 21-25 days, to a mean of approximately 14% by 56-60 days. This linear decrease was highly significant ("S1" = -210, z1 = 7.46, $p<0.00001$).

At the same time, there was a similarly marked increase in the relative frequency of sleeping alone or with other pups, as shown by a highly significant linear trend component ("S1" = 177, z1 = 6.29, $p<0.00001$). There was also a significant tritonic trend in the sleeping-alone data ("S3" = -62, z2 = 2.21, $p<0.05$); inspection of fig. 2.3 suggests that, from an initial mean level of nearly 27% of all observations, sleeping decreased to about 15% between 26-35 days (when weaning was apparently occurring), and then steeply increased to a mean peak of 38% between 56-60 days.

Despite these changes in the relative frequencies of sleeping with the mother or away from her, the overall frequency of resting in one form or another remained fairly constant with age, comprising approximately 50% of all observations (except in the first age-period, when maternal behaviour and sleeping, taken together, accounted for 63% of all behaviour).

2.3.2.2.1.2: Eating:

Fig. 2.4 shows the relative frequency of eating in each of the five-day periods studied. There seems to be some increase in eating up to 31-35 days of age, at which point eating accounted for approximately 14% of all behavioural observations. This is presumably associated with weaning which occurred at this time. There were no statistically significant trends in these data, however, the bitonic trend just failing to reach significance ("S2" = -53, z2 = 1.92, p<.06).

2.3.2.2.1.3: Grooming:

As can be seen from fig. 2.5, self-grooming showed a marked increase in frequency with age, from 4% at 21-25 days, up to about 15% of all behaviour at 46-50 days of age, after which there was some stabilisation or even a decline. Both the linear increase and the bitonic trend were highly significant ("S1" = 192, z1 = 6.82, p<0.0001; "S2" = -96, z2 = 3.5, p<0.0005).

2.3.2.2.2: Age-changes in non-social activity:

2.3.2.2.2.1: Olfactory investigation of the environment:

Fig. 2.6 shows age-changes in the relative frequency of olfactory investigation of the inanimate environment. When the data were pooled across sexes for a trend analysis, significant bitonic ("S2"= -108, z2= 3.94, p<0.0001) and tritonic ("S3" = 74, z3 = 2.65, p<0.01) trends were found. This suggests that the predominant

trend was for environmental olfaction to increase up to 31-35 days and then decrease thereafter, but that there was also some levelling-off from 46-50 days onwards, so that by the end of the observation-period this behaviour was being performed at more or less constant levels.

2.3.2.2.2.2: Locomotion:

Fig. 2.7 shows age-changes in the relative frequency of locomotion. A trend analysis revealed that there were significant linear ("S1" = -62, z1 = 2.18, $p<0.05$) and tritonic ("S3" = 62, z3 = 2.25, $p<0.025$) trends in these data, when combined across sexes. In other words, locomotion showed an overall tendency to decrease with increasing age; but within this, locomotion first increased from 21-25 days to its peak at 26-30 days (when it comprised approximately 5% of all behaviour), and then decreased until 41-45 days, after which the decrease stabilised.

2.3.2.2.3: Age-changes in social behaviours:

Age-changes in social behaviours will be discussed considering these behaviours both as percentages of the total amount of behaviour observed in each age-period, and as percentages of the total amount of social bhaviour observed in each age-block. The same trends are apparent, whichever method is used; only the units differ. The non-parametric trend analyses reported below were performed on the relative frequencies of social behaviours as percentages of total social behaviour, rather than as

percentages of all behaviour.

2.3.2.2.3.1: Social play:

Inspection of figs. 2.8 and 2.13 suggests that play increased in frequency up to a peak between 31-35 days of age, and then declined thereafter. A trend analysis confirmed this interpretation of a bitonic trend ("S2"= 154, z2 = 5.64, p<0.0001); no other trend components approached significance.

In terms of the percentage of total behaviour accounted for, play represented no more than a mean of approximately 4% at its peak and a mere 1.5% of all behaviour in the first and last age-periods. Play represented a considerable proportion of these animals' social behaviour, however; at 31-35 days, play amounted to just over 40% of all observed social behaviour, and accounted for over 25% of social behaviour in every age-period except the first and last. Play was thus a considerable source of social interaction in all age-periods, and at its peak was the predominant form of interaction.

2.3.2.2.3.2: Allo-grooming:

Fig. 2.14 and 2.15 show age-changes in the relative frequency of performing allo-grooming, and being allo-groomed, in comparison to other social behaviours.

Allo-grooming showed some increase in relative frequency with age, from under 5% of all social behaviour at 21-25 days, to a maximum of approximately 15% at 51-55 days ("S1" = 89, z1 3.17, p<0.002).

The frequency of being groomed showed an inverted "U"-shaped function, with a decrease from an initial high level of around 45% of all social behaviour, down to a low point between 41-45 days, after which the frequency of being groomed began to rise again. A trend analysis revealed significant monotonic ("S1"= -81, z1 = 2.86, $p<0.005$), bitonic ("S2" = 166, z2 = 6.10, $p<0.0001$) and polytonic ("S4" = -82, z4 = 2.99, $p<0.005$) components in the data on being groomed, compatible with this interpretation.

Allo-grooming and being allo-groomed accounted for relatively little behaviour overall; the former increased from representing 0.3% of all behaviour to a maximum of 1.2% at its peak between 51-55 days, and generally accounted for between 0.5 to 1% of all observations. Being allo-groomed accounted for 5.6% of all behaviour observations between 21-25 days; dropped to 0.3% at its lowest point; and then increased to just over 1% of observations from 51-55 days onwards.

The large discrepancies between the frequencies of allo-grooming and being grooomed are due to the fact that the great majority of observed instances of allo-grooming before 31-35 days were performed by the mother; when she ceased to do so, after weaning, the frequencies of grooming and being groomed became more comparable.

2.3.2.2.3.3: Social olfaction:

Fig. 2.16 shows age-changes in the relative frequency

of social olfaction in comparison to other social behaviours. Two components of the trend analysis were significant: a monontonic increase ("S1" = 178, z1 = 6.32, p<0.0001) and a bitonic trend ("S2" = -70, z2 = 2.54, p<0.02). This suggests that the main feature of this behaviour was for it to increase in frequency with age, but that after 41-45 days there was some levelling-off of this trend. In terms of the mean percentage of social behaviour accounted for, social olfaction thus rose from an initial minimum level of under 10%, to a more or less stable level of between 30-40% from 41-45 days onwards. Taken as percentages of all behaviour, these figures represent a rise from 1%, to just under 2.5% at its peak.

2.3.2.2.3.4: Agonistic behaviour:

Taking all agonistic and competitive behaviours together, fig. 2.16 shows that there was a steady decrease with age in the frequency of such behaviours compared to other social activities ("S1" = -159, z1 = 5.64, p<0.0001). From accounting for nearly 30% of all social behaviour at 21-25 days, agonistic interactions dropped to a low point of 5% at 51-55 days. In terms of the total amount of observations of behaviour in each age-block, this amounts to agonistic interactions decreasing from 3.5% of all behaviour between 21-25 days, to 0.4% at 51-55 days.

Consideration of the different behaviours encompassed under the global heading of "agonistic" behaviours

clarifies the interpretation of this trend.

The initial high levels of agonistic behaviour are mainly due to the often intense competition between pups for access to the mother's nipples. This was the most frequent form of agonistic interaction amongst pups, between 21-30 days. Competition for nipples was supplanted by three behaviours: jostling between pups for access to the food-hopper, jostling for access to the water-spouts, and food-stealing from each other. These behaviours together accounted for the majority of agonistic interactions between weaning and the development of sexual maturity. With the onset of the latter, from about 46 days onwards, came an increase in agonistic interactions arising as a consequence of frustrated attempts at mounting and a general increase in mutual intolerance and hostility. What these data do not reflect is that while the number of agonistic interactions decreased, the intensity of them increased: one serious fight might have more effect on social relationships than any number of competitions for nipple access or food.

2.3.2.2.3.5: Sexual behaviour:

Too few instances of sexual behaviour were observed for a trend analysis to be performed, or even for meaningful descriptive statistics to be computed. It will be simplest to discuss each of the three litters separately, especially as they differed so widely in the frequency with which sexual activities were observed.

In L1, two instances of attempted mounting were

FIG.2.13: AGE-CHANGES IN MEAN RELATIVE FREQUENCY OF SOCIAL PLAY (AS % OF TOTAL SOCIAL BEHAVIOUR IN EACH AGE-PERIOD)

FIG.2.14: AGE-CHANGES IN MEAN RELATIVE FREQUENCY OF ALLO-GROOMING (AS % OF TOTAL SOCIAL BEHAVIOUR IN EACH AGE-PERIOD)

FIG.2.15: AGE-CHANGES IN MEAN RELATIVE FREQUENCY OF BEING GROOMED (AS % OF TOTAL SOCIAL BEHAVIOUR IN EACH AGE-PERIOD)

FIG.2.16: AGE-CHANGES IN MEAN RELATIVE FREQUENCY OF SOCIAL OLFACTION (AS % OF TOTAL SOCIAL BEHAVIOUR IN EACH AGE-PERIOD)

FIG.2.17: AGE-CHANGES IN MEAN RELATIVE FREQUENCY OF AGONISTIC BEHAVIOUR (AS % OF TOTAL SOCIAL BEHAVIOUR IN EACH AGE-PERIOD)

FIG.2.18: AGE-CHANGES IN PERCENTAGES OF PLAY OCCURRING WITHIN AND BETWEEN SEXES (POOLING DATA FROM ALL SUBJECTS)

observed between 31-35 days, and two between 36-40 days, but the bulk of observed sexual activity occurred between 41-50 days (6 observations between 41-45 days, and 14 between 46-50 days. Two further observations of mounting were seen between 51-55 days.

The majority of mounts in L2 occurred between 36-40 days, when there were six observed instances. The remaining seven observations of sexual behaviour were distributed as follows: one each in the 26-30 ,31-35 and 56-60 day age-periods, two between 41-45 days and two between 51-55 days.

L3 showed only four instances of sexual behaviour: three between 36-40 days, and one between 46-50 days.

A tentative conclusion on the basis of these rather scanty data is that there was a peak of sexual activity at around 40 days, the precise timing obviously depending on the sexual cycle of the females and the maturational state of the male pups.

2.3.2.3: Age-related sex-differences in involvement in social behaviours, using data pooled across subjects:

This section looks at age differences in the extent to which males and females directed social behaviours towards their own sex or the opposite sex, using data pooled from all subjects. Only age-changes in the three most common social behaviours - play, allo-grooming and social olfaction - will be examined in this way.

2.3.2.3.1: Age-changes in social play:

Fig. 2.18 shows age-changes in the extent to which play occurred between males, between females, or between males and females, expressed as percentages of the total number of observations of play per age-period (combined across all litters, and regardless of the individuals under whose observation-periods the data were obtained).

It is clear from fig. 2.18 that, with increasing age, play between males and females markedly decreased in frequency, from a peak of nearly 80.% of all observed play between 21-25 days, to approximately 30% of observed play from 51 days onwards. Over the same period, the relative frequencies of male-male and female-female play increased, showing similar trends to each other except in the last age-period; between 56-60 days, females appear to have markedly reduced their levels of play, not only with males but also with each other. In this final age-period, there is a steep rise in the proportion of play that was performed between males, presumably as a consequence of the fact that the males had only each other as partners.

2.3.2.3.1.1: Age-changes in frequency of "on-top" position in play:

Fig. 2.19(a) displays age changes in the proportions of male-male play and female-female play in which one of the interactants was clearly on top of the other. Between males, the proportion of on-top behaviour markedly increased between 21-25 days (when it accounted for 29% of male-male play) and 26-30 days (when over 72% of

FIG.2.19(a): AGE-CHANGES IN PERCENTAGE OF 'ON-TOP' POSITION IN WITHIN-SEX PLAY (AS % OF TOTAL PLAY IN EACH AGE-PERIOD)

FIG.2.19(b): AGE-CHANGES IN PERCENTAGES OF 'ON-TOP' POSITION IN BETWEEN-SEX PLAY (AS % OF TOTAL PLAY IN EACH AGE-PERIOD)

male-male play involved one animal being clearly on top). After this point, the proportion of on-top behaviour remained at between 70-90% of between-male play in every age-period except at 41-45 days, when it dipped to 65% of male-male play. The age-trend in these data thus seems to consist of a rapid transition from low to high levels of on-top behaviour in within-sex play; but once this had occurred, there was no further trend with age towards increasing proportions of on-top behaviour.

A broadly similar trend is evident in the percentage of female-female play in each age-period that was accounted for by on-top behaviour, except that females showed the sudden change to high levels of pinning at a slightly later age, between 26-30 days and 31-35 days. Females also failed to show the marked decrease in the percentage of on-top behaviour that was shown by males at 41-45 days.

Fig. 2.19(b) compares the proportion of between-sex play in which males were on top, to the proportion of between-sex play in which females were in the superior position. There is some tendency for the former proportion to increase with age, and the latter to remain stable or even decline over time; but the main feature of these data is that males consistently pinned females more than females pinned males.

2.3.2.3.2: Age-changes in allo-grooming:

Fig. 2.20(a) shows the proportions of the total number of allo-grooming observations in each age-period,

FIG.2.20(a): AGE-CHANGES IN PERCENTAGE OF WITHIN-SEX ALLO-GROOMING (AS % OF TOTAL ALLO-GROOMING IN EACH AGE-PERIOD)

FIG.2.20(b): AGE-CHANGES IN PERCENTAGE OF BETWEEN-SEX ALLO-GROOMING (AS % OF TOTAL ALLO-GROOMING IN EACH AGE-PERIOD)

that were performed between members of the same sex. These data show no clear age-trends, except for reflecting the increase in allo-grooming betwen pups which occurred after weaning.

Fig. 2.20(b) shows age-changes in the frequency of between-sex allo-grooming, expressed as the percentages of all allo-grooming observations in each age-period which were performed between pups of the opposite sex. Male allo-grooming of females, and female allo-grooming of males, show different trends: the latter behaviour shows a consistent decrease with age, whereas the former displays a marked peak at 46-50 days, followed by an equally marked drop at 51-55 days.

Within-sex allo-grooming appears to increase in relative frequency with increasing age, both for male-male and female-female allo-grooming. However, as with the frequencies of between-sex allo-grooming, these trends are rather erratic.

At 51-55 days, both male-male and female-female allo-grooming occurred at well above the levels which would be expected by chance, and male-female and female-male allo-grooming were much less frequent than would be expected. This same pattern was repeated in the 56-60 day age-period.

The overall pattern of sex-differences in allo-grooming reported earlier, thus appears to stem largely from this marked preference for grooming same-sexed peers, shown from 51 days onwards.

FIG.2.21(a): AGE-CHANGES IN PERCENTAGE OF WITHIN-SEX SOCIAL OLFACTION (AS % OF TOTAL SOCIAL OLFACTION IN EACH AGE-PERIOD)

FIG.2.21(b): AGE-CHANGES IN PERCENTAGE OF BETWEEN-SEX SOCIAL OLFACTION (AS % OF TOTAL SOCIAL OLFACTION IN EACH AGE-PERIOD)

2.3.2.3.3: Age-changes in social olfaction:

Fig. 2.21(a) shows the frequencies of male-male and female-female olfactory investigation, expressed as percentages of the total number of instances of social olfaction observed in each age-period. Comparison of this graph with fig. 2.21(b) suggests that there may be a slight trend for the proportions of within-sex sniffing to decrease with age, and for between-sex sniffing to increase, but, as with allo-grooming, the data are fairly erratic.

2.3.2.4: Summary of results on age-changes in behaviour:

The most striking finding of these analyses is the clear ontogenetic trend in the relative frequency of social play, as shown in fig. 2.13. The frequency of play rises to a peak at 31-35 days, and then declines with increasing age. This inverted "U"-shaped pattern, also found by previous researchers (eg, Muller-Schwarze 1966, Panksepp 1981) under widely differing conditions of observation, appears to be a highly characteristic feature of social play in this species. The data in this chapter thus confirm previous studies, and extend them by placing this ontogenetic patterning of play into the wider context of the young rat's other social and non-social behaviours.

Many of the age-related changes observed in these animals' behaviour are broadly interpretable as reflections of the two major processes occurring within

this period in the pups' ontogeny: weaning, between 21-35 days; and the development of sexual maturation, from 40 days of age onwards. The animals' behaviour can thus be divided into two main phases corresponding to these phenomena.

1: Weaning:

Changes in behaviour which were associated with weaning include the abrupt decline in maternal behaviour between 21-35 days, and the temporary reduction in the relative frequency of sleeping between 26-35 days. The frequency of eating peaked at around 31-35 days (although not significantly so), and self-grooming began to increase steadily from this time on, presumably to compensate for the lack of maternal allo-grooming of pups. Allogrooming between pups, however, showed little change in frequency.

The first ten days of observation saw a dramatic reduction in the frequency of agonistic and competitive behaviours, primarily as a result of the decrease in competition for nipple access in suckling. Although other competitive behaviours emerged with the transition to solid food - food-stealing and competition for the water-spouts and food-hopper - they did not compare with jostling for nipples, at least not in sheer number of observations.

The increases in olfactory investigation of the environment and the parallel increase in social play (to its peak at 31-35 days) may have little to do directly

with weaning, but weaning may have provided the impetus to "trigger off" these behaviours, by inducing higher states of alertness in the pups than hitherto. Also, the rapidly-increasing mobility of the pups (which had emerged from the nest for the first time only a few days before the commencement of observations) meant that not only was the environment comparatively novel for the pups, but also that they were bringing themselves into contact with its novelty by ranging widely away from the nest.

In short, the behaviour measures of the first half of this study reflect the growing independence of the pups from their mother during weaning.

2: Transition to adulthood:

The second half of the study, from 41 days onwards, shows evidence of the development of sexual behaviour and the transition to adulthood. Maternal behaviour (which, by this time, can confidently be regarded simply as sleeping with the mother) continued to decrease, and sleeping alone or with other pups continued to increase. Self-grooming and eating stabilised to what presumably represent near-adult levels. Olfactory investigation of the environment declined during this period, probably because the rather unstimulating test-environment had exhausted its potential for novelty.

Amongst social behaviours, play decreased during this time, especially in females. The frequency of social olfaction remained relatively constant. Allo-grooming and being allo-groomed increased in frequency slightly.

Agonistic behaviours continued to decline in terms of frequency, although what the quantitative data do not reveal is the change in "mood" of the litter during this period, with social relations becoming more "tense" and agonistic encounters, when they did occur, becoming more "serious", as revealed by the growing incidence of fighting. (Although it must be noted that fighting was always comparatively rare, in all three litters studied). Most observations of sexual behaviour centred somewhere around 41-45 days, with sporadic instances long before this time, and also in the subsequent age-periods; however, sexual activities were recorded fairly infrequently.

3: Age-changes in partner-preferences:

Across the 21-60 day period, pups showed age-changes in their choice of partner for interactions, some (but not all) of these possibly reflecting the effects of weaning and the development of sexual maturity. The changes were most marked in social play, where there was an abrupt transition from low levels of pinning during play to high ones - so that approximately 80% of play observations involved one of the interactants clearly being on top of the other. This transition occurred at the same time as play reached its peak frequency, 31-35 days, after which levels of pinning remained more or less constant until the end of observations at 60 days. The overall tendency for males to pin females more than they themselves were pinned by females, was found to be a feature of mixed-sex

play in all age-periods, although perhaps this tendency shows some increase with age.

The main age-related sex-difference in playfulness was that over time, there was a decline in the initially-strong tendency for play to occur between the sexes, and a concomitant increase in within-sex play. By the end of the observation period, only male-male play was occurring with any appreciable frequency; females had dropped out of play both with males and with each other.

There were fairly consistent sex-differences in the other social behaviours, too; for example, there was a greater frequency of within-sex allo-grooming as opposed to grooming between pups of the opposite sex, although there was also a tendency for females to allo-groom more than males. The frequency of within-sex social olfaction stayed fairly constant over time, but the frequencies of between-sex sniffing varied erratically. This is somewhat surprising in view of the increae in anogenital aniffing which might have been expected to accompany sexual maturation. Males did sniff females disproportionately frequently, however.

These data thus confirm the picture provided by the overall analyses - ie, that there were few sex differences in the frequency with which pups of different sexes apportioned their time to social behaviours - but nevertheless show that there were some significant differences between male and female pups in their choice of partners for social activities. The net result of these

preferences is that male and female pups experience somewhat different social relationships from each other, by virtue of the different types of social behaviour which they both direct to their peers and in turn receive themselves.

## 2.3.3: The social behaviour of the mother:

Table 2.7 shows the overall frequencies of maternal social and non-social behaviours. A comparison of this to table 2.1 shows that there were few marked differences between the mothers and their pups in the overall frequencies of non-social behaviours. Consequently, only the mother's social behaviours will be discussed in any detail.

One result in table 2.7 which should be mentioned, however, is the apparent difference between mothers and pups on the measures of "maternal behaviour" and "sleeping". These two behaviours together accounted for approximately 47% of all observations on the mothers of Litters 1 and 2, and 58% of those for L3. While these figures are within the range of those shown by male and female pups (see table 2.1), each of the three mothers appears to show more "maternal behaviour" and less "sleep" than any of her pups. This is probably an artefactual consequence of the way in which "maternal behaviour" was scored whenever a mother was observed lying with any of her pups. Purely by chance, a mother was likely to be laying with at least one of her pups, and thus scored as showing "maternal behaviour". In contrast, it was easier for a pup to lay alone and be scored as "sleeping".

Comparisons between the mothers are valid, however, since all three mothers presumably had similar chances of laying with a pup or not. The marked difference between

TABLE 2.7: RELATIVE FREQUENCY OF OBSERVATION OF BEHAVIOUR CATEGORIES FOR MOTHERS: OVERALL, 21-60 DAYS:

(Percentages are of the total number of observations made per mother. "Envtl." = "environmental": "obsvns" = "observations").

| | Litter 1: | Litter 2: | Litter 3: | Overall Mean, S.D: |
|---|---|---|---|---|
| MATERNAL BEHAVIOUR: | 26.7 (1507) | 26.7 (1526) | 49.1 (2704) | 34.2 (12.9) |
| SLEEP: | 20.4 (1154) | 22.5 (1286) | 8.6 (471) | 17.2 (7.5) |
| DRINK: | 1.5 (87) | 1.6 (91) | 1.8 (97) | 1.6 (0.1) |
| EAT: | 10.0 (567) | 9.2 (522) | 8.9 (490) | 9.4 (0.6) |
| GROOM: | 13.7 (774) | 10.1 (577) | 10.2 (560) | 10.4 (1.7) |
| SOCIAL OLFACTION: | 1.2 (69) | 1.1 (63) | 0.7 (38) | 1.0 (0.3) |
| ALLO-GROOM: | 2.1 (121) | 2.2 (126) | 2.4 (130) | 2.2 (0.1) |
| BEING ALLO-GROOMED: | 0.8 (47) | 0.8 (46) | 0.4 (22) | 0.7 (0.2) |
| SOCIAL PLAY: | 0.4 (22) | 1.2 (66) | 1.2 (64) | 0.9 (0.5) |
| AGONISTIC BEHAVIOURS: | 0.7 (41) | 1.1 (62) | 0.4 (20) | 0.7 (0.3) |
| SEX: | 0.1 (7) | 0.1 (6) | 0.1 (1) | 0.1 (0.0) |
| ENVTL. OLFACTION: | 16.7 (941) | 15.8 (903) | 11.2 (616) | 14.6 (2.9) |
| LOCOMOTION: | 5.5 (312) | 7.5 (427) | 5.1 (282) | 6.0 (1.3) |
| OTHER: | 0.1 (3) | 0.1 (5) | 0.2 (12) | 0.1 (0.1) |
| TOTAL NO. OBSVNS.: | 100.0 (5652) | 100.0 (5706) | 100.0 (5508) | 100.0 |

the mother of L3 and the other two mothers (the former showing more "maternal behaviour" and less "sleep") may reflect the fact that this litter seemed more closely attached to its mother than did the other two, during the course of observations.

2.3.3.1: Overall frequency of social behaviours:

Table 2.7 shows the frequencies with which mothers performed social behaviours compared to all other behaviours, and table 2.8 shows the frequencies of maternal social behaviours relative to each other.

Most of the differences between the figures in these tables and those of the pups (see table 2.1) are predictable consequences of the maternal relationship - for example, the differences between mother and pups in terms of the relative frequencies of allo-grooming (mothers grooming pups much more than vice versa); and the lower levels of agonistic behaviours in mothers compared to pups (because of the predominance of competition for nipple access amongst the pups).

The main findings of interest in this section are the unexpectedly high levels of social play and sexual activity shown by mothers. A mean 16% of the social interactions of mothers consisted of social play (equivalent to a mean of just under 1% of their total behaviour), and a further 1.4% of their social behaviour consisted of sexual activity with their pups.

TABLE 2.8: RELATIVE FREQUENCY OF OBSERVATION OF SOCIAL BEHAVIOUR CATEGORIES FOR MOTHERS: OVERALL, 21-60 DAYS:

(Percentages are of the total number of observations of social behaviour per mother. Codes as for table 2.7).

| | Litter 1: | Litter 2: | Litter 3: | Overall Mean, SD: |
|---|---|---|---|---|
| SOCIAL OLFACTION: | 22.5 (69) | 17.1 (63) | 13.8 (38) | 17.8 (4.4) |
| ALLO-GROOM: | 39.4 (121) | 34.2 (126) | 47.3 (130) | 40.3 (6.6) |
| BEING ALLO-GROOMED: | 15.3 (47) | 12.5 (46) | 8.0 (22) | 11.9 (3.7) |
| SOCIAL PLAY: | 7.2 (22) | 17.9 (66) | 23.3 (64) | 16.1 (8.2) |
| AGONISTIC: | 13.4 (41) | 16.8 (62) | 7.3 (20) | 12.5 (4.8) |
| SEX: | 2.3 (7) | 1.6 (6) | 0.4 (1) | 1.4 (1.0) |
| TOTAL OBSVNS.: | 100.1 (307) | 100.1 (369) | 100.1 (275) | 100.0 |

2.3.3.2: Overall frequency of social play, using data pooled across all subjects:

Table 2.9(a) shows the relative frequency with which the mother of each litter participated in play with her pups, expressed as a percentage of the total number of observations of play recorded from each litter, regardless of which animal was actually under observation when the play was scored. This table also shows the extent to which mothers showed a preference for playing with sons or daughters, in terms of the percentages of the mothers' play which were with male or female pups.

The three mothers varied considerably in the extent to which they were involved in play. At one extreme was the mother of L1, involved in 15% of her litter's total play, and at the other extreme was L3's mother, who accounted for almost 32% of all observations of play in her litter. The mother of L2 was in between these two, at just under 20% of her litter's total play. The overall mean for maternal involvement in play thus amounts to 22.3% of all play observations.

2.3.3.2.1: Overall sex-differences in play between mothers and their litters:

Within these figures, there were no consistent tendencies for the mothers to play more with pups of one sex rather than the other - at least not consistent in the sense of being in the same direction for all three litters. In L1, 26.6% of the mother's total play was with her sons, and 73.4% with her daughters, a highly

TABLE 2.9: OVERALL FREQUENCY OF INVOLVEMENT OF MOTHERS IN SOCIAL PLAY, USING DATA POOLED ACROSS ALL SUBJECTS (21-60 DAYS):

(Raw data, in brackets, represent the frequency with which the mother of each litter was observed to be involved in play, when all play-observations were pooled across all members of the litter; percentages mare these figures as percentages of the total number of play-observations scored for that litter. '?' = number of play-observations where the partner could not be identified).

(a) OVERALL FREQUENCY OF INVOLVEMENT OF MOTHERS IN PLAY:

| | Play with male pups: | Play with female pups: | ? | Overall: |
|---|---|---|---|---|
| L1: | 4.0% (21) | 11.1% (58) | 0.0% (0) | 15.2% (79) |
| L2: | 10.9% (88) | 8.8% (71) | 0.2% (2) | 19.9% (161) |
| L3: | 20.8% (104) | 11.0% (55) | 0.0% (0) | 31.8% (159) |
| Mean: | 11.9% | 10.3% | - | 22.3% |
| SD: | (8.4%) | (1.3%) | | (8.6%) |

## 2.9(b): OVERALL FREQUENCY OF ON-TOP POSITION IN MOTHER-PUP PLAY:

(Raw data, in brackets, represent frequency with which each mother was observed to be clearly on-top or underneath during play with a pup, using data pooled from all members of the litter. Percentages are these data expressed as percentages of the total amount of play between the mother and the relevant sex-category of interactant, except in the case of the "overall" category, where the percentages are of the total amount of mother-pup play in that litter).

### (i) Relative frequency with which mother was on top in play with:

| | males: | females: | overall: |
|---|---|---|---|
| L1: | 28.6% (6) | 19.0% (11) | 21.5% (17) |
| L2: | 20.5% (18) | 11.3% (8) | 16.4% (26) |
| L3: | 24.0% (25) | 21.8% (12) | 23.3% (37) |
| Frequencies for mother on top, for all litters combined: | | | |
| Mean, SD: | 24.4% (4.1%) | 17.4% (5.4%) | 20.4% (3.6%) |

### (ii) Relative frequency with which mother was on bottom in play with:

| | males: | females: | overall: |
|---|---|---|---|
| L1: | 42.9% (9) | 44.8% (26) | 44.3% (35) |
| L2: | 46.6% (41) | 56.3% (40) | 50.3% (81) |
| L3: | 57.7% (60) | 54.5% (30) | 56.6% (90) |
| Frequencies for mother on bottom, for all litters combined: | | | |
| Mean, SD: | 49.1% (7.7%) | 51.9% (6.2%) | 50.4% (6.2%) |

significant preference (normal approximation to the binomial for N>25, z = -4.050, p<000.1). However, the mother in L3 showed the opposite extreme, performing 65.4% of her observed play with males and only 34.6% with females (z = -3.807, p<0.0001); and L2's mother showed no significant tendency to play with either sex, 55.3% of her play being with her sons and 44.7% with her daughters (z = -1.419, p>0.05). Taken over all three litters, the net result is thus that there were no significant differences in the mothers' involvement in play with either sex (z = -1.405, p>0.05).

Because it was possible only to record who was involved in play, rather than who initiated it, these data provide no information on whether the litter-specific preferences in maternal play result from the mother or the pups. Casual observation, however, suggested that mothers initiated play relatively infrequently, so that any recorded preferences are on the intiative of the pups rather than their mother.

2.3.3.2.2: Overall frequency of on-top behaviour in play between mothers and their litters:

Table 2.9(b) shows the relative frequency with which mothers were in the on-top and underneath positions in play, expressed as percentages of the total amount of play in which each mother was seen to be involved.

Overall, 71.8% of all observations of mother-litter play involved the mother being either on top or underneath a pup (65.8% for L1, 66.5% for L2 and 79.9% for L3). Of

* Binomial tests performed on these data (converted to normal approximations to the binomial, for $N > 25$) showed that, when data were pooled from all three litters, mothers were statistically significantly more likely to pin male pups than female pups ($z = -2.070$, $p = 0.04$). However, when analysed separately, only litter 2's mother showed a significant tendency to pin males more than females ($z = -2.160$, $p = 0.03$); the data for L1 approach significance ($z = -1.756$, $p = 0.08$), and the mother of L3 showed no preference for pinning pups of either sex ($z = -0.536$, $p = 0.60$).

these, table 2.9(b) shows that all three mothers, either singly or overall, were considerably more often in the underneath position than on top: overall, mothers were observed to be underneath in 50.4% of all observed mother-infant play, and on top in 20.4% of it.

There were no differences in the frequencies with which mothers were observed to be in the underneath position in play with male or female pups, but there did appear to be sex-differences in on-top behaviour: mothers pinned males more frequently than they pinned females, when these frequencies are taken as percentages of the total play with each sex. A mean 24.4% of play between mothers and males involved the former pinning the latter, whereas the mean percentage of on-top behaviour in interactions between mothers and females was only 17.4%. This pattern was consistently shown by all three mothers.*

The overall picture given by these results is thus that the main feature of mother-infant play is that the mother takes the "passive" role, adopting the underneath position considerably more frequently than might be expected, especially if her greater size and strength are taken into account. Within this, however, mothers pin their male offspring somewhat more frequently than they pin females.

2.3.3.3: Overall frequency of social olfaction, using data pooled across all subjects:

Table 2.10 shows the relative frequencies with which

TABLE 2.10: OVERALL FREQUENCY OF INVOLVEMENT OF MOTHERS IN SOCIAL OLFACTION, USING DATA POOLED ACROSS ALL SUBJECTS (21-60 DAYS):

(Raw data, in brackets, represent frequency with which each mother was observed to be involved in social olfaction with her pups, using data pooled from all members of the litter. Percentages in part (a) below show the percentages of the total amount of social olfaction within each litter that were performed by the mother towards her pups; those in part (b) are percentages of the total number of observations of social sniffing of the mother herself, by her pups. The fourth columns of each table represent percentages of the total social olfactory activity of each litter that were performed by the mother and directed towards the mother, respectively. "?" = number of observations where the mother's partner could not be identified).).

(a) Relative frequency of mother sniffing at:

| | males: | females: | ?: | overall: |
|---|---|---|---|---|
| L1: | 47.8%<br>(33) | 47.8%<br>(33) | 4.3%<br>(3) | 12.7%<br>(69) |
| L2: | 37.5%<br>(24) | 46.9%<br>(30) | 15.6%<br>(10) | 11.6%<br>(64) |
| L3: | 36.0%<br>(14) | 44.7%<br>(17) | 18.4%<br>(7) | 9.8%<br>(38) |

Frequencies for mother sniffing, all litters combined:

| | | | | |
|---|---|---|---|---|
| Mean: | 40.7% | 46.5% | 12.8% | 11.4% |
| SD: | (6.2%) | (1.6%) | (7.5%) | (1.5%) |

2.10(b): Relative frequency of mother being sniffed by:

| | males: | females: | ?: | overall: |
|---|---|---|---|---|
| L1: | 47.6% (121) | 52.4% (133) | 0.0% (0) | 46.8% (254) |
| L2: | 42.9% (97) | 57.1% (129) | 0.0% (0) | 40.9% (226) |
| L3: | 38.9% (79) | 61.1% (124) | 0.0% (0) | 52.6% (203) |

Frequencies for mother being sniffed, all litters combined:

| | | | | |
|---|---|---|---|---|
| Mean: | 43.1% | 56.9% | 0 | 50.4% |
| SD: | (4.3%) | (4.3%) | (0.0) | (6.2%) |

the mother of each litter sniffed at her pups and was sniffed by them, expressed as percentages of the total number of observations of social olfaction recorded from each litter, regardless of which animal was actually under observation when the behaviour was scored. As with table 2.9, the data are shown according to the sex of the interactants, ie, in terms of the percentages of the mothers' olfactory activity which was with male or female pups.

The three litters show a similar pattern. In all three cases, mothers performed a mean 11.4% of their litter's total social olfactory activity, but were the recipient of 50.4% of it. By chance, one would expect the mother to perform approximately 20% of the social olfactory activity of the litter, and in turn receive 20% of it. The observed frequencies differ markedly from these figures, and suggest that mothers sniffed other animals less frequently than would be expected and were themselves the subject of considerable proportion of the litter's total olfactory activity.

2.3.3.3.1: Overall sex-differences in olfactory activity between mothers and their litters:

Within these figures, table 2.10 shows that there were no consistent tendencies for the mothers to sniff pups of one sex more than the other, but there was a significant difference between male and female pups in the frequency with which they sniffed the mother. Of the total number of observations of olfactory activity which were

directed towards the mother, males performed a mean 43.1%, and females 56.9%. This sex-difference in olfactory investigation of the mother was consistent across all three litters.

2.3.3.4: Overall frequency of allo-grooming between mothers and pups, using data pooled across all subjects:

Table 2.11 shows the frequency with which mothers groomed pups of either sex, and were in turn groomed by them, using data pooled across all subjects within a litter. These show, as might be expected, that mothers allo-groomed pups more than they themselves were groomed, mothers performing a mean 66.6% of the total number of allo-grooming observations within a litter. A mean 15% of all allo-grooming observations involved the mother as a recipient, somewhat less than the 20% that might be expected by chance. Mothers showed no consistent preferences for grooming pups of one sex rather than the other; however, there were significant differences in the relative frequencies with which mothers were groomed by male and female pups. Females performed a mean 62.1% of the total number of allo-grooming observations in which the mother was the recipient of the grooming, whereas male pups performed only a mean 34.6%.

Taken together with the results of the previous section on social olfaction, this suggests that while there are no sex differences in the extent to which male

TABLE 2.11: OVERALL FREQUENCY OF INVOLVEMENT OF MOTHERS IN ALLO-GROOMING , USING DATA POOLED ACROSS ALL SUBJECTS (21-60 DAYS):

(Raw data, in brackets, represent frequency with which each mother was observed to be involved in allo-grooming with her pups, using data pooled from all members of the litter. Percentages in part (a) show the percentages of the total amount of allo-grooming within each litter that was performed by the mother towards her pups; data in part (b) are percentages of the total number of observations of allo-grooming of the mother herself, by her pups. The fourth columns of each table represent percentages of the total allo-grooming activity of each litter that were performed by the mother and directed towards the mother, respectively. "?" = number of observations where the mother's partner could not be identified).).

(a) Relative frequency of mother allo-grooming:

| | males: | females: | ?: | overall: |
|---|---|---|---|---|
| L1: | 38.5%<br>(169) | 40.5%<br>(178) | 21.4%<br>(94) | 60.3%<br>(439) |
| L2: | 41.4%<br>(228) | 44.3%<br>(244) | 14.3%<br>(79) | 71.0%<br>(551) |
| L3: | 41.4%<br>(163) | 36.3%<br>(143) | 22.3%<br>(88) | 67.8%<br>(394) |

Frequencies for mother sniffing, all litters combined:

| | | | | |
|---|---|---|---|---|
| Mean: | 40.4% | 40.4% | 12.8% | 66.6% |
| SD: | (1.7%) | (4.0%) | (7.5%) | (5.8%) |

2.11(b): Relative frequency of mother being allo-groomed by:

| | males: | females: | ?: | overall: |
|---|---|---|---|---|
| L1: | 22.1%<br>(31) | 77.1%<br>(108) | 0.7%<br>(1) | 19.2%<br>(140) |
| L2: | 43.9%<br>(43) | 56.1%<br>(55) | 0.0%<br>(0) | 12.6%<br>(98) |
| L3: | 37.7%<br>(29) | 53.2%<br>(41) | 9.1%<br>(7) | 13.3%<br>(77) |

Frequencies for mother being sniffed, all litters combined:

| | | | | |
|---|---|---|---|---|
| Mean: | 34.6% | 62.1% | 3.3 | 15.0% |
| SD: | (11.2%) | (13.0%) | (5.1) | (3.6%) |

and female pups play with the mother, female pups were involved in a considerably greater proportion of the total number of amicable non-playful social interactions with the mother that were observed in each litter. Furthermore, it was the females who took the initiative in these interactions, since the mothers themselves showed few consistent preferences for interacting with pups of either sex.

2.3.3.5: Overall frequency of fighting between mothers and pups, using data pooled across all subjects:

As mentioned in an earlier section, there were relatively few serious fights between pups in any of the litters, over the whole of the 21-60 day observation period. All three litters, however, showed fighting between mothers and pups, although the absolute numbers of fights are still very small. In Litter 1, the mother was involved in 15 of the 16 fights shown by her litter; in L2, the mother participated in 7 out of a total of 17 fights; and in L3, all of the four instances of fighting recorded involved the mother.

With such small numbers of interactions, it is difficult to assess preferences. In L1, 11 out of the 15 instances of fighting occurred between the mother and her female pups, with only three fights taking place between mother and males. (In the case of the one remaining fight, it was not possible to determine the other interactant's identity). This pattern was also shown by the mother of

L3, who was observed fighting with her female offpsring three times, and with a male only once. L2's mother showed exactly the opposite figures to L3, plus two observations of fighting in which the other animal could not be identified. The overall pattern, therefore, on the basis of these few data, is that mothers tended to fight more with their daughters than with their sons (8 fights with males to 15 with females, overall).

2.3.3.6: Overall frequency of sexual activity between mothers and pups, using data pooled across all subjects:

As mentioned before, observations of sexual behaviour were as uncommon as those of fighting. As with the latter, most of the sexual activity of each litter was directed towards the mother.

In L1, of the total 26 observations of sexual behaviour that were recorded, 15 were directed towards the mother by pups. There were also two mounts performed by the mother herself, one on a male pup and the other on a female. L2's mother received 10 of the total 13 mounts performed by her pups. In L3, which only showed 5 mounts in toto, two involved the mother.

In L1 and L2, as might be expected, it was the male pups who performed most of the mounts of their mother: 11 out of 15 in L1, and 8 out of 10 in L2. The two mother-directed mounts of L3 were performed by a female.

Again, as with the previous section, only tentative

conclusions can be drawn from such meagre data; however, the data suggest that the mother may represent a significant target of sexual activity by the male pups during this period. It was unclear whether the sexual activity shown by the female pups resulted from sexual motivation on their part (since adult females not infrequently mount other females when they are themselves in the peak of oestrus), or whether the mounts stemmed from some other factor such as attempts to establish dominance, etc.

2.3.3.7: Summary and conclusions:

These data must be interpreted with caution, since the conditions of observation may have been quite abnormal for adult female rats. It must be borne in mind that the mothers used in these studies were deprived of contact with any conspecifics other than their own pups, and housed in an environment which effectively prevented them from avoiding those pups entirely.

With this caveat in mind, these data at least draw attention to the possibility that the mother may be a significant source of social interactions of all kinds for her pups, something which has received scant attention in previous studies of play in the rat.

The most interesting finding is the extent to which mothers were involved in play with their litters, play accounting for a mean 16% of the mother's total number of social interactions, and representing one fifth of the

litter's total play. In L3, in which the mother-litter relationships appeared to be particularly close and amicable, the mother accounted for no less than 32% of her litter's total play. Within these play observations, mothers were seen to take a predominantly passive role, although a significant proportion of play (20%) involved the mother being in the on-top position.

The mothers were also extensively involved in non-playful but amicable social interactions, on average accounting for 50% of the social olfactory activity of each litter and most of the litter's recorded sexual behaviour, although mothers received somewhat less than the amount of allo-grooming which they would be expected to receive.

Although mothers showed no consistent preferences for interacting with either sex, the pups themselves showed sex-differences in their levels of interaction; males directed much of their sexual activity towards their mother, and females showed high levels of allo-grooming and olfactory activity towards her.

Finally, most fighting within each litter occurred between the mother and her pups, especially her female offspring.

The overall impression, however, is that the relationships between mothers and young were primarily amicable, especially in litter 3. The implications of these findings will be discussed in greater detail in the overall conclusion to this section, but in brief it

appears that the mother may serve an important role as a source both of playful and non-playful interactions. The playful and sexual aspects of these interactions may be particularly significant, although there are too few data on the latter to draw anything more than speculative conclusions.

### 2.3.4: Individual differences in social behaviour:

This section is concerned with two issues. Firstly, it will assess to what extent individuals showed marked differences in their social behaviours, and to what extent individual differences in one behaviour were also found in others (eg, to see whether particularly playful individuals were also frequently observed to be engaged in allo-grooming or other social behaviours). Secondly, the question of whether there were significant partner preferences for interactions will be looked at, and to what extent these preferences were the same for all behaviours.

All behaviour frequencies in this section were obtained by pooling the observation-points on social behaviours from all subjects within a litter. In other words, if an individual is said to have been involved in "x" percent of play, then the total from which that percentage is drawn, is the total number of observations of play in that litter, as opposed to the total number of observations of play by that particular individual when

they were the focal animal under scrutiny. The total used was obtained by combining all observations on play which were made in the course of studying a litter, regardless of which particular individual was under observation at the time.

2.3.4.1: Overall individual differences in playfulness:

Table 2.12 shows the percentages of the total number of play observations per litter in which each litter-member was involved; and also shows these figures broken down into the percentages spent in the on-top position, underneath or neither of these.

These data show that each of the three litters contained one particularly playful individual; in L1 and L2, this individual was male, and in L3 it was female. These animals were involved in approximately half of the total number of observations of play made on their litters (52.5%, 49.3% and 49.8% for L1, L2 and L3 respectively). The least playful individual in each litter was the mother, although in L3 the mother was involved in almost as many instances of play as her least playful pup.

Leaving the mothers aside, the observed frequencies of involvement in play were significantly different from those which would be expected if all individuals were involved in play equally (Chi-squared, with 3 df, = 16.92, $p<0.001$ for L1; 15.65, $p<0.01$ for L2; and 17.41 for L3, $p<0.001$).

TABLE 2.12: INDIVIDUAL DIFFERENCES IN OVERALL FREQUENCIES OF PLAY, 21-60 DAYS:

(Percentages in column 1 are of the total number of play-bouts observed for each litter, when the data were pooled from all subjects within a litter. Percentages in columns 2,3 and 4 are of the total number of bouts that each animal was seen to be involved in - ie, the numbers in column 1 - when data were pooled from all subjects in a litter).

(a) Litter 1:

| Identity: | No. bouts involved in: | No. bouts on top: | No.bouts equal: | No.bouts beneath: |
|---|---|---|---|---|
| Mother | 15.2 (79) | 21.5 (17) | 34.2 (27) | 44.3 (35) |
| Male 1 | 35.4 (184) | 35.9 (66) | 16.8 (31) | 47.3 (87) |
| Male 2 | 52.5 (272) | 46.7 (127) | 27.6 (75) | 25.7 (70) |
| Female 1 | 45.1 (234) | 34.6 (81) | 35.5 (83) | 29.9 (70) |
| Female 2 | 45.1 (234) | 30.8 (72) | 26.1 (61) | 43.2 (101) |

(b) Litter 2:

| Identity: | No. bouts involved in: | No. bouts on top: | No.bouts equal: | No.bouts beneath: |
|---|---|---|---|---|
| Mother | 19.9 (161) | 16.2 (26) | 33.5 (54) | 50.3 (81) |
| Male 1 | 49.3 (398) | 49.0 (195) | 27.6 (110) | 23.4 (93) |
| Male 2 | 47.2 (381) | 33.6 (128) | 36.2 (138) | 30.2 (115) |
| Female 1 | 37.5 (303) | 28.4 (86) | 35.3 (107) | 36.3 (110) |
| Female 2 | 41.8 (337) | 28.8 (97) | 31.7 (107) | 39.5 (133) |

(c) Litter 3:

| Identity: | No.bouts involved in: | No. bouts on top: | No.bouts equal: | No.bouts beneath: |
|---|---|---|---|---|
| Mother | 31.8 (159) | 23.3 (37) | 20.1 (32) | 56.6 (90) |
| Male 1 | 34.0 (170) | 43.5 (74) | 18.2 (31) | 38.2 (65) |
| Male 2 | 38.4 (192) | 51.6 (99) | 22.4 (43) | 26.0 (50) |
| Female 1 | 44.8 (224) | 39.7 (89) | 20.1 (45) | 40.2 (90) |
| Female 2 | 49.8 (249) | 39.4 (98) | 19.7 (49) | 41.0 (102) |

In L1 and L2, the most highly playful individual was also the one who showed the highest percentage of on-top behaviour in his play. This was not the case in L3, however, where the animal who showed the highest percentage of pinning in play came only third in the frequency of playing; and a correlation performed over all three litters, between the percentage of play engaged in and the percentage of that play which was spent in on-top behaviour, was not significant ("rho", converted to "t" for N>10, = 0.590; p>0.05).

This suggests that there is no clear relationship between readiness to be involved in play, and being on-top in the course of that play; however, this must remain a tentative conclusion, in view of the lack of data on who actually initiated the encounters. It is possible that the data on "involvement" confound data from individuals who both initiate frequently and pin frequently, with data from individuals who do not initiate play particularly often, but who are sought-after partners for play by other animals who then pin them frequently. The data do show, however, that although the relative frequencies of engagement in play did vary between individuals, every pup was involved in a considerable proportion of its litter's play - at least approximately 35% - and was seen both to pin and be pinned (no pup spent more than 50% of its play in the underneath position, and only one pup was observed to be on-top in more than 50% of its play). The difference in involvement between the least and most

playful pups of a litter was never more than 15%, although of course the actual behavioural significance of such differences may be important.

A final feature of table 2.12 is that it shows clearly the relationship between mother-pup and between-pup play, demonstrating the passive role adopted in play by mothers which was described earlier.

2.3.4.2: Consistency of individual differences in playfulness over time:

Table 2.12 deals with overall differences in playfulness, over the whole of the 21-60 day observation period; this section looks at the consistency of these differences over time.

Table 2.13(a) shows the amount of play in which each pup was involved (including play with mother) during each of the five-day age-periods between 21-60 days, expressed as a percentage of the total amount of play seen in their litter in that age-period. Also shown are their ranks in terms of playfulness (1 = most playful, 4 = least playful) compared to the other pups of their litter.

To examine whether individuals showed consistency in their playfulness, Spearman's "rho" was calculated between the percentages of play in which each individual was involved in one age-period, and the percentages in which they were involved in the next. This process was repeated for all eight age-periods, so that involvement in play between 21-25 days was correlated with play between 26-30

TABLE 2.13: AGE-CHANGES IN INDIVIDUAL DIFFERENCES IN INVOLVEMENT IN SOCIAL PLAY, WITHIN EACH LITTER:

(a) Age-changes in frequency of involvement in play:

(First number within brackets represents the total number of observations of play - summing play observations across all members of a litter - in which an individual pup was involved, including instances of play with the mother, and also instances where the other participant could not be identified. Percentages represent these figures expressed as a proportion of the total number of observations of play in the appropriate age-period. Second number in brackets shows the rank of each pup in terms of frequency of observed involvement in play in that age-period: 1 = most playful, 4 = least playful. Figures in row of table entitled "tot" are the total number of observations of play for the litter in that age-period, summing observations over all litter-members. "M" = male, "F" = female).

Litter 1:

| | Age-period: 21-25 | 26-30 | 31-35 | 36-40 | 41-45 | 46-50 | 51-55 | 56-60 | total |
|---|---|---|---|---|---|---|---|---|---|
| M1: | 52.9% (18:3) | 40.2% (33:4) | 31.9% (37:4) | 36.8% (21:3) | 27.1% (26:4) | 45.2% (19:1.5) | 64.8% (35:1) | 55.3% (21:1.5) | 40.5% (210) |
| M2: | 58.8% (20:2) | 47.6% (39:3) | 71.6% (83:1) | 31.6% (18:4) | 43.7% (42:2.5) | 42.9% (18:2) | 57.4% (31:2) | 55.3% (21:1.5) | 52.4% (272) |
| F1: | 64.7% (22:1) | 48.8% (40:2) | 35.3% (41:3) | 43.9% (25:2) | 59.4% (57:1) | 45.2% (19:1.5) | 35.2% (19:3) | 28.9% (11:4) | 45.1% (234) |
| F2: | 5.9% (2:4) | 50.0% (41:1) | 54.3% (63:2) | 70.2% (40:1) | 43.7% (42:2.5) | 33.3% (14:3) | 33.3% (18:4) | 36.8% (14:3) | 45.1% (234) |
| tot: | 34 | 82 | 116 | 57 | 96 | 42 | 54 | 38 | : 519 |

Litter 2:

| | Age-period: 21-25 | 26-30 | 31-35 | 36-40 | 41-45 | 46-50 | 51-55 | 56-60 | total |
|---|---|---|---|---|---|---|---|---|---|
| M1: | 42.1% (24:2) | 50.9% (57:2.5) | 52.1% (62:1) | 53.1% (95:1) | 44.0% (40:3) | 34.9% (37:4) | 49.4% (43:2) | 71.4% (40:1) | 47.8% (386) |
| M2: | 43.9% (25:1) | 50.9% (57:2.5) | 46.2% (55:2) | 44.1% (79:2) | 47.2% (43:2) | 39.6% (42:3) | 54.0% (47:1) | 54.0% (33:2) | 47.2% (381) |
| F1: | 29.8% (17:4) | 35.7% (40:4) | 41.2% (49:4) | 38.5% (69:4) | 38.5% (35:4) | 47.2% (50:1) | 43.7% (38:3) | 8.9% (5:4) | 37.5% (303) |
| F2: | 33.3% (19:3) | 57.1% (64:1) | 42.0% (50:3) | 39.1% (70:3) | 50.5% (46:1) | 42.4% (45:2) | 31.0% (27:4) | 28.6% (16:3) | 41.8% (337) |
| tot: | 57 | 112 | 119 | 179 | 91 | 106 | 87 | 56 | : 807 |

Litter 3:

| | Age-period: 21-25 | 26-30 | 31-35 | 36-40 | 41-45 | 46-50 | 51-55 | 56-60 | total |
|---|---|---|---|---|---|---|---|---|---|
| M1: | 44.2% (19:2.5) | 55.8% (24:1) | 46.8% (51:1) | 33.8% (23:2) | 31.5% (17:3) | 34.3% (12:3) | 8.1% (9:4) | 35.1% (13:4) | 40.5% (168) |
| M2: | 39.5% (17:4) | 46.5% (20:2) | 39.4% (43:3) | 30.9% (21:3) | 33.3% (18:2) | 25.7% (9:4) | 38.7% (43:3) | 56.8% (21:1) | 52.4% (192) |
| F1: | 44.2% (19:2.5) | 34.9% (15:3) | 37.6% (41:4) | 22.1% (15:4) | 50.0% (27:1.5) | 62.9% (22:2) | 64.0% (71:1) | 37.8% (14:2.5) | 45.1% (224) |
| F2: | 48.8% (21:1) | 18.6% (8:4) | 41.5% (44:2) | 70.6% (48:1) | 50.0% (27:1.5) | 68.6% (24:1) | 56.8% (63:2) | 37.8% (14:2.5) | 45.1% (249) |
| tot: | 43 | 43 | 109 | 68 | 54 | 35 | 111 | 37 | : 500 |

2.13(b) Values of Spearman's "rho" for correlations between ranks in successive age-periods:

(For all correlations, N=12, the total number of pups across all three litters. Probabilities are for the values of "t", and are two-tailed in all cases).

| Correlation between ranks at: | rho: | t: | prob. |
|---|---|---|---|
| 21-25 days and 26-30 days: | - 0.248 | -0.810 | ns |
| 26-30 days and 31-35 days: | 0.505 | 1.851 | ns |
| 31-35 days and 36-40 days: | 0.287 | 0.946 | ns |
| 36-40 days and 41-45 days: | 0.364 | 1.234 | ns |
| 41-45 days and 46-50 days: | 0.386 | 1.324 | ns |
| 46-50 days and 51-55 days: | 0.575 | 2.223 | $p<0.05$ |
| 51-55 days and 56-60 days: | 0.514 | 1.895 | ns |
| 21-25 days and 56-60 days: | 0.171 | 0.550 | ns |

days, 26-30 days was correlated with 31-35 days, and so on. A correlation test was also performed between the first and last age-periods. The results of these tests, shown in table 2.13(b), reveal that, with one exception (46-50 days and 51-55 days), there were no significant correlations between any adjacent age-periods, nor between the first and last age-periods. This suggests that the previously-mentioned individual differences in playfulness at an overall level conceal the fact that, within this period , individuals may vary considerably in their degree of involvement in play.

The overall individual differences appear to arise because in particular age-periods the most playful individuals were involved in a particularly large number of observations of play, rather than as a consequence of these animals being the most frequent players in all (or even many) age-periods. To take an example, male number 2 was the animal most involved in play in L1, taking all observations of play overall; however, he was not the most playful individual (or even the second most playful) in four of the eight age-periods, and owes his overall rank to the fact that he was involved in a particularly large number of observations of play between 31-35 days.

A similar picture is presented by the data on age-changes in individual differences in on-top behaviour. Table 2.14(a) shows the frequency with which each individual was seen to be in the on-top position during play, expressed as a percentage of the total play

TABLE 2.14: AGE-CHANGES IN INDIVIDUAL DIFFERENCES IN BEING "ON TOP" DURING SOCIAL PLAY, WITHIN EACH LITTER:

(a) Age-changes in frequency of being in the "on-top" position in play:

(First number within brackets represents the total number of observations of play by each pup in which that pup was on top, summing play observations across all members of a litter. This includes instances of play with the mother, and also instances where the other participant could not be identified. Percentages represent these figures expressed as a proportion of the total number of observations of play for the pup in question, in the appropriate age-period. Second number in brackets shows the rank of each pup in terms of how often he was on top in each age-period: 1 = most often on top, 4 = least often on top. Figures in row of table entitled "tot" are the total number of observations of play for the litter in that age-period, summing observations over all litter-members. "M" = male, "F" = female).

Litter 1:

| | Age-period: 21-25 | 26-30 | 31-35 | 36-40 | 41-45 | 46-50 | 51-55 | 56-60 | total |
|---|---|---|---|---|---|---|---|---|---|
| M1: | 22.2% (4:2) | 27.3% (9:4) | 27.0% (10:4) | 47.6% (10:4) | 26.9% (7:4) | 36.8% (7:2) | 45.7% (16:1) | 33.3% (7:3) | 33.3% (70) |
| M2: | 5.0% (1:3) | 51.3% (20:1) | 53.0% (44:1) | 11.1% (2:4) | 59.5% (25:1) | 44.4% (8:1) | 41.9% (13:2) | 71.4% (15:1) | 44.1% (128) |
| F1: | 31.8% (7:1) | 27.5% (11:2) | 39.0% (16:2.5) | 60.0% (15:1) | 35.1% (20:2) | 31.6% (6:3.5) | 42.1% (8:3) | 27.3% (3:4) | 36.8% (86) |
| F2: | 0.0% (0:4) | 24.4% (10:3) | 25.4% (16:2.5) | 35.0% (14:2) | 30.9% (13:3) | 42.9% (6:3.5) | 27.8% (5:4) | 57.1% (8:2) | 30.8% (72) |
| tot: | 12 | 50 | 86 | 41 | 65 | 27 | 42 | 33 | : 356 |

Litter 2:

| | Age-period: 21-25 | 26-30 | 31-35 | 36-40 | 41-45 | 46-50 | 51-55 | 56-60 | total |
|---|---|---|---|---|---|---|---|---|---|
| M1: | 25.0% (6:2) | 36.8% (21:1) | 38.7% (24:2) | 49.5% (47:1) | 70.0% (28:1) | 78.4% (29:1) | 48.8% (21:1) | 47.5% (19:1) | 50.5% (195) |
| M2: | 36.0% (9:1) | 28.1% (16:3) | 45.5% (25:1) | 45.6% (36:2) | 30.2% (13:2) | 26.2% (11:3) | 25.5% (12:3) | 18.2% (6:3) | 33.6% (128) |
| F1: | 0.0% (0:3.5) | 15.0% (6:4) | 36.7% (18:3) | 27.5% (19:4) | 34.3% (12:3) | 34.0% (17:2) | 34.2% (13:2) | 20.0% (1:4) | 28.4% (86) |
| F2: | 0.0% (0:3.5) | 29.7% (19:2) | 26.0% (13:4) | 42.9% (30:3) | 23.9% (11:4) | 22.2% (10:4) | 11.1% (3:4) | 68.8% (11:2) | 28.8% (97) |
| tot: | 15 | 62 | 80 | 132 | 64 | 67 | 49 | 37 | : 506 |

Litter 3:

| | Age-period: 21-25 | 26-30 | 31-35 | 36-40 | 41-45 | 46-50 | 51-55 | 56-60 | total |
|---|---|---|---|---|---|---|---|---|---|
| M1: | 26.3% (5:2) | 16.7% (4:1.5) | 66.7% (34:1) | 39.1% (9:3) | 29.4% (5:4) | 25.0% (3:4) | 77.8% (7:4) | 53.8% (7:3) | 44.0% (74) |
| M2: | 41.2% (7:1) | 20.0% (4:1.5) | 51.2% (22:3) | 57.1% (12:2) | 50.0% (9:3) | 77.8% (7:3) | 69.8% (30:2) | 38.1% (8:2) | 51.6% (99) |
| F1: | 15.8% (3:4) | 20.0% (3:3) | 26.8% (11:4) | 26.7% (4:4) | 51.9% (14:1) | 36.4% (8:2) | 49.3% (35:1) | 78.6% (11:1) | 39.7% (89) |
| F2: | 19.0% (4:3) | 0.0% (0:4) | 63.6% (28:2) | 50.0% (24:1) | 40.7% (11:2) | 45.8% (11:1) | 31.7% (20:3) | 0.0% (0:4) | 39.4% (98) |
| tot: | 19 | 11 | 95 | 49 | 39 | 29 | 92 | 26 | : 360 |

2.14(b) Values of Spearman's "rho" for correlations between ranks in successive age-periods:

(For all correlations, N=12, the total number of pups across all three litters. Probabilities are for the values of "t", and are two-tailed in all cases).

| Correlation between ranks at: | rho: | t: | prob. |
|---|---|---|---|
| 21-25 days and 26-30 days: | 0.336 | 1.127 | ns |
| 26-30 days and 31-35 days: | -0.194 | 0.626 | ns |
| 31-35 days and 36-40 days: | 0.245 | 0.798 | ns |
| 36-40 days and 41-45 days: | -0.014 | 0.004 | ns |
| 41-45 days and 46-50 days: | 0.741 | 3.492 | p<0.01 |
| 46-50 days and 51-55 days: | 0.280 | 0.921 | ns |
| 51-55 days and 56-60 days: | 0.224 | 0.726 | ns |
| 21-25 days and 56-60 days: | -0.100 | 0.317 | ns |

performed by that individual in the appropriate age-period. Once again, correlation tests between successive age-periods (shown in table 2.14b) revealed no consistent individual differences in this behaviour. Only one correlation was significant, that between on-top frequencies at 41-45 and 46-50 days ("rho" = 0.741, converted to t = 3.492, with 10 df; $p<0.01$).

This one significant correlation is difficult to account for, and may have arisen by chance, given the number of tests performed. All other correlations between adjacent ages were small - below 0.3 - and a correlation between the first and final age-periods was also not significant, at -0.10. Inspection of the ranks in table 2.14 does suggest, however, that individual frequencies of on-top behaviour were somewhat more consistent than individual levels of involvement in play, especially in L1 and L2, where those pups who showed most pinning overall also showed most pinning in the majority of age-periods.

The overall impression from these data is therefore that, although on an overall basis, some individuals were significantly more playful than others, and showed more on-top behaviour than others, these differences were not markedly consistent over time. If anything, the data suggest that each animal showed periods when it was heavily involved in play or rarely involved in it, and that at times, each pup showed a fair degree of on-top behaviour in its play.

2.3.4.3: Correlations between the frequency of play and other social behaviours:

This section examines whether an individual's degree of involvement in play was correlated with the extent to which he participated in other social behaviours. Each individual was ranked according to his frequency of participation in each behaviour within his own litter, and then these ranks were correlated using Spearman's "rho".

2.3.4.3.1: Play compared to all agonistic behaviours combined:

A correlation test was performed between each pup's rank on playfulness, and his rank for involvement in agonistic activities (taking all agonistic and competitive behaviours together). There was a negative, but non-significant, correlation between these two measures ("rho" = -0.425; converted to "t", for N>10, = 1.484, with 10 df; p>0.05), suggesting that highly playful individuals were not also generally highly aggressive or competitive. A correlation performed between the frequency with which pups were on top during play, and the frequency with which they were involved in all agonistic and competitive behaviours combined, was also not significant ("rho" = -0.448; t = 1.583, 10 df; p>0.05).

2.3.4.3.2: Play compared to specific agonistic behaviours:

While these results show that levels of playfulness, and being on top during play, are not related to overall levels of aggressiveness and

competitiveness, the possibility remains that playfulness may be associated with degree of involvement in one or more particular agonistic behaviours. Therefore correlation tests were performed between play and the more frequently-occurring agonistic behaviours - competition for access to the food-hopper, competition for access to the water-spouts, food-stealing, and actual fighting.

There was no significant correlation between level of involvement in play and the frequency of competing for access to the food-hopper ("rho" = $^{-}$0.371, t = 1.262, 10 df; p>0.05). The frequency of on-top behaviour bore even less relationship to this competitive behaviour ("rho" = $^{-}$0.037, t = 0.116, 10 df; p>0.05). Competing for access to the water-spout also showed no correlation with involvement in play ("rho" = $^{-}$0.103, t = 0.328, 10 df; p>0.05) or with levels of on-top behaviour in play ("rho" = $^{-}$0.173, t = 0.556, 10 df; p>0.05).

Food-stealing from another pup did, however, show a significant positive correlation with being on top in play ("rho" = 0.787, t = 4.030, 10 df; p<0.01), although not with play in general ("rho" = 0.570, t = 2.193, 10 df; 0.10 > p >0.05).

No significant correlation was found between play and the frequency with which pups were involved in fighting ("rho" = $^{-}$0.219, t = 0.708, with 10 df; p>0.05). Fighting was also unrelated to the frequency of being on-top during play ("rho" = $^{-}$0.194, t = 0.626, 10 df; p>0.05).

While these tests were based on relatively few data

in the case of fighting, they do suggest that the individuals who were most involved in play were not the same individuals who were most involved in agonistic behaviour, whether this is considered in terms of general aggressiveness and competitiveness, in terms of specific competitive behaviours (with the possible exception of food-stealing), or in terms of actual serious fighting. This represents further evidence that play is motivationally distinct from these behaviours.

2.3.4.3.3: Play compared to amicable behaviours:

The frequency of involvement in play, and in on-top behaviour in play, were correlated with the frequency of the two principal non-playful but amicable social behaviours: allo-grooming and social olfaction. Each of these will be discussed in turn.

There were no significant correlations between involvement in play and levels of allo-grooming ("rho" = -0.100, t = -0.317, with 10 df; $p>0.05$), or between the latter and the frequency of on-top behaviour in play ("rho" = -0.196, t = 0.631, with 10 df; $p>0.10$). There was, however, a weak but statistically-significant negative correlation between the frequencies of play and of being the recipient of allo-grooming ("rho" = -0.614, t = -2.457, with 10 df; $p<0.05$); ie, those animals who were most involved in play, were the ones who received the least allo-grooming from their peers. Too much importance should not be attached to this finding; in view of the

large number of correlations performed, one which is statistically significant only at the 5% level might well have arisen by chance. Nevertheless, the result is interpretable in terms of the animals' behaviour: an animal which is playing is highly active, and active animals might be less likely to be involved in a relatively "quiet" activity such as grooming. There is certainly not a strong relationship between playfulness and involvement in allo-grooming, however.

The same holds true for the relationship between playfulness and involvement in social olfactory activity; no significant correlations were found between these two measures, whether the test was performed between the frequency of sniffing conspecifics (including the mother), and involvement in play ("rho" = 0.288, t = 0.953, 10df; p>0.05); between the frequency of being sniffed by other conspecifics, and play ("rho" =-0.061, t = -0.194, 10df; p>0.05); between the frequency of on-top behaviour in play, and the frequency of sniffing others ("rho" = -0.005, t =-0.066, 10df; p>0.05); or between on-top behaviour and the frequency of being sniffed oneself ("rho" = -0.255, t = -0.835, 10 df; p>.05). Play clearly bore no apparent relationship to non-playful social investigation.

2.3.4.4: Individual partner-preferences for play and other behaviours:

The preceding sections show that levels of

playfulness, overall, were not related to the frequency with which other non-playful behaviours were performed. This section looks at another aspect of the issue of individual differences, examining whether subjects (a) expressed individual preferences for interacting with particular members of their group; and (b) if so, whether these preferences were the same for all behaviours - so that, for example, an animal who preferred a certain individual for play interactions also preferred the same partner for non-playful social behaviour. This will be looked at in terms of what percentages of a pup's total play, allo-grooming, etc, were allocated to interacting with each of his peers, regardless of the absolute number of interactions in which he engaged. In the same way as the previous section, the relationship between partner-preferences for play and for aggressive encounters will be examined, and then the relationship between play and more amicable non-playful behaviours.

2.3.4.4.1: Preferences for play-partners:

Since the identity of the initiator of each play interaction was not recorded, but merely which two animals were involved, play-partner preference could only be measured in terms of whether particular pairings of animals were observed to play together more or less frequently thn would be expected by chance. Following Poole and Fish (1976), binomial tests were performed to determine whether the total amount of play between each posible pairing of subjects within a litter was

significantly greater or smaller than would occur by chance. For the purpose of these tests, the "total" amount of play against which these frequencies were compared, consisted of all instances of play ocurring within the appropriate litter, including those with the mother but excluding any in which one of the interactants could not be identified.

The results of the binomial tests, shown in table 2.15, suggest that in each litter, subjects showed marked preferences for playing with some of their peers and for not playing with others. Individuals did not play with each other at random. The pattern of these partner-preferences showed some similarities between L1 and L2, but L3 showed a completely different pattern.

In L1, the frequencies of both male-male and female-female play were significantly higher than would be expected by chance. The frequency of play between male number one and both females amounted to significantly less than expected levels, whereas the amount of play between male two and his female siblings was at chance levels. This explains why male two was the most playful pup, and male one the least playful, overall, in L1; male two played with all other pups, but especially with male one, whereas male one largely restricted his play to male two.

In L2, the two males again displayed a strong preference for playing with each other rather than with their female siblings. Both males played with one of their

TABLE 2.15: OVERALL PARTNER PREFERENCES FOR SOCIAL PLAY BETWEEN PUPS (21-60 DAYS):

(Unbracketed number is the number of times the individuals in question were observed to play together, over the whole of the period of study. Bracketed figure is the result of a binomial test, to ascertain whether or not this frequency of play was greater or less than would be expected by chance: a figure preceded by a plus sign shows that frequency is greater than chance, a figure preceded by a minus shows the frequency is less than would occur by chance. N for each test was the total number of observations of play in the litter concerned, where both partners could be identified. "*" = that the result of the test is significant at $p<0.05$; "**" = $p<0.02$; "***" = $p<0.0005$; "****" = $p<0.0001$. All tests are two-tailed. "M" = male, "F" = female).

(a) Litter 1:

| | M1 | M2 | F1 | F2 |
|---|---|---|---|---|
| M1 | - | 111 **** (+4.975) | 42 *** (-3.807) | 41 *** (-3.936) |
| M2 | - | - | 81 (+1.101) | 72 (-0.062) |
| F1 | - | - | - | 84 (+1.488) |
| F2 | - | - | - | - |

(b) Litter 2:

| | M1 | M2 | F1 | F2 |
|---|---|---|---|---|
| M1 | - | 149 **** (+4.924) | 79 ** (-2.543) | 110 (+0.703) |
| M2 | - | - | 82 * (-2.219) | 104 (+0.054) |
| F1 | - | - | - | 90 (-1.353) |
| F2 | - | - | - | - |

2.15(c): Litter 3:

| | M1 | M2 | F1 | F2 |
|---|---|---|---|---|
| M1 | - | 50<br>(-0.798) | 27 ****<br>(-4.167) | 53<br>(-0.358) |
| M2 | - | - | 44<br>(-1.677) | 30 ****<br>(-3.728) |
| F1 | - | - | - | 131 ****<br>(+10.922) |
| F2 | - | - | - | - |

sisters at chance levels (female two) and the other sister at below chance levels. Since there was also significantly less play between the two females than might be expected, this suggests that most of these results stem from the fact that female two was particularly unplayful.

The situation in L3 was completely different: as in L1 and L2, two of the pups showed a marked preference for playing with each other, but in this case it was the two females of the litter, not the two males. (The latter actually showed slightly less than chance levels of playing together, although this was not statistically significant). The pattern of play-interactions shown by this litter seem to result from the two males being particularly unplayful, both to each other and to their sisters.

On the basis of a similar analysis, Poole and Fish (1976) suggest that highly playful animals tend to prefer to play together. This was indeed the case for L2 and L3 in this study. In L2, the most playful pairing were males one and two, who performed 24.3% of the total number observations of between-pup play in their litter. Their ranks on overall frequency of involvement in play were first and second, respectively. In L3, the two females were the most playful members of their litter, and 39.1% of their litter's total play occurred between them. This was not the case in L1, however, where the most play occurred between the two males (25.8% of the between-pup total) despite the fact that one of the males had the

lowest overall rank for involvement in play of any of the pups in his litter.

On a more general level, these data show that the observed frequency-distribution of play within a litter is determined by the play-partner preferences of the members of the group; an obvious fact, but one which tends to be ignored in the face of claims of "sex-differences" in play. These results suggest that sex-differences in playfulness may be of secondary importance compared to the preferences for interaction of the pups individually.

2.3.4.4.2: Play-partner preferences in relation to partner preferences for other social behaviours:

This section investigates whether the play-partner preferences just discussed are specific to play, or whether they are a manifestation of more general social relationships, so that for example, individuals who prefer each other as partners for play also prefer each other for allo-grooming or for social olfactory activity.

2.3.4.4.2.1: Play and allo-grooming:

The individual partner preferences for allo-grooming were analysed, using the same procedure as that for studying play-partner preferences. The results of the binomial tests performed are shown in table 2.16. These revealed that, within each litter, there were marked deviations from the pattern of interactions between individuals which would be expected to occur if they had shown no preferences. Furthermore, broadly the same

pattern of preferences was found in all three litters. Males preferred to allo-groom males, amd females preferred to allo-groom females; these interactions occurred at well above chance levels in all litters. In contrast, mixed-sex interactions all occurred at chance or below-chance levels, except for allo-grooming between male two and female one in L2, and between male two and female one in L3 - and in both of these cases, the above-chance observed frequencies were due to the female of the pair grooming the male, the male showing chance (L2) or below-chance (L3) levels of allo-grooming in return. The consistency across litters in these individual differences gives rise to the sex-differences in allo-grooming behaviour which were reported in an earlier section.

To determine whether the partner-preferences for allo-grooming were similar to those found in play, two sets of correlations were performed. The first group compared the overall frequencies of play and allo-grooming between each pair of subjects, (ignoring the question of which of the two animals in a pair actually performed the allo-grooming). The second set compared the overall frequencies of on-top behaviour in play and allo-grooming between each subject-pair, taking into account the identities of the peformer and the recipient of the behaviour in each case. The results of all these tests are summarised in table 2.17.

The first set yielded a positive correlation between the frequency with which each pair of subjects played

TABLE 2.16: OVERALL PARTNER PREFERENCES FOR ALLO-GROOMING BETWEEN PUPS (21-60 DAYS):

(Unbracketed numbers represent the number of times each individual groomed each of the other pups in his litter. Names of initiators of grooming are shown on the left of the table, and names of recipients are shown over the columns. Each bracketed figure is the result of a binomial test, to ascertain whether or not this frequency of grooming differed from that which would be expected by chance: a figure preceded by a plus sign shows a frequency is greater than chance, a figure preceded by a minus shows a frequency is less than would occur by chance. N for each test was the total number of observations of allo-grooming in the litter concerned, where both partners could be identified. "*" = that the result of the test is significant at $p<0.05$; "**" = $p<0.02$; "***" = $p<0.01$; "****" = $p<0.0005$; "*****" = $p<0.0001$. All tests are two-tailed. "M" = male, "F" = female).

(a) Litter 1:

| | M1 | M2 | F1 | F2 |
|---|---|---|---|---|
| M1 | - | 7 (+1.306) | 4 (-0.171) | 2 (-1.058) |
| M2 | 40 ***** (+6.288) | - | 6 ***** (-3.283) | 8 *** (-2.703) |
| F1 | 9 (-1.247) | 10 (-0.910) | - | 21 ** (+2.460) |
| F2 | 7 (-1.459) | 10 (-0.378) | 18 * (+2.144) | - |

(b) Litter 2:

| | M1 | M2 | F1 | F2 |
|---|---|---|---|---|
| M1 | - | 21 *** (+2.905) | 10 (-0.599) | 6 * (-2.001) |
| M2 | 7 (+1.563) | - | 4 (-0.283) | 1 (-1.514) |
| F1 | 6 ** (-2.421) | 17 (+0.868) | - | 19 (+1.526) |
| F2 | 1 *** (-2.960) | 7 (-0.451) | 18 ***** (+3.729) | - |

2.16(c): Litter 3:

| | M1 | M2 | F1 | F2 |
|---|---|---|---|---|
| M1 | - | 14 ***** (+3.798) | 1 * (-2.231) | 3 (-1.226) |
| M2 | 24 ***** (+5.080) | - | 0 **** (-3.725) | 7 (-1.045) |
| F1 | 11 (-1.422) | 19 (+0.709) | - | 19 (+0.709) |
| F2 | 1 (-0.418) | 0 (-1.288) | 5 * (+2.193) | - |

together, and the frequency with which they allo-groomed each other, when the data from all three litters was combined ("rho" = 0.509, $p<0.05$). However, correlations between the two variables for each litter separately, suggest that this was a litter-specific effect, since although there was a high correlation for L1 ("rho" = 0.943, $p<0.02$), the other two litters showed no correlation between play and grooming preferences

The second set of correlations, between each possible pairing's observed frequencies of allo-grooming of each other and on-top behaviour in play with each other, also revealed no significant relationship between the two factors, either for each litter separately or over all three litters combined.

Thus, overall, there appears to be little obvious relationship between preferences for allo-grooming, and preferences for social play.

2.3.4.4.2.2: Play and social olfaction:

The same procedure as used in the previous section, was employed to see if there were any individual preferences for olfactory activity. In none of the three litters studied did the frequency of sniffing between any pair of animals show any differences from the values which would be expected to occur by chance (see table 2.18). It is to be expected from this that there would be no significant correlations between the frequencies of either play or on-top behaviour in play, and social olfaction; and this was indeed the case, both within and across

TABLE 2.17: SPEARMAN'S RANK CORRELATION COEFFICIENTS BETWEEN INDIVIDUAL PARTNER PREFERENCES FOR DIFFERENT SOCIAL BEHAVIOURS (21-60 DAYS):

(a) Correlations between individual partner preferences for play and allo-grooming:

| | Rho | N | p (2-tailed) |
|---|---|---|---|
| Litter 1: | 0.943 | 6 | <0.02 |
| Litter 2: | 0.200 | 6 | ns |
| Litter 3: | 0.257 | 6 | ns |
| 3 litters combined: | 0.509 (t=2.367) | 18 | <0.05 |

(b) Correlations between individual partner preferences for "on top" behaviour in play, and allo-grooming:

| | Rho | t | N | p (2-tailed) |
|---|---|---|---|---|
| Litter 1: | 0.535 | 2.002 | 12 | ns |
| Litter 2: | 0.313 | 1.042 | 12 | ns |
| Litter 3: | 0.159 | 0.509 | 12 | ns |
| 3 litters combined: | 0.251 | 1.512 | 36 | ns |

(c) Correlations between individual partner preferences for "on top" behaviour in play, and social olfaction:

| | Rho | t | N | p (2-tailed) |
|---|---|---|---|---|
| Litter 1: | 0.142 | 0.452 | 12 | ns |
| Litter 2: | 0.666 | 2.824 | 12 | <0.02 |
| Litter 3: | 0.030 | 0.094 | 12 | ns |
| 3 litters combined: | 0.429 | 2.770 | 36 | <0.01 |

(d) Correlations between individual partner preferences for allo-grooming and social olfaction:

| | Rho | t | N | p (2-tailed) |
|---|---|---|---|---|
| Litter 1: | -0.177 | 0.567 | 12 | ns |
| Litter 2: | 0.260 | 0.853 | 12 | ns |
| Litter 3: | 0.054 | 0.172 | 12 | ns |
| 3 litters combined: | 0.109 | 0.642 | 36 | ns |

TABLE 2.18: OVERALL PARTNER PREFERENCES FOR SOCIAL OLFACTION BETWEEN PUPS (21-60 DAYS):

(Unbracketed numbers represent the number of times each individual sniffed each of the other pups in his litter. Names of initiators of grooming are shown on the left of the table, and names of recipients are shown over the columns. Each bracketed figure is the result of a binomial test, to ascertain whether or not this frequency of sniffing differed from that which would be expected by chance: a figure preceded by a plus sign shows a frequency is greater than chance, a figure preceded by a minus shows a frequency is less than would occur by chance. N for each test was the total number of observations of social olfaction in the litter concerned, where both partners could be identified. None of these tests was significant at the 5% level, two-tailed. "M" = male, "F" = female).

(a) Litter 1:

| | M1 | M2 | F1 | F2 |
|---|---|---|---|---|
| M1 | - | 19 (+0.100) | 19 (+0.100) | 17 (-0.186) |
| M2 | 17 (-0.143) | - | 18 (+0.029) | 18 (+0.029) |
| F1 | 22 (+0.101) | 16 (-1.228) | - | 26 (+1.164) |
| F2 | 17 (+1.236) | 10 (-0.807) | 12 (-0.126) | - |

2.18(b): Litter 2:

| | M1 | M2 | F1 | F2 |
|---|---|---|---|---|
| M1 | - | 26 (-0.095) | 33 (+1.450) | 21 (-1.165) |
| M2 | 15 (-1.181) | - | 23 (+0.741) | 22 (+0.467) |
| F1 | 15 (-0.396) | 17 (-0.098) | - | 19 (+0.497) |
| F2 | 13 (-0.718) | 15 (-0.104) | 20 (+1.123) | - |

(c) Litter 3:

| | M1 | M2 | F1 | F2 |
|---|---|---|---|---|
| M1 | - | 12 (-0.446) | 14 (-0.118) | 16 (+0.538) |
| M2 | 8 (-0.297) | - | 8 (-0.297) | 12 (+0.908) |
| F1 | 13 (+0.596) | 9 (-0.515) | - | 11 (-0.144) |
| F2 | 9 (-0.627) | 11 (-0.080) | 14 (+0.832) | - |

litters, as shown by the results of the correlations in table 2.17. There was also no significant correlation between partner-preferences for allo-grooming, and those for social olfaction.

2.3.4.5: Summary of data on individual differences in social behaviour:

Two main features arise from this survey of individual differences in the litters' social behaviours.

The first relates to the individual differences in play itself. Taken over the whole of the 21-60 day age-period, there were marked individual differences amongst pups in terms of their playfulness. Each of the three litters studied contained one individual who accounted for nearly half of the litter's total play. In L1 and L2, but not L3, the most playful individual was also the one showing the most on-top behaviour in play.

However, at the same time, it must be noted that every pup was involved in a considerable proportion of their litter's play, and every animal was seen both to pin and be pinned on numerous occasions. This includes the mother, who in all cases was involved in a sizeable minority of her litter's total play. Furthermore, individuals did not show very marked consistency across age-periods either in the extent to which they were involved in play, or in the extent to which they were on-top during it (although there was slightly more consistency on the former measure). The overall impression, then, is that

while individuals varied considerably in their overall involvement in play, the marked degree of reciprocity between animals in play has to be appreciated.

The second important result to emerge from these analyses, is the lack of relationship between play and other social behaviours, whether the latter are amicable or agonistic. There were no correlations between each individual's involvement in play, and their participation in allo-grooming, social olfaction or agonistic activities (whether or not these last behaviours are considered jointly or severally). The only significant correlation of this kind was a weak (.6) negative one, between involvement in play and the frequency of receiving allo-grooming.

Not only were there no relationships between an individual's involvement in play and his involvement in other social behaviours, but also there was no correlation between his preferences for other individuals for different types of social interaction. Marked partner-preferences for both allo-grooming and play were found (in the latter case with some indications that highly playful individuals may prefer to play with each other), but these were not for the same individuals in each case. No individual preferences were observed for social olfaction. The implication that follows from these results is that play is a unique dimension of behaviour, not just one of a number of facets of "amicable" behaviour.

## 2.4: DISCUSSION:

### 2.4.1: Overall summary of the results of this chapter:

This section briefly recaps the main points to emerge from these longitudinal observations, and relates them to the results of previous studies on social play in the rat. In this discussion, the main emphasis will be on social behaviours, especially play. It should be noted, however, that the overall frequencies of non-social behaviours and the age-changes seen in them, can be seen as a continuation of the observations of Bolles and Woods (1964); many of the behaviour-frequencies are closely similar between the two studies, when allowance is made for variation caused by differences in the sampling methods used and in the definitions of the behaviours sampled.

#### 2.4.1.1: Overall frequency of behaviours:

Firstly, these studies provide some perspective on the relative frequency of social interactions. The exact frequencies with which different behaviours were recorded are obviously heavily dependent on the particular observation-times chosen. Within certain limits however, these results do suggest that the majority of activities shown by young rats are non-social in nature, and concerned with immediate survival. Only 8% of all

observations made between 21-60 days consisted of "social" behaviour, and play itself accounted for only 2.5% of the total behaviour of pups during this period of life.

Even so, play represented the predominant form of social interaction during this period, comprising approximately 30% of the pups' social behaviour. The data suggest that the other social interactions observed during this period were mainly amicable in nature, consisting largely of allo-grooming and social olfactory investigation. Agonistic and competitive activities of all kinds accounted for less than 20% of social behaviour observations; and of these, most instances consisted of competition for access to the mothers' nipples, or other resources. Few observations of "serious" fighting were recorded. Sexual activity was also rarely observed, accounting for less than 1% of the total number of observations of social behaviour.

2.4.1.2: Overall frequency of within- and between-sex interactions:

While there were few sex differences in the frequency of involvement in different behaviours, there were some interesting differences in the frequencies of different kinds of social interaction within and between the sexes.

There was significantly more play and allo-grooming between pups of the same sex than between the sexes. In mixed-sex play, males pinned females more frequently

than they were themselves pinned. In mixed-sex allo-grooming, the opposite trend was evident, with females grooming males more than vice versa. 37% of social olfactory activity involved males sniffing females, although this was not a statistically-significant difference.

2.4.1.3: Age-changes in the frequency of behaviours:

There were numerous age-related changes in behaviour which were presumably related to the two processes of weaning and sexual maturation, both of which occurred within the time-span of these observations. The main conclusion to be drawn from these observations is that social play and exploration (in the sense of olfactory investigation of the inanimate environment) showed similar age-trends, with both of these behaviours increasing in frequency up to 31-35 days and subsequently declining. This trend is particularly striking in the case of social play, and taken together with similar findings by previous researchers, would appear to be a highly characteristic feature of play in this particular species.

These trends were very different from those shown by other social and non-social behaviours. In the case of the other commonly-occurring amicable behaviours, allo-grooming showed a steady decrease with age (although much of this was attributable to the reduction in maternal care, with weaning), and social olfaction showed a steady

increase. Agonistic behaviours, taken overall, showed a consistent decrease with advancing age; and considered individually, their occurrence bore no relation to the pattern shown by play. As mentioned earlier, sexual behaviour was rarely seen; however, the few instances that were recorded show something of an increase in frequency of sexual activities from around 40 days onwards.

2.4.1.4: Age-changes in within- and between-sex interactions:

Some age-trends were found within behaviour-categories also. Play between male and female pups was very common at 21-25 days, but this declined with increasing age, so that within-sex play became most frequent. Females came to participate less and less in play, both with males and with each other, until by the end of observations they were dropping out of play altogether. There were age-related changes in the nature of the play observed, also; on-top behaviour in play increased markedly at weaning, and then remained at consistently high levels. There was some increase with age in the tendency for males who were participating in mixed-sex play to pin females more than they were pinned by females; however, the main trend in this respect was for males to be consistently "dominant" over females in play.

In the case of allo-grooming, there was a general trend for between-sex grooming to decline with age (except

for an abrupt peak at 46-50 days in the frequency of females grooming males); within-sex allo-grooming correspondingly increased over time. The frequency of social olfaction between the sexes varied erratically across age-periods, whereas within-sex olfaction remained fairly constant with age.

2.4.1.5: Social interactions involving the mother:

Mothers were found to play an important role in their litters' social behaviour, accounting for many of the agonistic intractions (especially fights) and about 16% of their litters' total play. Mothers showed no consistent preferences for interacting with pups of either sex, but female pups directed both more amicable and agonistic interactions towards her than did male pups. While mothers varied widely in the degree to which they interacted with their pups, the overall tone of the relationship was amicable.

2.4.1.6: Individual differences in social behaviours:

Finally, we have seen that there were consistent individual differences in social behaviours, including play. However, it is notable that no pup was involved in less than 35% of their litter's total play, nor in more than about 50% of it; all animals both pinned and were pinned, on numerous occasions; and there were no consistent changes with age - any individual differences

were overall ones, not found in every age-period. There were no relationships between the individual differences dfound in play, and those found in other social behaviours, whether these latter were of an amicable or agonistic/competitive nature.

2.4.2: Relationship of play to other behaviours:

These results both differentiate play from other behaviours, and highlight the relationships between different activities.

2.4.2.1: Play compared to agonistic and competitive behaviours:

Play displayed a characteristic and distinctive ontogenetic pattern, in terms of the frequency with which it was observed compared to other social and non-social behaviours. The inverted - "U" shaped frequency distribution of play which was found in this study resembles that reported by previous researchers (Meaney and Stewart 1981, Muller-Schwarze 1966). This pattern was quite different from that shown by agonistic and conpetitive behaviours, whether these latter interactions are considered as a group or individually (ie, as separate behaviours such as competition for nipple access, competitive behaviours associated with access to resources, and fighting).

Play not only peaked and declined in frequency at

different ages to agonistic behaviours, but also showed a different pattern of sex-differences and individual differences.

2.4.2.2: Play compared to other amicable behaviours:

The above features - play's ontogenetic distribution, sex-differences and individual differences - also serve to distinguish play from the other most commonly-occurring social behaviours, allo-grooming and social olfaction. (It is significant that the three most frequent forms of social interaction were amicable ones).

The time-sampling convention that only one behaviour could occur at a time, conceals the fact that these three behaviours are inter-related more than one might conclude on the basis of the quantitative data. Apart from the wrestling behaviour-patterns which make play so morphologically distinctive, play also was seen to contain large elements of allo-grooming and olfactory activity. This may partly explain the relatively low levels of these two behaviours during the study, since the bulk of them occurred during what was scored as "play" rather than separately from it. What the data show is that play has a distinctive patterning from "serious" allo-grooming and "serious" social olfaction, (ie, grooming and sniffing occurring entirely outside of a playful context), but not that play has no relation to these behaviours at all. It is quite possible that the

kinds of grooming and sniffing occurring within play are different (in form or motivation) from those occurring outside of it, so that it is no more valid to consider the playful forms as "borrowed" from "serious" grooming and sniffing than it is to regard the wrestling components of play as "borrowed" from serious aggressive behaviour.

2.4.2.3: Play compared to "exploration":

Play also showed differences from , and yet relationships to, olfactory investigation of the inanimate environment, which may be considered broadly equivalent to "exploration". The differences consist of the fact that the individuals who were most playful were not also the most exploratory, and that the pattern of sex differences in the latter did not correspond to those shown by the former.

However, in terms of ontogenetic patterning, the two behaviours show some similarities, since exploration was the only other behaviour category to show an inverted-U age-distribution similar to that of play. The fact that two behaviours show a similar ontogenetic patterning does not mean that they necessarily share a common motivation, however. The patterning of environmental olfaction may be an artifact of the relatively impoverished physical environment in which the animals were raised. The initial increase in exploration may have occurred because before weaning, the cage was relatively unfamiliar to the pups. As the pups matured, they rapidly became more

mobile, and more far-ranging in their excursions from the nest, so that there was more to be investigated. With increasing age came increasing familiarity with the environment. If it were not for the fact that much of the olfaction was actually concerned with investigating scents laid down by the other animals (and sniffing at the experimenter, as much as they were able to), then one suspects that levels of olfactory actvity would have declined more markedly after the initial period of exploration was over.

Nevertheless, some of the relationship between play and exploration seems to have been more real than apparent. It is perhaps suggestive that, on a daily basis, the peak of play occurred at around the time the light-cycle changed from light to dark and vice versa, since this represented the greatest amount of environmental change experienced by these animals.

Overall. however, these data do not support Muller-Scwarze's (1966) contention that play and exploration show different ontogenetic profiles, although there are numerous possible procedural differences which might account for the discrepant results. These include the fact that the present study ended at 65 days, whereas Muller-Schwarze continued for longer; possible differences in the definitions of "play" and "exploration" (it is difficult enough to compare studies of one ambigously-defined behaviour, let alone two); and differences in the animals themselves, since

Muller-Schwarze used animals given daily opportunities for play with each other, rather than animals which were conitnually housed together as in this study, so that the environment may have been relatively less familiar to his animals.

## 2.4.3: Relation of these results to those of previous studies:

### 2.4.3.1: The frequency of play:

The inverted "U"-shaped frequency distribution of play found in the present observations closely resembles that reported by Muller-Schwarze (1966, cited in Panksepp 1981) and Panksepp (1981). Given that these studies employed very different techniques (in that Panksepp and Muller-Schwarze obtained their data from pairing isolates in small and unfamiliar cages for short periods, whereas the present investigations were made on undisturbed social groupings in familiar environments), this distribution of play would appear to be a highly consistent and reliable feature of rat social behaviour between 21-60 days of age. Muller-Schwarze (1966) found that, out of a total of five hour's social contact per day, his rats spent a maximum of 5% of their time in play; this compares well with the peak figure of 4.5% in the present study, when allowance is made for procedural differences.

The timing of the peak frequency of play is similar across studies; Muller-Schwarze (1966) and Panksepp's

(1981) reports of maximal levels of play between 31-40 days, were confirmed in the present work. If Baenninger's (1967) categories of "fighting", "dominating" and "submitting" were actually descriptions of play, then her observations also agree with the present study, since these behaviours showed an inverted "U"-shaped function with a peak at 30-36 days.

Although other studies show less consistency concerning the ontogenetic distribution of play, these discrepancies are easily explained. Bolles and Woods (1964) for example, mention a peak in "fighting" (a term which they apparently use in the sense that other workers use the word "play") at between 22-29 days. However, they obtained only a qualitative description of their subjects' behaviour up to 36 days; quantitative records were made only up to day 23. The qualitative data can thus provide us with no detailed information on the frequency of play; and the quantitative study ended before the peak of play would have occurred. At least their results confirm the impression that play increases markedly around the time that weaning occurs.

Poole and Fish (1976) found no significant differences between the amount of play shown at different ages in their cross-sectional study. However, this could simply be an artifact of an unfortunate choice of age-samples; since they observed play at 21-25 days and 35-49 days, they might well have missed a peak in play activity if it occurred in between those two age-periods.

It is quite possible that Poole and Fish's subjects could have shown a peak of play activity between 31-35 days, as in the present study.

Meaney and Stewart (1981) looked at age-changes in different components of play, rather than using a blanket category of "play" as in the present study. They report that the various behaviours which they considered to be "playful" followed different time-courses during development. "Pouncing" was found to increase markedly up to 26-30 days and then remain stable; "wrestling" and "on the back/kicking" decreased with age; "lateral display", "boxing" and "on the back" increased with age; and "on-top" and "neck-grooming" showed no age-changes.

In the present investigation, some of these behaviours were lumped together in the category of "play" ("pouncing", "wrestling", "on the back/kicking", "on-top" and "neck-grooming"); some were considered to be primarily agonistic behaviours ("lateral display"); and others ("on-top", "boxing" and "on the back") were classified under either category, largely depending on the context within which they were seen to occur. (Early "boxing" appeared to be playful, whereas later boxing was a somewhat different behaviour which appeared to be more "agonistic". This point will be returned to, and discussed at greater length, in a subsequent section).

The time-sampling conventions used in the present study were probably more likely to record the incidence of longer-duration behaviours such as "wrestling" and "on the

back/kicking" than they were to reflect the occurrence of very brief events such as the initial "pounce". If this was indeed the case, then possibly there is some disagreement between the present observations and those of Meaney and Stewart (1981), since although the present data show similar age-changes to those found in the latter's observations on pouncing, they do not support Meaney and Stewart's claim that wrestling decreases with age. However, given the definitional differences between the two studies, it is pointless to make too precise a comparison between them. In fact, summing together Meaney and Stewart's data for the overall frequencies of "wrestling", "pounce", "on the back/kicking" and "on top" in each age-period (ie, those behaviours which would have been unequivocally categorised as "play" in the present work) reveals substantial agreement between the two sets of data, except that the peak for "play" in Meaney and Stewart's study came slightly earlier, at 26-30 days.

The overall conclusion is therefore that social rough and tumble play in the rat shows a distinctive ontogenetic patterning, with a marked peak around 30-35 days.The fact that the results of different studies show such close agreement on this point, despite the diversity of the social and environmental conditions under which the subjects were housed, suggests that age-changes in the frequency and distribution of play are under the influence of endogenous factors rather than governed by the animals' environment.

2.4.3.2: Sex differences in play:

Although the overall patterning of play is highly consistent across studies, there is less agreement on the question of whether or not there are sex differences in playfulness.

The present study found no sex differences in the frequency with which pups were involved in play, except that females showed more of a decline in play at the end of the study (51-60 days). There were, however, sex-differences in the choice of partners for play; more play occurred between interactants of the same sex than would be expected by chance. This tendency increased with age; before weaning, (ie, between 21-30 days), mixed-sex play was most frequently observed, but this showed a progressive decline. Differences in on-top behaviour within play were also observed, with males consistently pinning females more than females pinned males.

The net conclusion from these results seems to be that there were some sex differences in play, but that they were minor and only began to manifest themselves towards the end of the study. There were no sex differences in involvement in play; but of course, due to the lack of data on who actually initiated the observed interactions, the possibility remains that males might have initiated more play than females. (This would explain the relative increase in male-male play at the end of the

study, since if females became increasingly unresponsive to playful solicitations, then males would be forced to turn to each other for play).

Some of the previous studies on rat social behaviour report no sex-differences in playfulness. Panksepp and Beatty (1981) found no reliable sex differences in the playfulness of Long-Evans rats, and Bolles and Woods (1964) observed no systematic sex-differences in any social behaviour. However, Panksepp and Beatty's results may have been affected by the fact that they used rats housed in social isolation except for sporadic opportunities for play, and their findings should not be relied upon too heavily as a record of normal behavioural development. Bolles and Woods ceased observations at 36 days, before the onset of sexual maturation; and in the present work, those sex differences which were observed became statistically significant only towards the end of the study, from 51 days onwards.

The more substantial studies of play in the rat - those of Poole and Fish (1976) and Meaney and Stewart (1981) - both recorded sex differences in play. Poole and Fish (1976) found that males showed more "solitary" play and a larger number of elements of social play than did females. Both males and females carried out more play elements if the partner was male. Rats of both sexes spent more time playing with males, so that females were less involved in social play. The difference of approach from the present work - ie, in counting "elements" rather than

time-sampling behaviour - makes Poole and Fish's results difficult to compare to those described in this section, and there may be no contradiction between the two studies that cannot be accounted for in terms of procedural differences. The claim that females were less involved in social play, however, is not supported by the present data.

Meaney and Stewart (1981) reported sex differences in a number of different social behaviours; as we have seen, some of these correspond to "play" in the present study and some do not. Between 21-55 days, all of the patterns which they considered as "play" (including "pouncing" and "wrestling", the behaviours regarded as most unequivocally "playful" in the current study) were more frequently observed to be performed by males rather than by females, although not always to a statistically-significant extent.

Meaney and Stewart also noted a number of age-related sex differences in pups' choice of partners for "play". At all ages, males were seen to initiate play (ie, by pouncing) more frequently than females, an observation which in itself is not incompatible with the results of the present study, in which the identity of the initiator in play was not recorded. Males preferred to initiate play with other males, except between 36-40 days (when they showed a preference for pouncing on females instead), and between 41-45 and 46-50 days (when there were slight and statistically non-significant preferences for males initiating play with females, and females initiating play

with males, respectively).

As with Poole and Fish's study, direct comparisons betwen Meaney and Stewart's results and those of the present work are difficult. However, it does seem that Meaney and Stewart's subjects displayed somewhat more marked sex differences in their play than the animals whose behaviour is discussed in this chapter, even when consideration of Meaney and Stewart's results is confined solely to those behaviours which were considered to be definitely "playful" in the present work.

In short, Meaney and Stewart's (1981) results suggest that play is an activity performed mainly by - and between - males; and although the limitations of the present observations preclude the possibility of assessing the claim that males initiate more play than females, the present data do contradict the statements that (a) male rats prefer to play mainly with other males, (except towards the very end of the age-period studied) and (b) that males show an overall greater degree of involvement in play than do females. Clearly, the existence of sex-differences in the play of young rats is subject to much greater variability than the ontogenetic patterning of the behaviour.

2.4.3.3: "Dominance" in play; sex and individual differences:

Another controversial issue is the extent to which consistent "on-top" relationships are established in play.

There are two issues at stake here. Firstly, there is the problem of whether or not consistent individual differences or sex differences in "on-top" behaviour are in fact an important aspect of rat play. The second problem is, if such differences are found, what do they represent? Describing them in terms of "dominance", even as a shorthand measure, is potentially misleading, as it begs many questions about the motivation of the behaviour concerned. This section will confine itself to the issue of whether or not consistent differences exist in "on-top" behaviour, and the question of what these differences represent will be returned to in a later section.

Poole and Fish (1976) found no evidence of consistent "dominance" relationships in play, either between the sexes or on the basis if individual animals. Out of thirty-nine pups from eight litters, only two subjects showed a greater number of "offensive" elements in play than was expected by chance, and only three showed a greater number of "submissive" elememts than expected. Poole and Fish concluded that "...Rats which adopted a consistent role, were, therefore, in the minority".

Other studies have not supported this conclusion. The strongest evidence for the existence of consistent on-top relationships in play comes from the work of Panksepp (1981), who claimed that stable "dominance hierarchies" developed during play; isolates paired every 4 days or so initially pinned each other equally frequently, but with increasing age one animal in each pair came to pin the

other about 70% of the time. Occasionally, reversals of dominance occurred, which were heralded by decreases in play. Whether or not these effects are a feature of normal rats' play is questionable; the unnaturalness of Panksepp's rearing conditions have already been discussed. Also, Panksepp used only male subjects, so that his data touch only on the question of whether or not there are individual differences in on-top behaviour.

However, further support for Panksepp's claims comes from the work of Meaney and Stewart (1981), using mixed-sex litter-groups. They not only confirmed Panksepp's results by observing the establishment of stable "dominance" hierarchies with age, but also suggested that there are sex differences in this behaviour.

Meaney and Stewart found that from about 46 days of age onwards, there was a major change in on-top behaviour during play. Up to this age, "males engaged in more dominance-related behaviours than females", and on-top behaviour was evenly distributed amongst them. However, from 46 days onwards, the performance of on-top behaviour became largely restricted to one male pup per litter. Also, the rankings of male pups in terms of this behaviour were virtually identical for the last two age-periods (ie, between 46-50 days, and 51-55 days). Meaney and Stewart concluded from these results that a stable dominance hierarchy is formed in the play of older males.

Meaney and Stewart also reported a sex-difference in the probability with which an "on-top/on the back" relationship was likely to occur during play. In play between pups of the same sex, the probability of observing such a relationship remained more or less constant over age, and there were no consistent differences between male-male and female-female play. However, although the probabilities of on-top/on-back behaviour in between-sex play and within-sex play were initially similar, after 40 days of age play between males and females became increasingly less likely to result in an "on top/ on the back" relationship.

Meaney and Stewart's interpretation of this latter effect is rather misleading. By writing that "...Thereafter, [ie, after 40 days] male-male play-bouts are about twice as likely to result in an OT/OB relation as are male-female play-bouts" (paragraph one, page 40) they imply that it is the male-male play which is showing an age-change, in the direction of increasing "dominance". Their graph on page 40, however, suggests that this difference between male-male and mixed play stems not from any age-changes in the former's behaviour, but from a change in the nature of the latter; between-sex play clearly shows a progressive reduction in on-top/on-back behaviour from the consistent pattern shown in within-sex play.

In other words, it is not the case that male-male play is increasingly likely to involve on-top/on-back

relationships, but rather that with increasing age, mixed-sex play becomes less likely to involve such behaviour. Thus "dominance", as expressed by on-top/on-back, is showing no age-changes in play between animals of the same sex, and is becoming less frequent in play between the sexes. This is a rather different interpretation from that implied by Meaney and Stewart.

Another point worthy of note is that, although Meaney and Stewart observed their animals from 21 days onwards, they only provide information on the probability of on-top/on-back relations from 26 days on - and yet in the present study, it was during this first few days that the most marked changes in on-top behaviour were observed, with the frequency of on-top increasing from less than 30% of play to over 70%, a result which does not fit so neatly with a concept of increasing "dominance" in play over age.

It thus appears that consistent on-top relationships do not necessarily occur during play, if Poole and Fish's (1976) results are valid; and that, even when they do occur, they are confined to the behaviour of older animals (ie, over 50 days), as shown by Panksepp (1981) and Meaney and Stewart (1981). Furthermore, despite suggestions to the contrary, there is no firm evidence that males engage in such behaviour to a greater extent than females.

The data reported in this chapter thus support and contradict different aspects of all three of these previous studies. There is support from the present study for Meaney and Stewart's finding that roughly 60-80% of

within-sex play involves on-top relations, and that there are no changes in this pattern between 26-55 days (although the present work shows a marked increase in such behaviour between 21-30 days). However, the current work contradicts Meaney and Stewart (1981) and Panksepp (1981), and supports Poole and Fish (1976), in finding no evidence for individual differences in on-top behaviour. The claim that "dominance" relationships develop in the play of older pups is also not supported by these data. Sex-differences in on-top behaviour (in that males were consistently on top of females rather than vice versa) were found in the present study, but they did not show the downward trend displayed by Meaney and Stewart's pups.

In short, the present data support the suggestion that much of play involves one animal being on top of the other (this after all, was largely how play was defined). However there is little support for claims that these relationships are consistent between individuals, or that there is an increase in such behaviour with increasing age (at least, not an increase during the age-period suggested by Meaney and Stewart and Panksepp).

### 2.4.4: Methodological limitations of the current study:

The time-sampling conventions employed produced an objective and systematic estimate of the relative frequencies with which different behaviours occurred;

however use of the instantaneous sampling technique carried with it a number of limitations which restrict the informativeness of the data obtained.

2.4.4.1: Problems in determining who initiated social interactions:

The major drawback of the spot-sampling method used was that the identity of the initiator of social behaviours could not be identified. This difficulty affected different social behaviours to varying extents, for two reasons.

Firstly, there are problems associated with the fact that there were differences between the social behaviours in the extent to which they were liable to involve role reversals. The more likely the possibility of role-reversal, the more risky it is to conclude that the animal performing the behaviour at a particular instant is the one who actually initiated it.

In the case of social olfaction, the animal scored as "sniffing" obviously initiated the behaviour, although he was not necessarily the animal who initiated the actual interaction within which the sniffing occurred. For allo-grooming, assuming that the performer of the behaviour at the instant of sampling was also the initiator of that interaction is more chancy, because often there were cases in which one animal began to groom another and then the recipient switched to grooming the initiator.

This difficulty was potentially most marked in play, because this behaviour is reputed to involve role-reversals; however, the subjective impression obtained from watching the animals is that the animal on top was in many cases also the one who had initiated the play. This means that while the frequency of observations of "play" tell us nothing about who actually initiated the interaction, the frequency of the "on-top" position within play may provide a very crude estimate of the relative frequency of initiation. Identifying the initiator of fighting and other agonistic behaviours (except for chasing) is difficult because there is nothing in the behaviour itself - at the moment of sampling - which reliably identifies the initiator of the interaction.

The second factor in this problem is that the behaviour categories scored represent different levels of interaction: play and fighting are "sets" of behaviours (pouncing, wrestling, rearing, sniffing, grooming in the case of play); allo-grooming represents more of a unitary expression of a partcular behaviour-pattern; and social olfaction is a brief, single behaviour-pattern. In other words, at one extreme there are "categories" of behaviours (play and fighting) and at the other, behaviours which can for all practical purposes be regarded as single behaviour patterns, eg sniffing. Allo-grooming falls somewhere in between, since the behaviours involved are sufficiently homogeneous to warrant regarding the activity as "one" behaviour, while the prolonged duration of the whole

allo-grooming interaction means that it is better to regard allo-grooming as a "state" rather than as a single behaviour-pattern or "event".

2.4.4.2: Problems in comparing the frequencies of different behaviours:

The last point made above, brings us to a more general difficulty of the time-sampling technique, that there are considerable problems in making valid comparisons between different behaviours in terms of their frequency of occurrence.

The greatest difficulty has already been briefly mentioned, that different levels of behavioural analysis may be occurring within the same study: some behaviour-categories scored as single behaviours - eg, "play" - actually consist of a constellation of different behaviours (albeit with a common motivational basis). This is less obviously the case for other behaviours, such as "sleeping" or "sniffing", which on the same (intuitively-derived) level of analysis as that applied to play, may effectively be considered as "single" behaviours.

This is not to say that sleeping and sniffing do not themselves consist of different behaviour patterns; obviously they do. Any behaviour can be investigated at a number of different levels of analysis, ranging from studies of the movement of individual muscles up to very gross categories such as "play" or even "activity"; the

problems come in making comparisons between different behaviours, since it is difficult to know whether the level of complexity at which one behaviour is scored, is the same level as that being used in the recording of others.

The second difficulty is that time-sampling appears to be biassed towards detecting and recording the occurrence of "states" (continuous behaviours of relatively long duration) rather than "events" (briefly-occurring behaviours). "Sleeping", for example, is more likely to be recorded than "sniffing" because the former occurs continuously over prolonged periods whereas the brevity of the latter means that in practice it is as likely to occur between two spot-samples as it is to coincide with a sampling-point and be scored.

For practical purposes, one is dealing with levels of confidence in making behavioural comparisons. Comparisons of the frequencies of a single behaviour-category, eg "play", either within or between individuals seems to be quite valid, since the units of analysis are effectively the same throughout.

Comparisons between different "states", or between different "events", are more or less accurate, so that for example "eating", "self-grooming" and "sleeping" (states) can be compared to each other, and "sniffing", "fighting" and "play" (events) can be compared.

Potentially, the greatest problems arise in comparing the relative frequencies of states and events, since the

frequencies of the former may be systematically biased compared to the frequencies of the latter. A deliberate attempt to minimise the severity of this bias was made by reducing the gap between time-samples to the minimum possible without sacrificing reliability. However, even with a 10-second time-sample, it was felt that quite a few instances of play and sniffing were missed because they started and finished between consecutive samples. The recorded levels of play, sniffing and fighting are thus probably underestimates of the actual levels of these behaviours, if they were measured directly. One alternative strategy is to score brief behaviours at the nearest time-sample to their actual occurrence, but this method was not used since it was felt that it would merely introduce a different, and more complex, source of bias into the study.

2.4.4.3: Problems caused by the mutual exclusivity of categories:

One possible problem of the time-sampling technique used is that only one behaviour could be scored as occurring at any one instant. While it is difficult to determine precisely what effect this had on the results obtained, the majority of observations were probably unaffected to any significant extent. The net effect, however, is to introduce a further element of imprecision into the results, which must be recognised when evaluating the validity of the conclusions drawn from them.

### 2.4.4.4: Limitations of the behaviour categories used:

A final practical difficulty which could, with hindsight, have been remedied is that the behaviour categories used were too gross, even allowing that the aim was to compare behaviours in very general terms. More data could have been obtained from these studies at relatively little extra cost in terms of time and effort, if a greater number of behavioural categories had been used. This applies especially to the social behaviour categories; age-changes in the quality of play have not been detected by the present studies, but might have been if more fine-grain categories had been used. However, the categories actually employed were chosen with a view to maximising the reliability of the observations made, considering the difficulties of time-sampling five rapidly-moving animals at ten-second intervals, without the aid of video. Selection between a greater number of categories than that actually used would have required more decision-time, and this might have resulted in a reduction in the reliability of the obtained data.

## 2.5: CONCLUSION:

In some respects, the results of the time-sampling studies described in this chapter corroborate those of

earlier reports, in suggesting that striking features of play are a highly characteristic ontogenetic patterning, and the "endogenous" nature of its motivation. However, they also appear to conflict with previous studies which stress the relationship of play to "dominance" and "aggressiveness", and which find prominent variations in playfulness as a function of age, sex and individual differences.

The conception of play suggested by the current data is that play is predominantly an amicable behaviour which is quite distinct from all other social behaviours, both motivationally and morphologically. This is in contrast to the way in which previous researchers have envisaged play, as a distorted, preparatory version of adult aggressive patterns. However, as we have seen in the previous discussion, the results obtained from these time-sampling studies concerning individual differences in playfulness and "dominance", suffer from a number of drawbacks due to the constraints imposed by the time-sampling techniques employed.

The aim of the following section, therefore, is to confirm and amplify the impressions obtained from the present chapter, by means of direct observation of the play interactions themselves rather than by using time-sampling techniques.

Whereas the present chapter was primarily concerned with looking at play in relation to other behaviours on a broad level, chapter three will focus more closely on the

fine details of the play itself, although (in line with the "ecological" approach to play which is a prime concern of this thesis) also studying the relationship of play to the behaviours occurring immediately around it. Direct observation of play will not only supply more information on the aspects of play already examined, such as "dominance" and the question of sex differences in playfulness, but will also provide data on aspects of play which time-sampling techniques either could not measure at all, or else could investigate only in gross terms. These include such features as the duration of individual play-bouts, the number of role reversals occurring within a play-bout, the percentage of play spent by each animal on top or underneath, etc. Above all, direct observation of play will enable information to be obtained on the issue of who intiates play, the most serious drawback of the current chapter.

# CHAPTER THREE: LONGITUDINAL STUDIES OF SOCIAL PLAY:

## 3.1: INTRODUCTION:

Chapter two investigated the wider context in which play occurs, namely the way in which play fits into the general patterning of the young rats' social and non-social activities. This chapter looks more closely at various specific features of play which could not be investigated with a time-sampling technique, and examines more closely the way in which play fits into the stream of behaviour occurring immediately before and after it.

As with chapter two, this section is primarily concerned with obtaining normative data on variations in play occurring as a function of the age and sex of the participants. As a result of the conclusions drawn from the previous section however, particular attention will be paid to three additional aspects of play:

(a) The relationship of play to other behaviours, especially amicable social behaviours (allo-grooming and social olfaction), agonistic and competitive behaviours, and exploration.

(b) The question of whether there are marked variations in "dominance" in play, in terms of asymmetries in the frequency and duration of pinning during play.

(c) The question of whether or not there are marked sex differences in playfulness.

* The film of each play-bout selected for analysis was examined a number of times. All measurements of play were double-checked for accuracy. In the case of measures of duration ( bout duration, amount of time spent in the "on-top" position by each of the participants, etc.), measurements were repeatedly checked and re-checked until a consistent timing was obtained on two or more successive attempts. Since the video-machine used had a slow-motion facility, this was often used to confirm initial impressions of where each animal was and what he was doing before and after the bout concerned (something which was often difficult to ascertain at normal tape-speed, due to the rapidity of movement in young rats).

Each play-bout took about 15 minutes or more (sometimes half-an-hour) to analyse in this fashion.

Occasionally, bout-measures were re-checked after a few days had elapsed, to check on observer consistency over time.

Another precaution against systematic changes in observer behaviour with time, was that tapes were analysed in a random order with respect to their date of filming. This precluded the development of any consistent observer biases over time (as a function of increased familiarity with the animals' behaviour, etc) which might otherwise have developed, and which might have confounded any "true" developmental effects in the phenomena under investigation. (See also Appendix One).

## 3.2: PROCEDURE:

Three separate litters were filmed on video. The whole of the period from 30 minutes before dusk, to 3 hours after dusk, was filmed each day, between 21 and 60 days of age. Wrestling bouts were then subsequently selected for analysis if they satisfied the criteria outlined below. This resulted in a total of 700 play-bouts being analysed: 246 for Litter 1 (L1); 272 for Litter 2 (L2); and 182 for Litter 3 (L3). (Note that these are not the same three litters as used for the studies in chapter two). *

### 3.2.1: Definition of play:

For the purposes of this chapter, only play in the form of wrestling was considered. A wrestling-bout was defined as any interaction occurring between two subjects which began with a pounce, and in which one of the two was held down on his back by the other. The beginning of a bout was considered to be the initial pounce. A bout was considered to have ended when, for more than three seconds, the two animals ceased to maintain ventral-ventral contact. "Play-chasing" was analysed only if it occurred within a wrestling bout. Only exclusively dyadic interactions were analysed; and of these, only those were selected in which the two animals were in complete view for a period of at least ten seconds before and ten seconds after the interaction.

### 3.2.2: Apparatus:

PVG hooded rats were used. Each litter was run singly: each pregnant mother was placed in the observation cage described below, so that her litter was wholly raised under the conditions (light-cycle etc) in which it would be observed. The Litter was culled to six pups (three male, three female) and the mother removed at 21 days, after which they were left undisturbed in the test environment, until observations ended at 60 days. Subjects were identified on the basis of their natural coat markings.

Subjects were housed in the same enclosure, and under the same lighting conditions, as in the studies described in chapter two.

### 3.2.3: Variables Studied :

The following measures were taken for each wrestling-bout analysed. Each of these aspects of play will be examined in the light of the issues mentioned in the introduction to this chapter, ie in terms of sex differences, age differences, and the extent to which they reflect "dominance" and "aggressive" tendencies.

#### 3.2.3.1: Contextual Features:

##### 3.2.3.1.1: Identity of the initiator and recipient of play:

The identity and sex of each of the participants in

the wrestling bout were recorded. The animal which performed the initial pounce which was defined as commencing the interaction, was designated the initiator of the bout (A1). The animal who was pounced upon was considered to be the recipient of the wrestlng (A2). Note that designation as A1 or A2 was completely independent of who was actually on top during the encounter, since an animal which pounced on another but which was then held down for the rest of the encounter could truly be considered to be the "recipient" of the wrestling in one sense, but was by this definition nevertheless the initiator of it.

3.2.3.1.2: Number of role reversals:

For each bout, a record was made of the number of times that the interactants switched positions, so that the animal on top became the animal underneath and vice versa. A "role reversal" was operationally defined as having taken place when the animal which had been on top, pinning down his partner, was himself then pinned down.

3.2.3.1.3: Antecedents of play:

A note was made of what each animal was doing in the three seconds immediately prior to the beginning of the interaction. Antecedents of play could fall into any one of the following categories, which were set up beforehand,

1: Non-playful social behaviours:

(a) "Agonistic" encounters:

As in chapter one, most of these would more properly be called "potentially-agonistic", or "competitive": situations such as food-stealing, or competing for access to resources such as the food-hopper, water-spout, a particular area of the cage which appeared olfactorily-interesting to the interactants, or sexual partner.

(b) Allogrooming:

Grooming by the subject of another animal, not necessarily the play-partner.

(c) Sexual behaviour:

This category included sexual behaviour-patterns such as attempted mounting, mounting, intromission and ejaculation. Anogenital sniffing proved slightly difficult to classify. If it occurred in an obviously-sexual context, then it was included in this category; otherwise, it was scored as olfactory investigation of the animal concerned.

2: Playful behaviours:

(a) Wrestling with the same individual.

(b) Wrestling with a different individual.

3: Olfactory behaviours:

(a) Olfactory invetigation of the inanimate environment:

This was scored if the animal's snout was in contact with some part of the environment for the majority of the

three-second period.

(b) Olfactory investigation of the play-partner:

In some circumstances this would be counted as "sexual behaviour", as described above.

(c) Olfactory investigation of a different animal to the one with which play had just occurred.

4: Locomotion:

Gross motor activity of the subject which did not involve obvious olfactory behaviour, was classified under this category: ie, running, leaping, and climbing.

5: Self-grooming.

6: Ingestive activities:

This category was comprised of drinking and eating, including coprophagy.

7: Other behaviours:

The relatively few behaviours which could not meaningfully be assigned to any of the previous categories were scored here, for example "lying motionless".

3.2.3.1.4: Consequences:

Using the same categories employed in recording the antecedents of each bout, a note was made of what each animal was doing in the first three seconds immediately following the end of the bout.

3.2.3.1.5: How the bout ended:

A record was made of what behaviour by either of the participants actually appeared to terminate the

interaction. Again, on the basis of preliminary observations, a number of categories were set up which accounted for the majority of bout-endings:

1: Either of the interactants simply moving away:

This might be by running away from the partner or sometimes merely by walking away.

2: Distraction of either interactant:

This category included either animal breaking off the current interaction in order to participate in a fresh one with a different animal. For example, a common ending was for the animal on top to break off from his wrestling activities and chase after a different animal in order to play with him.

3: Olfactory investigation of the environment:

Either animal might suddenly "switch off" from wrestling, and engage in prolonged sniffing of the immediate surroundings.

4: Olfactory investigation of the other interactant:

Either animal might cease wrestling and engage in prolonged sniffing of the wrestling-partner.

5: Self-grooming:

Either animal might break off to groom himself.

6: Sexual behaviours:

Sexual activity directed by one of the participants towards the other effectively ended the wrestling interaction.

7: Other:

Any behaviours which ended the bout but which did not

fall into any of the above categories.

For each of these categories, a note was made of which animal was responsible for terminating the bout.

3.2.3.1.6: Proximity of interactants:

Whether or not the two animals were in close proximity before and after the interaction was recorded. "Proximity" was defined as the two interactants being within 6 inches of each other; "before" and "after" as consisting of the 3 seconds before and after the interaction respectively.

3.2.3.1.7: Location within the environment:

The location of the interaction within the cage, and the proximity of the interactants to the nearest wall or cover, was noted. Proximity to wall was scored as being within 10 cm ("close"); between 10-20 cm ("intermediate"); or over 20 cm ("no proximity"). Wrestling interactions within a single bout could often occur at a number of different locations. Therefore, proximity was taken as the distance from cover at which most of the wrestling occurred, ignoring any chases which might take place within a bout. Although chases could result in the interactants moving away from cover for very brief periods, it was considered that the important factor was where the wrestling itself occurred.

3.2.3.1.8: Who approached whom:

This was classified according to whether the initiator of the bout approached the recipient, the recipient approached the initiator, both were already adjacaent to each other, or both independently moved towards each other.

3.2.3.2: Duration of Interaction:

3.2.3.2.1: Overall duration:

The overall duration of each wrestling interaction was measured, from the initial pounce which was defined as beginning the bout, to the cessation of ventral-ventral contact for more than three seconds which was defined as ending the bout.

3.2.3.2.2: Amount of time each animal was in an "active" role during play:

For each wrestling bout, a note was made of the total amount of time that each interactant spent in an "active", rather than "passive", role. Taking an "active" role consisted of being on top during wrestling and holding the other animal down; chasing rather than being chased; and thrusting forward and pawing more vigorously, during episodes of rearing up or "boxing".

The amount of time that each animal was in an "active" role was also considered in terms of the percentage of the total bout duration it represented, thus

enabling bouts of differing durations to be compared.

## 3.3. RESULTS:

### 3.3.1: Frequency of play:

#### 3.3.1.1: Age-differences in the number of play-bouts observed:

Table 3.1 shows the number of play-bouts selected from each litter for analysis, in each of the ten-day periods between 21 and 60 days. If the ease with which bouts could be selected for analysis is an accurate reflection of the underlying frequency with which the subjects played, (and there is no reason to suppose that it is not) then these data suggest that play was most frequent between 31-50 days, with fewer bouts being recorded before or after this period. In the case of L3, the peak of play came between 31-40 days; the other two litters showed a slightly later peak, between 41-50 days.

#### 3.3.1.2: Sex-differences in the number of bouts observed:

Table 3.2 shows the overall frequencies with which males and females were observed to initiate play with their own sex or the opposite sex. These frequencies are expressed as percentages of the total number of bouts recorded, combining the data from all three litters studied.

TABLE 3.1: NUMBER OF PLAY-BOUTS OBSERVED IN EACH AGE-PERIOD:

(Percentages are of the total number of bouts shown by each Litter)

| | L1 | L2 | L3 | OVERALL |
|---|---|---|---|---|
| 21-30 days: | 16.7%<br>(41) | 15.1%<br>(41) | 37.4%<br>(68) | 21.4%<br>(150) |
| 31-40 days: | 22.4%<br>(55) | 18.4%<br>(50) | 39.0%<br>(71) | 25.1%<br>(176) |
| 41-50 days: | 44.3%<br>(109) | 49.6%<br>(135) | 14.3%<br>(26) | 38.6%<br>(270) |
| 51-60 days: | 16.7%<br>(41) | 16.9%<br>(46) | 9.3%<br>(17) | 14.9%<br>(104) |
| overall total: | 100.1%<br>(246) | 100.0%<br>(272) | 100.0%<br>(182) | 100.0%<br>(700) |

TABLE 3.2: SEX-DIFFERENCES IN INVOLVEMENT IN PLAY:

(Percentages are of the total no. of bouts shown in each age-period, combining the data for all three Litters. "M" = males; "F" = females; "A1" = initiator; "A2" = recipient; "Chi Sq." = Chi-Squared test on whether the observed frequencies of play within and between the sexes in each age-period differ significantly from the frequencies which would be expected by chance; all tests have 3 df. First figure within brackets represents the observed frequency on which the percentage is based. Second figure within brackets represents the expected frequency of the type of interaction in question, allowing for the fact that the probabilities of within- and between-sex play are different - for details see text).

| | MA1-MA2 | FA1-FA2 | MA1-FA2 | FA1-MA2 | Chi-Sq. |
|---|---|---|---|---|---|
| 21-30: | 33.8%<br>(38,30) | 2.9%<br>(25,30) | 33.8%<br>(48,45) | 29.4%<br>(39,45) | 3.97<br>n.s. |
| 31-40: | 53.5%<br>(55,35) | 4.2%<br>(32,35) | 19.7%<br>(48,53) | 22.5%<br>(41,53) | 14.87<br>P<0.01 |
| 41-50: | 42.3%<br>(64,54) | 19.2%<br>(37,54) | 19.2%<br>(103,81) | 19.2%<br>(66,81) | 15.96<br>P<0.01 |
| 51-60: | 17.6%<br>(22,21) | 11.8%<br>(25,21) | 47.1%<br>(39,31) | 23.5%<br>(18,31) | 8.33,<br>P<0.05 |
| 21-60: | 25.6%<br>(179,140) | 17.0%<br>(119,140) | 34.0%<br>(238,210) | 23.4%<br>(164,210) | 27.82<br>p<0.001 |

A Chi-squared test was performed to determine whether these observed frequencies differed from those which would be expected by chance. (Note that, in calculating the expected frequencies, allowance had to be made for the fact that between-sex play was more likely to occur than within-sex play simply as a function of chance, since a given individual had a choice of three opposite-sex partners with which to play, but only two like-sex partners). This revealed that, taking the frequency of play over the whole of the 21-60 day observation-period, there were significant differences between the sexes in their involvement in play (Chi-Squared = 27.82, 3 df; $p<0.001$).

Inspection of Table 3.2 reveals that males initiated play with each other and with females more frequently than would be expected by chance. Conversely, females initiated play with each other and with males less frequently than chance would predict. The net result of this was that males were involved in more play-bouts than females: the former were involved in 81.9% of all play, whereas the latter were involved in 73.3%.

3.3.1.3: Age x Sex differences in the number of bouts observed:

Table 3.2 also shows the number of play-bouts performed by each category of interactant (male-male, female-female, male-female, female-male) in each of the four age-periods studied, combining data from the three

litters studied. The results of Chi-squared tests on these frequencies are also shown.

These figures suggest that the overall pattern described in the previous section was a fairly consistent feature of playful interactions in all four age periods. At all ages - though not significantly so between 21-30 days - males initiated a greater number of bouts with each other and with females than would be expected by chance, and females initiated less play either with males or with other females. The one exception was that play between females occurred at higher than expected levels between 51-60 days.

### 3.3.2: Duration of play-bouts:

#### 3.3.2.1: Overall Duration of Play :

Ignoring age and sex differences, the median overall duration of play-bouts was 11.1 seconds, with an inter-quartile range of 15.3 seconds. As the latter figure suggests, there was wide variation in the duration of bouts, from a minimum of 1.1 seconds to a maximum of 149 seconds.

Since the variation in bout-durations is so large, it is more informative to look at the frequency-distribution of different bout-lengths. Figure 3.1 shows the overall bout-length distribution for all three litters combined, grouping bout-lengths into 10-second blocks. This reveals that the majority of bouts were short. Nearly half (46.4%)

FIG.3.1: FREQUENCY-DISTRIBUTION OF PLAY-BOUT DURATIONS
(21-60 DAYS, MALES AND FEMALES COMBINED: NO.BOUTS = 700)

FIG.3.2: LOG SURVIVORSHIP PLOT OF PLAY-BOUT DURATIONS
(MALES AND FEMALES COMBINED, 21-60 DAYS: (NO.OF BOUTS =700)

of bouts lasted 10 seconds or less; over a quarter (26.7%) were between 11 and 20 seconds long; and 12.7% lasted between 21 and 30 seconds. Only 14.1% of bouts lasted longer than 30 seconds.

Whilst grouping the bout-durations into 10-second blocks serves to emphasise the brevity of most play-bouts, it should not be thought that these categories represent any natural discontinuities in the data, ie that the distribution of durations is actually step-like. To examine the actual distribution of bout-durations, a cumulative frequency graph was plotted of the number of bouts surviving to a length of one second, two seconds, etc., and a regression line fitted (Fig. 3.2). If the termination of play-bouts were randomly determined the regression line would be a straight line. Conversely, non-linearity would imply that termination of play was not random, but was more likely at a particular point in time than at others. Fig. 3.2 suggests that, when bout-durations are considered across all ages and regardless of sex, termination of play-bouts is a random process.

3.3.2.2: Age-differences in the duration of play :

Table 3.3 (a) shows the medians, inter-quartile ranges and absolute ranges of play-bout durations for each of the four age-periods studied, combining the data for both sexes. There were no systematic age-differences in the median durations of play-bouts, especially when one

TABLE 3.3: AGE-CHANGES IN DURATION OF PLAY-BOUTS (MALES AND FEMALES COMBINED):

(a) Median duration of play-bouts in each age-period:

| | AGE-PERIOD (DAYS) | | | |
|---|---|---|---|---|
| | 21-30 | 31-40 | 41-50 | 51-60 |
| Median duration: | 11.4 | 11.7 | 10.4 | 10.4 |
| Inter-quartile range: | 16.2 | 16.7 | 12.8 | 14.8 |
| Number of bouts: | 150 | 176 | 270 | 104 |
| Minimum duration: | 1.1 | 1.7 | 2.0 | 1.7 |
| Maximum duration: | 78.3 | 115.9 | 149.0 | 78.6 |

3.3(b): Frequency distribution of play-bout lengths, in each age-period:

(Percentages are of the total number of play-bouts analysed for each age-period; bracketed figures represent the raw totals on which the percentages are based. All durations are in seconds).

| Number of bouts with durations of: | AGE-PERIOD (DAYS) 21-30 | 31-40 | 41-50 | 51-60 |
|---|---|---|---|---|
| under 10 s: | 46.0% (69) | 43.2% (76) | 47.8% (129) | 49.0% (51) |
| 11-20 s: | 24.7% (37) | 26.7% (47) | 28.9% (78) | 24.0% (25) |
| 21-30 s: | 14.0% (21) | 11.9% (21) | 13.0% (35) | 11.5% (12) |
| 31-40 s: | 8.0% (12) | 9.7% (17) | 3.7% (10) | 10.6% (11) |
| 41-50 s: | 2.0% (3) | 3.4% (6) | 3.0% (8) | 1.0% (1) |
| 51-60 s: | 1.3% (2) | 0.6% (1) | 1.5% (4) | 2.9% (3) |
| 61-70 s: | 1.3% (2) | 2.3% (4) | 1.1% (3) | 0.0% (0) |
| 71-80 s: | 2.7% (4) | 1.7% (3) | 0.4% (1) | 1.0% (1) |
| 81-90 s: | 0.0% (0) | 0.0% (0) | 0.4% (1) | 0.0% (0) |
| 91-100 s: | 0.0% (0) | 0.0% (0) | 0.0% (0) | 0.0% (0) |
| over 100 s: | 0.0% (0) | 0.6% (1) | 0.4% (1) | 0.0% (0) |

considers the large ranges involved.

Table 3.3 (b) shows age-related variations in the frequency distribution of different bout-lengths, again combining the data across sexes. This reveals that there were no consistent age-changes in the distribution of bout-durations; ie, there was no tendency for there to be a greater proportion of shorter than longer bouts (or vice-versa) at any particular stage in ontogeny.

3.3.2.3: Sex-differences in the duration of play:

Table 3.4 (a) shows the medians, inter-quartile ranges and absolute ranges of the duration of play-bouts within and between the sexes, combining the data over the whole of the 21-60 age-period. The median duration of male-male play was 15.3 seconds; this was somewhat higher than the medians for the other three categories of interactant (ie, all those in which females were involved), which ranged from 9.7 to 11.6 seconds. There are considerable ranges accompanying these figures, however.

An examination of the frequency-distribution of these data, shown in table 3.4 (b), suggests that these sex-differences result from the fact that there was a different pattern of bout-durations for play between males, compared to play involving females (whether between females, or between males and females). There appears to be little difference between male-male play and the other categories of player in the proportion of bouts lasting

TABLE 3.4: SEX-DIFFERENCES IN DURATION OF PLAY-BOUTS (OVERALL, 21-60 DAYS):

(a) Median duration of play-bouts, according to sex of interactants:

("M" = males, "F" = females, "A1" = initiator, "A2" = recipient)

| | SEX OF PLAYERS | | | |
|---|---|---|---|---|
| | MA1-MA2 | FA1-FA2 | MA1-FA2 | FA1-MA2 |
| Median duration: | 15.3 | 11.6 | 9.7 | 10.2 |
| Inter-quartile range: | 19.4 | 15.3 | 12.2 | 14.1 |
| Number of bouts: | 179 | 119 | 238 | 164 |
| Minimum duration: | 2.1 | 1.7 | 1.1 | 2.3 |
| Maximum duration: | 149.0 | 87.9 | 70.1 | 115.9 |

3.4(b): Frequency distribution of play-bout lengths, according to sex of interactants:

(Percentages are of the total number of play-bouts analysed for each age-period, for each category of interactants; bracketed figures represent the raw totals on which the percentages are based. All durations are in seconds).

| Number of bouts with durations of: | SEX OF PLAYERS: | | | |
|---|---|---|---|---|
| | MA1-MA2 | FA1-FA2 | MA1-FA2 | FA1-MA2 |
| under 10 s: | 36.3% (65) | 47.1% (56) | 51.7% (123) | 49.4% (81) |
| 11-20 s: | 25.1% (45) | 25.2% (30) | 28.1% (67) | 27.4% (45) |
| 21-30 s: | 17.3% (31) | 14.3% (17) | 10.9% (26) | 9.1% (15) |
| 31-40 s: | 11.7% (21) | 5.9% (7) | 5.9% (14) | 4.9% (8) |
| 41-50 s: | 2.2% (4) | 3.4% (4) | 1.2% (3) | 4.3% (7) |
| 51-60 s: | 0.6% (1) | 2.5% (3) | 0.8% (2) | 2.4% (4) |
| 61-70 s: | 2.8% (5) | 0.8% (1) | 0.8% (2) | 0.6% (1) |
| 71-80 s: | 3.3% (6) | 0.0% (0) | 0.4% (1) | 1.2% (2) |
| 81-90 s: | 0.0% (0) | 0.8% (1) | 0.0% (0) | 0.0% (0) |
| 91-100 s: | 0.0% (0) | 0.0% (0) | 0.0% (0) | 0.0% (0) |
| over 100 s: | 0.6% (1) | 0.0% (0) | 0.0% (0) | 0.6% (1) |

for between 11-20 seconds. However when males played together, rather than with females, they showed a higher proportion of bouts lasting between 21-40 seconds (and especially between 31-40 seconds), and a correspondingly lower percentage of bouts lasting under 10 seconds. When females participated in play, there was a higher proportion of bouts lasting under 10 seconds, and fewer bouts lasting over 31 seconds. Nearly 12% of bouts between males lasted for between 31-40 seconds, compared to only 5-6% of play involving females. There appear to be few sex-differences in the frequencies with which play-bouts lasted for anything over 40 seconds, but bouts of this length appear to be relatively unusual in any case.

3.3.2.4: Age x Sex differences in the duration of play:

Table 3.5 (a) shows the median, inter-quartile range and absolute range of bout-durations of MM, MF, FF and FM play-bouts in each of the four ageblocks studied, and table 3.5 (b) displays the corresponding frequency distributions of bout-lengths. Due to the considerable variation in duration of the play shown by each category of interactant, and the differing numbers of bouts available for calculating each age by sex distribution, it is difficult to draw firm conclusions from these data.

With some fluctuations, the duration of male-male play in all age-periods appears to be somwehat longer than

TABLE 3.5: AGE-RELATED SEX-DIFFERENCES IN DURATION OF PLAY-BOUTS:

(a) Age-changes in median duration of play-bouts, according to sex of interactants:

("M" = males, "F" = females, "A1" = initiator, "A2" = recipient. "IQR" = inter-quartile range. All medians and IQR's are in seconds. "N" = number of bouts performed between individuals of the sexes concerned, in the age-period concerned).

| | | SEXES OF PLAYERS | | | |
|---|---|---|---|---|---|
| | | MA1-MA2 | FA1-FA2 | MA1-FA2 | FA1-MA2 |
| 21-30 days: | Median: | 15.9 | 12.0 | 8.2 | 10.2 |
| | IQR: | 19.2 | 12.8 | 7.1 | 16.2 |
| | N: | 38 | 25 | 48 | 39 |
| 31-40 days: | Median: | 22.5 | 8.6 | 11.1 | 11.5 |
| | IQR: | 25.9 | 10.9 | 11.6 | 13.0 |
| | N: | 55 | 32 | 48 | 41 |
| 41-50 days: | Median: | 12.1 | 12.6 | 9.0 | 9.1 |
| | IQR: | 10.7 | 16.5 | 13.2 | 12.6 |
| | N: | 64 | 37 | 103 | 66 |
| 51-60 days: | Median: | 16.4 | 9.6 | 10.1 | 9.5 |
| | IQR: | 15.5 | 11.1 | 14.5 | 12.4 |
| | N: | 22 | 25 | 39 | 18 |

3.5(b): Age-changes in the frequency distribution of play-bout lengths, according to sex of interactants:

(Percentages are of the total number of play-bouts analysed for each age-period, for each permutation of players' sexes; bracketed figures represent the raw totals on which the percentages are based)

| | SEXES OF INTERACTANTS | | | |
|---|---|---|---|---|
| | MA1-MA2 | FA1-FA2 | MA1-FA2 | FA1-MA2 |
| **21-30 days:** | | | | |
| under 10 secs: | 34.2% (13) | 40.0% (10) | 56.3% (27) | 48.7% (19) |
| 11-20 secs: | 23.7% (9) | 28.0% (7) | 27.1% (13) | 20.5% (8) |
| 21-30 secs: | 21.0% (8) | 20.0% (5) | 6.3% (3) | 12.8% (5) |
| 31-40 secs: | 10.5% (4) | 8.0% (2) | 4.2% (2) | 10.3% (4) |
| 41-50 secs: | 0.0% (0) | 0.0% (0) | 2.1% (1) | 5.1% (2) |
| over 50 secs: | 10.5% (4) | 4.0% (1) | 4.2% (2) | 2.6% (1) |
| **31-40 days:** | | | | |
| under 10 secs: | 30.9% (17) | 53.1% (17) | 47.9% (23) | 46.3% (19) |
| 11-20 secs: | 16.4% (9) | 21.9% (7) | 35.4% (17) | 34.2% (14) |
| 21-30 secs: | 21.8% (12) | 12.5% (4) | 6.3% (3) | 4.9% (2) |
| 31-40 secs: | 20.0% (11) | 3.1% (1) | 6.3% (3) | 4.9% (2) |
| 41-50 secs: | 3.6% (2) | 6.3% (2) | 2.1% (1) | 2.4% (1) |
| over 50 secs: | 7.2% (4) | 3.1% (1) | 2.1% (1) | 7.3% (3) |

3.5(b) continued:

| | SEXES OF INTERACTANTS | | | |
|---|---|---|---|---|
| | MA1-MA2 | FA1-FA2 | MA1-FA2 | FA1-MA2 |
| **41-50 days:** | | | | |
| under 10 secs: | 40.6% (26) | 40.5% (15) | 52.4% (54) | 51.5% (34) |
| 11-20 secs: | 35.9% (23) | 29.7% (11) | 26.2% (27) | 25.8% (17) |
| 21-30 secs: | 9.4% (6) | 13.5% (5) | 16.5% (17) | 10.6% (7) |
| 31-40 secs: | 4.7% (3) | 8.1% (3) | 1.9% (2) | 3.0% (2) |
| 41-50 secs: | 3.1% (2) | 5.4% (2) | 1.0% (1) | 4.5% (3) |
| over 50 secs: | 6.2% (4) | 2.7% (1) | 1.9% (2) | 4.5% (3) |
| **51-60 days:** | | | | |
| under 10 secs: | 40.9% (9) | 56.0% (14) | 48.7% (19) | 50.0% (9) |
| 11-20 secs: | 18.2% (4) | 20.0% (5) | 25.6% (10) | 33.3% (6) |
| 21-30 secs: | 22.7% (5) | 12.0% (3) | 7.7% (3) | 5.6% (1) |
| 31-40 secs: | 13.6% (3) | 4.0% (1) | 17.9% (7) | 0.0% (0) |
| 41-50 secs: | 0.0% (0) | 0.0% (0) | 0.0% (0) | 5.6% (1) |
| over 50 secs: | 4.5% (1) | 8.0% (2) | 0.0% (0) | 5.6% (1) |

that of play involving females, especially between 31-40 days when male-male play had a median duration of 22.5 seconds. However, Kruskal-Wallis tests comparing the durations of MM, FF, MF and FM play, in each of the four age-periods, were statistically significant only for the first two age-periods (21-30 days: "H" = 9.347, $p<0.025$; 31-40 days: "H" = 12.426, $p<0.01$, both with 3 df) and not the last two (41-50 days: "H" = 3.826; 51-60 days, "H" = 1.841, both with 3 df and $p>.10$).

3.3.2.5: Summary:

These data suggest that, despite wide variation, play-bouts between young rats are essentially brief events, the majority (two-thirds) lasting less than 20 seconds. The probability of play ending appears to be randomly determined. No age-changes were found in the duration of play. There was however some evidence of sex-differences in the length of bouts; play between males tended to last somewhat longer than play bouts involving females, mainly due to the former category of interactant showing a higher proportion of bouts lasting between 31-40 seconds. These sex-differences were statistically significant only for the first two age-periods.

## 3.3.3: Percentage of "on top" behaviour in play:

### 3.3.3.1: Overall percentage of "on top" in play:

For each play-bout, a record was taken of the total amount of time that each interactant spent in beng "on top", ie, pinning down the play-partner by laying over him, or behaving in such a way as to move into this position. This procedure yielded two scores for each bout: the length of time within the bout that the initiator ("A1") of the play spent in the "on top" position, and a corresponding measure for the recipient ("A2") of the play. These figures were then converted into percentages of the total duration of the bout to which they belonged.

Table 3.6 shows the median, inter-quartile range, absolute range and frequency distribution of the percentage of play spent in the "on top" position by A1 and A2, considering all ageblocks and both sexes together.

These data reveal clearly that in the majority of bouts, the initiator was in the "on top" position for longer than the recipient of the play. A1 was on top for a median 70.4% of each bout, compared to only 7.9% for A2. As with the duration of play, there was wide variation in these figures, and an examination of the frequency distributions of on top behaviour for A1 and A2 is more informative. These show that nearly 70% (69.4%) of all

TABLE 3.6: OVERALL FREQUENCY OF "ON TOP" IN PLAY (MALES AND FEMALES COMBINED, 21-60 DAYS):

Median percentage of play spent in the "on top" position by the initiator and recipient:

| | Median: | IQR: | Minimum: | Maximum: |
|---|---|---|---|---|
| Initiator of play (A1): | 70.4 | 47.5 | 0.6 | 100.0 |
| Recipient of play (A2): | 7.9 | 36.1 | 0.0 | 99.5 |

Frequency distribution of the percentage of being on top during play:

(Percentages represent the frequency with which interactants were in the on-top position for the proportions of the bout duration specified on the left-hand side of the table; bracketed figures represent raw data).

| Percentage of play spent in on-top bvr: | Initiator: | Recipient: |
|---|---|---|
| 10% of bout or less: | 5.9% (41) | 52.1% (365) |
| 11-20% of bout: | 6.7% (47) | 9.3% (65) |
| 21-30% of bout: | 5.7% (40) | 7.9% (55) |
| 31-40% of bout: | 5.9% (41) | 7.7% (54) |
| 41-50% of bout: | 6.4% (45) | 5.0% (35) |
| 51-60% of bout: | 8.0% (56) | 4.9% (34) |
| 61-70% of bout: | 11.1% (78) | 4.4% (31) |
| 71-80% of bout: | 13.1% (92) | 3.6% (25) |
| 81-90% of bout: | 13.0% (91) | 3.6% (25) |
| 91-100% of bout: | 24.1% (169) | 1.6% (11) |
| 99% of bout or more: * | 14.6% (102) | 0.3% (2) |

(* Note that this frequency is a sub-set of the "91-100%" category)

bouts involved A1 being on top for over 50% of the time. In nearly a quarter of all play-bouts (24.1%), the initiator was on top for over 90% of the bout; and in 15% of all play (14.6%), the initiator was on top for 99% of the bout or more.

In contrast, the recipient of play was on top for more than 50% of the time in only 19.6% of all instances of play; and cases where the recipient immediately reversed the relationship between the two interactants and then remained on top for the rest of the encounter hardly ever occurred. In only 13 out of 700 bouts (1.9%) was A2 on top for more than 90% of the time, and only 2 bouts involved A2 being on top for more than 99% of the bout. In over half of all the bouts observed (52.1%), the recipient was on top for no more than 10% of the time - whereas the corresponding figure for the initiator was less than 6% of all observed bouts (5.9%).

Thus the overall picture presented by these data is that in the majority of instances of play, the initiator of a bout tended to remain on top during it, to a greater or lesser extent. Within a particular bout, there was little reciprocity in terms of who was in the on-top position.

3.3.3.2. Age-differences in percentage of "on-top" behaviour in play:

Table 3.7 (a) shows age-changes in the median, inter-quartile range and absolute range of the percentage

TABLE 3.7: AGE-CHANGES IN THE MEDIAN FREQUENCY OF "ON TOP" IN PLAY (MALES AND FEMALES COMBINED):

| | | PERCENTAGE OF BOUT SPENT IN ON-TOP POSITION: | | | | |
|---|---|---|---|---|---|---|
| Age-period: | | Median: | IQR: | No. bouts: | Min. | Max. |
| 21-30 DAYS: | A1 : | 66.2 | 50.7 | 150 | 1.9 | 100.0 |
| | A2 : | 12.0 | 38.7 | | 0.0 | 98.1 |
| 31-40 DAYS: | A1 : | 74.1 | 53.6 | 176 | 2.5 | 100.0 |
| | A2 : | 11.1 | 41.6 | | 0.0 | 97.1 |
| 41-50 DAYS: | A1 : | 69.9 | 42.8 | 270 | 0.6 | 100.0 |
| | A2 : | 6.7 | 35.4 | | 0.0 | 99.7 |
| 51-60 DAYS: | A1 : | 71.1 | 41.5 | 104 | 1.6 | 100.0 |
| | A2 : | 0.0 | 25.4 | | 0.0 | 99.0 |

TABLE 3.8: AGE-CHANGES IN THE FREQUENCY DISTRIBUTION OF "ON TOP" IN PLAY (MALES AND FEMALES COMBINED):

(Percentages represent the frequency with which interactants were in the on-top position for the proportions of the bout duration specified on the left-hand side of the table; bracketed figures represent raw data).

(a) Percentage of play spent in on-top position by the initiator of play:

| | Age-period: 21-30: | 31-40: | 41-50: | 51-60: |
|---|---|---|---|---|
| <10%: | 6.7% (10) | 6.8% (12) | 5.2% (14) | 4.8% (5) |
| 11-20%: | 5.3% (8) | 4.0% (7) | 8.2% (22) | 9.6% (10) |
| 21-30%: | 6.0% (9) | 7.4% (13) | 5.6% (15) | 2.9% (3) |
| 31-40%: | 7.3% (11) | 8.5% (15) | 4.1% (11) | 3.9% (4) |
| 41-50%: | 8.7% (13) | 4.0% (7) | 7.4% (20) | 4.8% (5) |
| 51-60%: | 8.0% (12) | 9.1% (16) | 7.0% (19) | 8.7% (9) |
| 61-70%: | 12.0% (18) | 6.3% (11) | 13.0% (35) | 13.5% (14) |
| 71-80%: | 10.7% (16) | 14.8% (26) | 14.8% (40) | 9.6% (10) |
| 81-90%: | 10.7% (16) | 10.2% (18) | 14.4% (39) | 17.3% (18) |
| 91-100%: | 24.7% (37) | 29.0% (51) | 20.4% (41) | 25.0% (26) |
| * 99% or more: | 10.0% (15) | 17.6% (31) | 13.3% (36) | 19.2% (20) |

(* Note that this frequency is a sub-set of the "91-100%" category)

(b) Percentage of play spent in on-top position by the recipient of play:

| | Age-period: 21-30: | 31-40: | 41-50: | 51-60: |
|---|---|---|---|---|
| <10%: | 44.7% (64) | 47.2% (83) | 54.1% (146) | 66.4% (69) |
| 11-20%: | 13.3% (20) | 8.5% (15) | 9.3% (25) | 4.8% (5) |
| 21-30%: | 8.0% (12) | 7.4% (13) | 7.0% (19) | 10.6% (11) |
| 31-40%: | 10.7% (16) | 10.2% (18) | 6.7% (18) | 1.9% (2) |
| 41-50%: | 7.3% (11) | 6.3% (11) | 3.3% (9) | 3.9% (4) |
| 51-60%: | 4.0% (6) | 5.7% (10) | 5.2% (14) | 3.9% (4) |
| 61-70%: | 4.0% (6) | 5.7% (10) | 4.8% (13) | 1.9% (2) |
| 71-80%: | 2.7% (4) | 4.0% (7) | 4.4% (12) | 1.9% (2) |
| 81-90%: | 3.3% (5) | 2.9% (5) | 4.1% (11) | 3.9% (4) |
| 91-100%: | 2.0% (3) | 2.3% (4) | 1.1% (3) | 1.0% (1) |
| * 99% or more: | 0.0% (0) | 0.0% (0) | 0.4% (1) | 1.0% (1) |

(* Note that this frequency is a sub-set of the "91-100%" category)

of on-top behaviour performed by A1 and A2 during play, combining the data from all sex-categories of interactant. Tables 3.8(a) and 3.8(b) display the associated frequency-distributions of being in the on-top position, for A1 and A2 respectively.

There were no systematic age-changes in the median percentages of on-top behaviour shown by A1 during play, the medians for all age-periods fluctuating around the overall 70% figure. The percentages of on-top behaviour shown by A2 did show a small but consistent decrease with age, however. Although both of these sets of figures were associated with large ranges, an examination of the frequency-distributions underlying these data (shown in table 3.8(a) and 3.8(b)) confirms the picture provided by the medians.

Table 3.8 (a) shows that there were few age-related changes in the frequency distribution of the various percentage categories of A1 being on top, except that with increasing age there was some increase in the relative frequency of bouts in which A1 was on top for between 81-90% of the time. Table 3.8 (b) suggests that, over the four age-periods studied, there was an increase in the proportion of play-bouts in which A2 was on top for less than 10% of the time, and a concomitant decrease in the proportions of bouts in which A2 occupied the on top position for larger percentages (11-20%, 31-40%) of play.

In short, with increasing age there was some suggestion of a trend for A1 to be on top during play for

TABLE 3.9: OVERALL SEX-DIFFERENCES IN THE MEDIAN FREQUENCY OF "ON TOP" IN PLAY (21-60 DAYS):

(a) Sex-differences in the overall (21-60 days) median percentage of play spent in the "on top" position by the initiator and recipient:

("M" = males, "F" = females; "A1" = initiator of play, "A2" = recipient)

| Interactants' sexes: | | PERCENTAGE OF BOUT SPENT ON-TOP: Median: | IQR: | N: | Minimum: | Maximum: |
|---|---|---|---|---|---|---|
| MA1-MA2: | A1 : | 65.9 | 57.9 | 179 | 2.5 | 100.0 |
| | A2 : | 13.9 | 43.4 | | 0.0 | 97.1 |
| FA1-FA2: | A1 : | 73.1 | 42.9 | 119 | 2.7 | 100.0 |
| | A2 : | 5.7 | 32.3 | | 0.0 | 99.7 |
| MA1-FA2: | A1 : | 72.6 | 37.7 | 238 | 1.6 | 100.0 |
| | A2 : | 0.0 | 30.2 | | 0.0 | 99.0 |
| FA1-MA2: | A1 : | 65.7 | 57.8 | 164 | 0.6 | 100.0 |
| | A2 : | 13.2 | 44.1 | | 0.0 | 98.1 |

3.9(b): Sex-differences in the overall (21-60 days) frequency distribution of different percentages of "on-top" behaviour by the initiator and recipient:

(i) Percentage of on-top behaviour by initiators of play:

| | Sexes of interactants: | | | |
|---|---|---|---|---|
| | MA1-MA2 | FA1-FA2 | MA1-FA2 | FA1-MA2 |
| <10%: | 7.3% (13) | 4.2% (5) | 4.2% (10) | 7.9% (13) |
| 11-20%: | 7.3% (13) | 5.0% (6) | 4.2% (10) | 11.0% (18) |
| 21-30%: | 6.7% (12) | 5.0% (6) | 5.9% (14) | 4.9% (8) |
| 31-40%: | 7.3% (13) | 5.9% (7) | 3.4% (8) | 7.9% (13) |
| 41-50%: | 3.9% (7) | 5.9% (7) | 7.6% (18) | 7.9% (13) |
| 51-60%: | 9.5% (17) | 9.2% (11) | 6.7% (16) | 7.3% (12) |
| 61-70%: | 11.7% (21) | 13.4% (16) | 13.9% (33) | 4.9% (8) |
| 71-80%: | 11.2% (20) | 11.8% (14) | 15.6% (37) | 12.8% (21) |
| 81-90%: | 10.1% (18) | 15.1% (18) | 16.0% (38) | 10.4% (17) |
| 91-100%: | 25.1% (45) | 24.4% (29) | 22.7% (54) | 25.0% (41) |
| * 99% or more: | 14.5% (26) | 14.3% (17) | 15.6% (37) | 13.4% (22) |

(* Note that this frequency is a sub-set of the "91-100%" category)

(ii) Percentage of on-top behaviour by recipients of play:

| | Sexes of interactants: | | | |
|---|---|---|---|---|
| | MA1-MA2 | FA1-FA2 | MA1-FA2 | FA1-MA2 |
| <10%: | 43.6% (78) | 54.6% (65) | 61.8% (147) | 45.7% (75) |
| 11-20%: | 11.7% (21) | 12.6% (15) | 6.7% (16) | 7.9% (13) |
| 21-30%: | 9.5% (17) | 7.7% (9) | 5.9% (14) | 9.1% (15) |
| 31-40%: | 8.4% (15) | 6.7% (8) | 8.8% (21) | 6.1% (10) |
| 41-50%: | 5.6% (10) | 3.4% (4) | 2.5% (6) | 9.1% (15) |
| 51-60%: | 5.6% (10) | 4.2% (5) | 4.2% (10) | 5.5% (9) |
| 61-70%: | 6.7% (12) | 5.0% (6) | 2.5% (6) | 4.3% (7) |
| 71-80%: | 3.9% (7) | 2.5% (3) | 3.8% (9) | 3.7% (6) |
| 81-90%: | 3.3% (6) | 2.5% (3) | 2.9% (7) | 5.5% (9) |
| 91-100%: | 1.7% (3) | 0.8% (1) | 0.8% (2) | 3.0% (5) |
| * 99% or more: | 0.0% (0) | 0.8% (1) | 0.4% (1) | 0.0% (0) |

(* Note that this frequency is a sub-set of the "91-100%" category)

a greater percentage of the bout, and stronger evidence of a tendency for A2 to be on top for smaller percentages of the bout; however, neither of these effects was very marked, when the large variations in on-top behaviour are taken into account.

3.3.3.3: Sex-differences in the percentage of "on-top" behaviour:

Table 3.9 (a) shows the median frequencies of on-top behaviour in relation to the sex of the interactants, taking all age-periods together. The overall pattern described previously, with A1 on-top for approximately two-thirds of the bout and A2 on-top for a quarter of the bout, appears to hold regardless of whether play was within or between the sexes. This absence of sex-differences also appears to apply to the overall frequency-distributions of the percentage of play spent in the on-top position, broken down in table 3.9 (b) according to the players' sexes.

3.3.3.4: Age x sex differences in the percentage of "on-top" behaviour:

Table 3.10 shows the median percentage of on-top behaviour shown by the initiator and recipient in male-male, female-female, male-female and female-male play, in each of the four age-periods studied. Table 3.11 gives the frequency-distributions of on-top behaviour, broken down by sex of interactant for each of

TABLE 3.10: AGE-RELATED SEX-DIFFERENCES IN MEDIAN PERCENTAGE OF "ON-TOP" BEHAVIOUR IN PLAY:

(Figures preceding brackets are medians; bracketed figures are inter-quartile ranges. All medians and IQR's refer to the percentage of time interactants spent in the "on-top" position during play-bouts within the age-period concerned. "N" = number of bouts performed between individuals of the sexes concerned, in the age-period concerned).

(a) Male initiator with male recipient:

| | Age-period: | | | |
|---|---|---|---|---|
| | 21-30: | 31-40: | 41-50: | 51-60: |
| A1: | 65.7 (52.0) | 65.9 (68.1) | 64.4 (49.5) | 78.5 (44.3) |
| A2: | 12.4 (43.2) | 22.2 (51.2) | 19.0 (44.6) | 0.0 (20.5) |
| N: | 38 | 55 | 64 | 22 |

(b) Female initiator with female recipient:

| | Age-period: | | | |
|---|---|---|---|---|
| | 21-30: | 31-40: | 41-50: | 51-60: |
| A1: | 65.9 (42.3) | 74.7 (46.8) | 75.6 (41.3) | 76.2 (28.7) |
| A2: | 12.3 (26.1) | 11.7 (35.3) | 5.2 (45.2) | 0.0 (5.7) |
| N: | 25 | 32 | 37 | 25 |

(c) Male initiator with female recipient:

| | Age-period: | | | |
|---|---|---|---|---|
| | 21-30: | 31-40: | 41-50: | 51-60: |
| A1: | 69.1 (40.1) | 76.0 (46.3) | 71.5 (33.4) | 76.7 (34.3) |
| A2: | 8.5 (33.7) | 2.0 (32.9) | 0.0 (25.9) | 0.0 (14.4) |
| N: | 48 | 48 | 103 | 39 |

(d) Female initiator with male recipient:

| | Age-period: | | | |
|---|---|---|---|---|
| | 21-30: | 31-40: | 41-50: | 51-60: |
| A1: | 55.9 (62.9) | 72.0 (46.1) | 72.8 (57.4) | 40.4 (57.8) |
| A2: | 27.1 (46.6) | 13.8 (42.4) | 8.5 (41.1) | 28.5 (44.0) |
| N: | 39 | 41 | 66 | 18 |

TABLE 3.11: AGE-RELATED SEX DIFFERENCES IN THE FREQUENCY DISTRIBUTION OF "ON TOP" IN PLAY:

(Percentages represent the frequency with which interactants were in the on-top position for the proportions of the bout duration specified on the left-hand side of the table; bracketed figures represent raw data. Note that in all cases the "99% or more" category is a sub-set of the "91-100%" category; all other categories are mutually exclusive).

(a) Male-male play (MA1-MA2):

(i) Percentage of play spent in on-top position by the initiator of play between males:

| Percentage on-top: | Age-period: 21-30: | | 31-40: | | 41-50: | | 51-60: | |
|---|---|---|---|---|---|---|---|---|
| <10%: | 0.0% | (0) | 12.7% | (7) | 9.4% | (6) | 0.0% | (0) |
| 11-20%: | 5.3% | (2) | 7.3% | (4) | 9.4% | (6) | 4.5% | (1) |
| 21-30%: | 10.5% | (4) | 5.4% | (3) | 4.7% | (3) | 9.1% | (2) |
| 31-40%: | 10.5% | (4) | 9.1% | (5) | 6.3% | (4) | 0.0% | (0) |
| 41-50%: | 5.3% | (2) | 0.0% | (0) | 4.7% | (3) | 9.1% | (2) |
| 51-60%: | 7.9% | (3) | 10.9% | (6) | 7.8% | (5) | 13.6% | (3) |
| 61-70%: | 13.2% | (5) | 5.4% | (3) | 20.3% | (13) | 0.0% | (0) |
| 71-80%: | 10.5% | (4) | 7.3% | (4) | 14.1% | (9) | 13.6% | (3) |
| 81-90%: | 13.2% | (5) | 7.3% | (4) | 6.3% | (4) | 22.7% | (5) |
| 91-100%: | 23.7% | (9) | 34.5% | (19) | 17.2% | (11) | 27.3% | (6) |
| >99%: | 13.2% | (5) | 20.0% | (11) | 7.8% | (5) | 22.7% | (5) |

(ii) Percentage of play spent in on-top position by the recipient of play in play between males:

| Percentage on-top: | Age-period: 21-30: | | 31-40: | | 41-50: | | 51-60: | |
|---|---|---|---|---|---|---|---|---|
| <10%: | 39.5% | (15) | 45.4% | (25) | 35.9% | (23) | 68.2% | (15) |
| 11-20% | 21.1% | (8) | 3.6% | (2) | 15.6% | (10) | 4.5% | (1) |
| 21-30% | 2.6% | (1) | 7.3% | (4) | 10.9% | (7) | 22.7% | (5) |
| 31-40% | 7.9% | (3) | 10.9% | (6) | 9.4% | (6) | 0.0% | (0) |
| 41-50% | 13.2% | (5) | 5.4% | (3) | 3.1% | (2) | 0.0% | (0) |
| 51-60% | 2.6% | (1) | 5.4% | (3) | 9.4% | (6) | 0.0% | (0) |
| 61-70% | 10.5% | (4) | 5.4% | (3) | 6.3% | (4) | 4.5% | (1) |
| 71-80% | 2.6% | (1) | 9.1% | (5) | 1.6% | (1) | 0.0% | (0) |
| 81-90% | 0.0% | (0) | 3.6% | (2) | 6.3% | (4) | 0.0% | (0) |
| 91-100% | 0.0% | (0) | 3.6% | (2) | 1.6% | (1) | 0.0% | (0) |
| >99% | 0.0% | (0) | 0.0% | (0) | 0.0% | (0) | 0.0% | (0) |

3.11(b): Female-female play (FA1-FA2):

(i) Percentage of play spent in on-top position by the initiator of play between females:

| Percentage on-top: | Age-period: 21-30: | | 31-40: | | 41-50: | | 51-60: | |
|---|---|---|---|---|---|---|---|---|
| <10% | 8.0% | (2) | 6.3% | (2) | 2.7% | (1) | 0.0% | (0) |
| 11-20% | 8.0% | (2) | 0.0% | (0) | 5.4% | (2) | 8.0% | (2) |
| 21-30% | 4.0% | (1) | 9.4% | (3) | 5.4% | (2) | 0.0% | (0) |
| 31-40% | 4.0% | (1) | 6.3% | (2) | 5.4% | (2) | 8.0% | (2) |
| 41-50% | 12.0% | (3) | 3.1% | (1) | 8.1% | (3) | 0.0% | (0) |
| 51-60% | 4.0% | (1) | 12.5% | (4) | 10.8% | (4) | 8.0% | (2) |
| 61-70% | 20.0% | (5) | 6.3% | (2) | 8.1% | (3) | 24.0% | (6) |
| 71-80% | 8.0% | (2) | 21.9% | (7) | 10.8% | (4) | 4.0% | (1) |
| 81-90% | 8.0% | (2) | 9.4% | (3) | 18.9% | (7) | 24.0% | (6) |
| 91-100% | 24.0% | (6) | 25.0% | (8) | 24.3% | (9) | 24.0% | (6) |
| >99% | 8.0% | (2) | 15.6% | (5) | 16.2% | (6) | 16.0% | (4) |

(ii) Percentage of play spent in on-top position by the recipient of play in play between females:

| Percentage on-top: | Age-period: 21-30: | | 31-40: | | 41-50: | | 51-60: | |
|---|---|---|---|---|---|---|---|---|
| <10%: | 44.0% | (11) | 40.6% | (13) | 59.5% | (22) | 76.0% | (19) |
| 11-20%: | 16.0% | (4) | 21.9% | (7) | 5.4% | (2) | 8.0% | (2) |
| 21-30% | 16.0% | (4) | 6.3% | (2) | 5.4% | (2) | 4.0% | (1) |
| 31-40% | 12.0% | (3) | 9.4% | (3) | 2.7% | (1) | 4.0% | (1) |
| 41-50% | 0.0% | (0) | 3.1% | (1) | 8.1% | (3) | 0.0% | (0) |
| 51-60% | 4.0% | (1) | 3.1% | (1) | 5.4% | (2) | 0.0% | (0) |
| 61-70% | 4.0% | (1) | 9.4% | (3) | 5.4% | (2) | 0.0% | (0) |
| 71-80% | 4.0% | (1) | 3.1% | (1) | 2.7% | (1) | 0.0% | (0) |
| 81-90% | 0.0% | (0) | 3.1% | (1) | 2.7% | (1) | 4.0% | (1) |
| 91-100% | 0.0% | (0) | 0.0% | (0) | 2.7% | (1) | 0.0% | (0) |
| >99% | 0.0% | (0) | 0.0% | (0) | 2.7% | (1) | 0.0% | (0) |

3.11(c): Male-female play (MA1-FA2):

(i) Percentage of play spent in on-top position by male initiators of between-sex play:

| Percentage on-top: | Age-period: 21-30: | | 31-40: | | 41-50: | | 51-60: | |
|---|---|---|---|---|---|---|---|---|
| <10% | 4.2% | (2) | 2.1% | (1) | 2.9% | (3) | 10.3% | (4) |
| 11-20% | 4.2% | (2) | 4.2% | (2) | 4.9% | (5) | 2.6% | (1) |
| 21-30% | 4.2% | (2) | 10.4% | (5) | 6.8% | (7) | 0.0% | (0) |
| 31-40% | 4.2% | (2) | 2.1% | (1) | 3.9% | (4) | 2.6% | (1) |
| 41-50% | 12.5% | (6) | 8.3% | (4) | 5.8% | (6) | 5.1% | (2) |
| 51-60% | 6.3% | (3) | 8.3% | (4) | 5.8% | (6) | 7.7% | (3) |
| 61-70% | 16.7% | (8) | 6.3% | (3) | 15.5% | (16) | 15.4% | (6) |
| 71-80% | 12.5% | (6) | 12.5% | (6) | 19.4% | (20) | 12.8% | (5) |
| 81-90% | 14.6% | (7) | 14.6% | (7) | 16.5% | (17) | 17.9% | (7) |
| 91-100% | 20.8% | (10) | 31.3% | (15) | 18.4% | (19) | 25.6% | (10) |
| >99% | 8.3% | (4) | 20.8% | (10) | 15.5% | (16) | 17.9% | (7) |

(ii) Percentage of play spent in on-top position by female recipients of between-sex play:

| Percentage on-top: | Age-period: 21-30: | | 31-40: | | 41-50: | | 51-60: | |
|---|---|---|---|---|---|---|---|---|
| <10% | 50.0% | (24) | 54.2% | (26) | 66.0% | (68) | 74.4% | (29) |
| 11-20% | 14.6% | (7) | 6.3% | (3) | 4.9% | (5) | 2.6% | (1) |
| 21-30% | 4.2% | (2) | 8.3% | (4) | 5.8% | (6) | 5.1% | (2) |
| 31-40% | 14.6% | (7) | 10.4% | (5) | 7.8% | (8) | 2.6% | (1) |
| 41-50% | 4.2% | (2) | 8.3% | (4) | 0.0% | (0) | 0.0% | (0) |
| 51-60% | 4.2% | (2) | 4.2% | (2) | 3.9% | (4) | 5.1% | (2) |
| 61-70% | 2.1% | (1) | 2.1% | (1) | 3.9% | (4) | 0.0% | (0) |
| 71-80% | 2.1% | (1) | 0.0% | (0) | 6.8% | (7) | 2.6% | (1) |
| 81-90% | 4.2% | (2) | 4.2% | (2) | 1.0% | (1) | 5.1% | (2) |
| 91-100% | 0.0% | (0) | 2.1% | (1) | 0.0% | (0) | 2.6% | (1) |
| >99% | 0.0% | (0) | 0.0% | (0) | 0.0% | (0) | 2.6% | (1) |

3.11(d): Female-male play (FA1-MA2):

(i) Percentage of play spent in on-top position by female initiators of between-sex play:

| Percentage on-top: | Age-period: 21-30: | | 31-40: | | 41-50: | | 51-60: | |
|---|---|---|---|---|---|---|---|---|
| <10% | 15.4% | (6) | 4.9% | (2) | 6.1% | (4) | 5.6% | (1) |
| 11-20% | 5.1% | (2) | 2.4% | (1) | 13.6% | (9) | 33.3% | (6) |
| 21-30% | 5.1% | (2) | 4.9% | (2) | 4.5% | (3) | 5.6% | (1) |
| 31-40% | 10.3% | (4) | 17.1% | (7) | 1.5% | (1) | 5.6% | (1) |
| 41-50% | 5.1% | (2) | 4.9% | (2) | 12.1% | (8) | 5.6% | (1) |
| 51-60% | 12.8% | (5) | 4.9% | (2) | 6.1% | (4) | 5.6% | (1) |
| 61-70% | 0.0% | (0) | 7.3% | (3) | 4.5% | (3) | 11.1% | (2) |
| 71-80% | 10.3% | (4) | 21.9% | (9) | 10.6% | (7) | 5.6% | (1) |
| 81-90% | 5.1% | (2) | 9.8% | (4) | 16.7% | (11) | 0.0% | (0) |
| 91-100% | 30.8% | (12) | 21.9% | (9) | 24.2% | (16) | 22.2% | (4) |
| 99% | 10.3% | (4) | 12.2% | (5) | 13.6% | (9) | 22.2% | (4) |

(ii) Percentage of play spent in on-top position by male recipients of between-sex play:

| Percentage on-top: | Age-period: 21-30: | | 31-40: | | 41-50: | | 51-60: | |
|---|---|---|---|---|---|---|---|---|
| <10% | 43.6% | (17) | 46.3% | (19) | 50.0% | (33) | 33.3% | (6) |
| 11-20% | 2.6% | (1) | 7.3% | (3) | 12.1% | (8) | 5.6% | (1) |
| 21-30% | 12.8% | (5) | 7.3% | (3) | 6.1% | (4) | 16.7% | (3) |
| 31-40% | 7.7% | (3) | 9.8% | (4) | 4.5% | (3) | 0.0% | (0) |
| 41-50% | 10.3% | (4) | 7.3% | (3) | 6.1% | (4) | 22.2% | (4) |
| 51-60% | 5.1% | (2) | 9.8% | (4) | 3.0% | (2) | 5.6% | (1) |
| 61-70% | 0.0% | (0) | 7.3% | (3) | 4.5% | (3) | 5.6% | (1) |
| 71-80% | 2.6% | (1) | 2.4% | (1) | 4.5% | (3) | 5.6% | (1) |
| 81-90% | 7.7% | (3) | 0.0% | (0) | 7.6% | (5) | 5.6% | (1) |
| 91-100% | 7.7% | (3) | 2.4% | (1) | 1.5% | (1) | 0.0% | (0) |
| >99% | 0.0% | (0) | 0.0% | (0) | 0.0% | (0) | 0.0% | (0) |

the four age-periods studied.

There appear to be some indications in these data of an age-related sex-difference in on-top behaviour. In the case of MM, FF and MF play, play appears to be more one-sided in the final age-period than at earlier ages, with A1 on top for approximately 75-80% of a bout, and A2 showing no on-top behaviour at all. Mixed-sex play initiated by females appears to show a different pattern, with females remaining on top for only 40% of a bout, and their male partners managing to get on top for nearly 30% of the time.

These data perhaps suggest that males (who were, by 51-60 days, noticeably bigger and heavier than females) were using their greater strength to resist being pinned down by a female partner, or in order to maintain their on-top position if they were pinning a female.

However, in interpreting these data,

One must take note of the large ranges accompanying each median. The net conclusion must therefore be that there are no marked age-related sex-differences in rat play.

3.3.3.5: Summary:

The main conclusions to be drawn from this section are that play-bouts displayed little evidence of reciprocity within a bout, in that the initiator of a

given instance of play tended to remain in the on-top position for most (roughly two-thirds) of the interaction. There were no major differences between the sexes in this respect when play was considered over all age-periods. However, there were some indications of age-related sex-differences in these data. Play-bouts appeared to become more one-sided in the final age-period (51-60 days): recipients of play at this age performed relatively little on-top behaviour within a play-bout, except in the case of female-male play, when male recipients performed a considerable proportion (30%) of on-top behaviour. These changes in play as a function of age and sex must be considered with great caution, however, since they were relatively small in comparison to the large ranges accompanying the data.

### 3.3.4: Role reversals within play:

The data of the previous section suggest that the initiator of a play bout tended to assume the on-top position for a high proportion of the total duration of that bout. However, these figures provide no information on how this on-top behaviour was arranged - ie, whether the initiator adopted the on-top position and remained there for one uninterrupted period of time, or whether there were numerous interchanges of position between the players but with the initiator merely tending to remain on top for longer whenever he was on top. Accordingly, in

TABLE 3.12: NUMBER OF ROLE REVERSALS WITHIN PLAY-BOUTS:

(a) Overall frequencies of role-reversals within play (21-60 days, males and females combined):

(percentages are of the total number of bouts observed)

| Number of role-reversals within a bout: | | | | | | | |
|---|---|---|---|---|---|---|---|
| none: | 1: | 2: | 3: | 4: | 5: | 6: | total: |
| 64.6% | 24.4% | 8.9% | 1.6% | 0.3% | 0.1% | 0.1% | 100.0% |
| (452) | (171) | (62) | (11) | (2) | (1) | (1) | (700) |

(b) Age-differences in the number of role reversals shown in play (male and females combined):

(percentages are of the total no.of bouts observed in each age-period)

| No.of rr's: | Age-period 21-30 | 31-40 | 41-50 | 51-60 |
|---|---|---|---|---|
| 0: | 62.0% (93) | 66.5% (117) | 61.8% (167) | 72.1% (75) |
| 1: | 27.3% (41) | 21.0% (37) | 27.0% (73) | 19.2% (20) |
| 2: | 5.3% (8) | 10.2% (18) | 10.4% (28) | 7.7% (8) |
| 3: | 4.0% (6) | 1.7% (3) | 0.4% (1) | 1.0% (1) |
| 4: | 0.7% (1) | 0.0% (0) | 0.4% (1) | 0.0% (0) |
| 5: | 0.0% (0) | 0.6% (1) | 0.0% (0) | 0.0% (0) |
| 6: | 0.7% (1) | 0.0% (0) | 0.0% (0) | 0.0% (0) |
| total: | 100.0% (150) | 100.0% (176) | 100.0% (270) | 100.0% (104) |

(c) Overall sex-differences in the number of role reversals shown in play (21-60 days):

(percentages are of the total no.of bouts observed for interactants of the sexes concerned, over the whole of the 21-60 day study-period)

| No.of rr's: | Sexes of interactants MA1-MA2: | FA1-FA2: | MA1-FA2: | FA1-MA2: |
|---|---|---|---|---|
| 0: | 58.1% (104) | 75.6% (90) | 70.6% (168) | 54.9% (90) |
| 1: | 29.0% (52) | 13.4% (16) | 19.7% (47) | 34.1% (56) |
| 2: | 11.7% (21) | 7.6% (9) | 8.0% (19) | 7.9% (13) |
| 3: | 0.6% (1) | 3.4% (4) | 0.8% (2) | 2.4% (4) |
| 4: | 0.0% (0) | 0.0% (0) | 0.8% (2) | 0.0% (0) |
| 5: | 0.0% (0) | 0.0% (0) | 0.0% (0) | 0.6% (1) |
| 6: | 0.6% (1) | 0.0% (0) | 0.0% (0) | 0.0% (0) |
| tot.: | 100.0% (179) | 100.0% (119) | 100.0 (238) | 100.0% (164) |

order to answer this question, a record was kept for each play-bout of the number of role reversals which occurred within it. A role reversal was defined as occurring when the animal on top during wrestling became the animal underneath.

3.3.4.1: Overall frequency of role reversals:

Table 3.12 (a) shows the relative frequency with which different numbers of role reversals were observed to occur within a play-bout, combining all age and sex classes. Approximately 65% of bouts showed no role reversals at all; 25% showed one reversal; and under 10% involved two reversals. The frequency with which three or more role reversals occurred was very small, comprising a mere 2% of all bouts (15 out of 700).

3.3.4.2: Age-differences in the number of role-reversals in play:

Table 3.12 (b) shows the frequency of 0, 1, 2 and 3 or more role reversals in each of the four age-periods, combining the data from males and females. There appear to be no systematic or marked age-changes in the number of role reversals which occurred within play; the pattern described in the previous section appears to hold true for each age-period considered separately.

3.3.4.3: Overall sex-differences in the number of role-reversals in play:

Table 3.12 (c) shows the relative frequencies with which role reversals were observed to occur in MM, FF, MF and FM play, combining the data for all age-periods. Again, the overall pattern was shown by each category of interactants. There do appear to be slight sex-differences, however, in the relative frequencies of occurrence of either one role reversal or none. Over 70% of female-female and male-female play showed no role-reversals in play. In contrast, in male-male and female-male play, there was a higher frequency of bouts involving one role reversal, and a corrspondingly lower frequency of play totally lacking in reversals. This was particularly so in the case of play initiated by females with males, where only 55% of bouts involved no role reversals and 34% involved one role reversal.

This suggests that in the case of bouts initiated by females with males, the females were somewhat less likely to maintain their initial on-top position than would be the case in within-sex play or in cases where males intiated play with females. However, on-top relationships in male-male play also appear to be relatively more labile in the same way.

3.3.4.4. Age x Sex differences in the number of role-reversals in play:

Table 3.13 shows the number of role-reversals shown

TABLE 3.13: AGE-RELATED SEX DIFFERENCES IN NUMBER OF ROLE REVERSALS WITHIN PLAY-BOUTS:

(Percentages are of the total number of bouts observed for each permutation of players' sexes, in each age-period. "M" = "males", "F" = "females", "A1" = "initiator", "A2" = "recipient", "rr's" = "role reversals", "tot" = "total").

(a) MA1-MA2:

| No.of rr's: | Age-period: 21-30 | 31-40 | 41-50 | 51-60 |
|---|---|---|---|---|
| 0: | 63.2% (24) | 58.2% (32) | 48.4% (31) | 77.3% (17) |
| 1: | 31.6% (12) | 29.1% (16) | 35.9% (23) | 4.6% (1) |
| 2: | 0.0% (0) | 12.7% (7) | 15.6% (10) | 18.2% (4) |
| 3: | 2.6% (1) | 0.0% (0) | 0.0% (0) | 0.0% (0) |
| 4: | 0.0% (0) | 0.0% (0) | 0.0% (0) | 0.0% (0) |
| 5: | 0.0% (0) | 0.0% (0) | 0.0% (0) | 0.0% (0) |
| 6: | 2.6% (1) | 0.0% (0) | 0.0% (0) | 0.0% (0) |
| tot: | 100.0% (38) | 100.0% (55) | 100.0% (64) | 100.0% (22) |

(b) FA1-FA2:

| No.of rr's: | Age-period: 21-30 | 31-40 | 41-50 | 51-60 |
|---|---|---|---|---|
| 0: | 68.0% (17) | 81.3% (26) | 73.0% (27) | 80.0% (20) |
| 1: | 24.0% (6) | 3.1% (1) | 16.2% (6) | 12.0% (3) |
| 2: | 4.0% (1) | 9.4% (3) | 10.8% (4) | 4.0% (1) |
| 3: | 4.0% (1) | 6.2% (2) | 0.0% (0) | 4.0% (1) |
| tot: | 100.0% (25) | 100.0% (32) | 100.0% (37) | 100.0% (25) |

(c) MA1-FA2:

| No.of rr's: | Age-period: 21-30 | 31-40 | 41-50 | 51-60 |
|---|---|---|---|---|
| 0: | 64.6% (31) | 68.7% (33) | 70.9% (73) | 79.5% (31) |
| 1: | 25.0% (12) | 18.8% (9) | 18.4% (19) | 17.9% (7) |
| 2: | 8.3% (4) | 10.4% (5) | 8.7% (9) | 2.6% (1) |
| 3: | 0.0% (0) | 2.1% (1) | 1.0% (1) | 0.0% (0) |
| 4: | 2.1% (1) | 0.0% (0) | 1.0% (1) | 0.0% (0) |
| tot: | 100.0% (48) | 100.0% (48) | 100.0% (103) | 100.0% (39) |

(d) FA1-MA2:

| No.of rr's: | Age-period: 21-30 | 31-40 | 41-50 | 51-60 |
|---|---|---|---|---|
| 0: | 53.8% (21) | 63.4% (26) | 54.5% (36) | 38.9% (7) |
| 1: | 28.2% (11) | 26.8% (11) | 37.9% (25) | 50.0% (9) |
| 2: | 7.7% (3) | 7.3% (3) | 7.6% (5) | 11.1% (2) |
| 3: | 10.3% (4) | 0.0% (0) | 0.0% (0) | 0.0% (0) |
| 4: | 0.0% (0) | 0.0% (0) | 0.0% (0) | 0.0% (0) |
| 5: | 0.0% (0) | 2.4% (1) | 0.0% (0) | 0.0% (0) |
| tot: | 100.0% (39) | 99.9% (41) | 100.0% (66) | 100.0% (18) |

in play, considered according to the age and sex of the interactants. There were no consistent age-related sex-differences in the number of role reversals occurring in play, especially when acccount is taken of the fact that the percentages are often drawn from markedly different frequencies of bouts in each age/sex category; the overall trends described in the previous section, are apparent in each separate age-period.

3.3.4.5: Summary:

As with the percentage of time spent by each of the players in the on-top position, these data on the number of role-reversals in play suggest that there was little reciprocity between interactants. In two-thirds of observed play-bouts, the animal who initiated the play tended to stay on top, uninterruptedly. It was comparatively rare for more than one role-reversal to occur within a single bout. There were few age- or sex-differences in these data, except that more role-reversals tended to occur in male-male and female-male play.

3.3.5: Relationships between bout duration, on-top behaviour and role-reversals:

For each age-period, Spearman's rank correlations were performed between the duration of a bout; the percentage of on-top behaviour shown within it by the

initiator and the recipient; and the number of role reversals which occurred within it. These were intended to address the issue of whether the length of play bouts was significantly related to the degree of "reciprocity" of on-top behaviour shown by the interactants.

3.3.5.1: Relationship between percentage of "on-top" behaviour and the duration of bouts:

Table 3.14 (a) shows the results of Spearman's rank-order correlation tests performed between the duration of a bout and the percentage of that bout spent in the on-top position by the bout's initiator, combining the data from both sexes but considering each age-period individually. In each age-period except the last, there was a very low but statistically significant negative correlation (ranging from 0.2 to 0.35) between these two variables; ie, the longer the bout lasted, the less time spent by A1 in the on-top position. (The correlation between the two factors between 51-60 days was in the same direction, but failed to reach significance).

A similar but complementary relationship to that above was found in the correlation between bout-duration and the percentage of time spent by A2 in the on-top position: the longer the bout, the more time A2 spent on top ("rho" ranged from 0.27 to 0.35; $p<0.001$ in all age-periods except the last, when $p<0.01$). These data are summarised in table 3.14 (b).

Finally, for each bout, the percentage of time spent

TABLE 3.14: CORRELATIONS BETWEEN DURATION OF PLAY, PERCENTAGE OF TIME SPENT ON-TOP BY EACH OF THE PARTICIPANTS, AND THE NUMBER OF ROLE-REVERSALS OCCURRING WITHIN THE BOUT:

(Data shown are the results of correlation tests performed for each of the four age-periods studied, combining the data across sexes. "Rho" was converted to "t", since large samples were involved; the probabilities refer to the "t" values, with degrees of freedom equal to infinity except for tests on data for the 51-60 day period, where df= N-2. All tests are two-tailed).

(a) Results of Spearman's rank-order correlation tests between bout duration and the percentage of the bout spent in the on-top position by A1:

| age-period: | "rho": | "t": | No. bouts: | probability: |
|---|---|---|---|---|
| 21-30 days: | -0.199 | 2.466 | 150 | p<0.02 |
| 31-40 days: | -0.350 | 4.925 | 176 | p<0.001 |
| 41-50 days: | -0.262 | 4.442 | 270 | p<0.001 |
| 51-60 days: | -0.132 | 1.342 | 104 | n.s. |

(b) Results of Spearman's rank-order correlation tests between bout duration and the percentage of the bout spent in the on-top position by A2:

(Conventions as for table 3.14a).

| age-period: | "rho": | "t": | No. bouts: | probability: |
|---|---|---|---|---|
| 21-30 days: | 0.275 | 3.483 | 150 | p<0.001 |
| 31-40 days: | 0.345 | 4.846 | 176 | p<0.001 |
| 41-50 days: | 0.372 | 6.560 | 270 | p<0.001 |
| 51-60 days: | 0.307 | 3.261 | 104 | p<0.01 |

3.14(c): Results of Spearman's rank-order correlation tests between bout duration and the disparity in on-top behaviour between A1 and A2 (percentage of on-top shown by A1, minus percentage of on-top shown by A2):

(Conventions as for table 3.14a).

| age-period: | "rho": | "t": | No. bouts: | probability: |
|---|---|---|---|---|
| 21-30 days: | -0.223 | 2.777 | 150 | p<0.01 |
| 31-40 days: | -0.346 | 4.870 | 176 | p<0.001 |
| 41-50 days: | -0.290 | 4.964 | 270 | p<0.001 |
| 51-60 days: | -0.161 | 1.643 | 104 | n.s. |

(d) Results of Spearman's rank-order correlation tests between bout duration and the number of role-reversals occurring with a bout:

(Conventions as for table 3.14a).

| age-period: | "rho": | "t": | No. bouts: | probability: |
|---|---|---|---|---|
| 21-30 days: | 0.453 | 6.190 | 150 | p<0.001 |
| 31-40 days: | 0.586 | 9.546 | 176 | p<0.001 |
| 41-50 days: | 0.434 | 7.888 | 270 | p<0.001 |
| 51-60 days: | 0.367 | 3.991 | 104 | p<0.001 |

by A2 in on-top behaviour was subtracted from the percentage of time spent by A1 in on-top behaviour, to give a measure of the disparity in on-top behaviour between the players. A score of zero would thus indicate total equality between the interactants; positive deviations from this (up to a maximum of 100) would show an inequality in on-top behaviour in favour of A1; and negative deviations would show a similar bias in A2's favour (up to a maximum of 99%, since by definition A2 could not dominate a bout for 100% of it). This score was then correlated with its associated bout's duration, using Spearman's "rho" as before, to determine if there were any systematic relationship between the extent of inequality in on-top behaviour within a bout, and the duration of that bout: ie, to investigate whether increasing one-sidedness in on-top behaviour was associated with either increasing or decreasing bout-length.

In all age-periods except the last, there was a significant negative correlation between the duration of a bout and the disparity between the interactants: ie, the more one-sided the bout (whether it was in A1 or A2's favour), the shorter it lasted. As before, these correlations were low but statistically significant. (See table 3.14 (c) for the correlation coefficients and associated probabilities).

3.3.5.2: Correlation between bout-duration and the number of role-reversals within a bout:

For each age-period, a Spearman rank correlation was performed between the duration of each bout and the number of role reversals occurring within it. Table 3.14 (d) shows the results of these tests. In all four age periods, highly significant correlations were found between these two variables: the more reversals which occurred, the longer the bout ("rho" ranged from 0.37 to 0.59; $p<0.001$ in all cases).

3.3.5.3: Summary:

There appears to be some degree of relationship between the duration of a play-bout, and the degree of reciprocity between the interactants (the latter as expressed by the percentage of the bout spent in the on-top position by either the initiator or recipient of play, or by the difference between these two percentages). Correlations between these variables are weak, however, and only attain statistical significance due to the large numbers of values involved. A stronger relationship was found between play-bout duration and the number of role reversals occurring within it, suggesting that if players are sensitive to asymmetries of on-top behaviour within play, then the opportunity for pinning per se is more important than the actual length of the pins themselves.

As with all correlations, however, the precise interpretation of these results remains equivocal. Longer

bouts may show more "reciprocity" (both in terms of percentage of on-top behaviour, and number of role-reversals) simply because they are longer; if the probability of a role reversal occurring, or of being in the on-top position, is constant over time, then longer bouts will show more of these phenomena purely as a function of chance. Alternatively, bout length might depend on the degree of reciprocity within the interaction, so that a lack of reciprocity is perceived by one of the interactants, who then terminates the encounter prematurely.

If this latter view is correct, and the maintenance of a play interaction is directly dependent on both players having opportunities for being on top, then one might expect a stronger relationship between duration and reciprocity than was found in practice; the weakness of the relationship between asymmetry in play and the length of play-bouts instead suggests that such effects have only minor importance in determining bout duration compared to other undetermined influences. The lack of age-changes in these relationships, at any rate, certainly fails to support any hypotheses that players become more sensitive to asymmetries in play with increasing age.

### 3.3.6: The antecedents of play:

#### 3.3.6.1: Overall antecedents of play (21-60 days, males and females combined):

Taking the data for all age-periods and both sexes together, fig. 3.3 shows the relative frequencies with which different categories of activity by the initiator (A1) were observed to occur in the three seconds immediately preceding play. Fig. 3.4 shows the corresponding overall relative frequencies with which various behaviours were seen to precede play in the case of the recipient animal (A2).

By far the most frequent antecedent of play for A1 was olfactory investigation of the inanimate environment: this preceded approximately 37% of all play-bouts. The next most commonly-occurring antecedent was playing with a different partner, which preceded 18% of play. Playing with the same partner, locomotion (running, walking, climbing) and olfactory investigation of the play-partner before beginning to play with him, were all seen to precede just under 10% of play-bouts. More "sedentary" activities - eating and drinking, allogrooming and self-grooming - were observed to precede A1's play only infrequently; none of these categories of activity preceded more than 3% of bouts. Sleep (operationally defined as laying motionless) was never observed in the three seconds before a play-bout commenced. Sexual and agonistic behaviours, and olfactory investigation of an

Explanation of the abbreviations and conventions used for the Figures in Chapter Three:

The abbreviations used for figures 3.3 to 3.6 are as follows:

"AGON" : "agonistic behaviours".
"PLS" : "play with the same partner".
"PLD" : "play with a different partner".
"EAT" : "eating and drinking".
"SGM" : "self-grooming".
"AGM" : "allo-grooming".
"LOCO" : "locomotion".
"SEX" : "sexual behaviours".
"OPP" : "olfactory investigtion of the play partner".
"ODP" : "olfactory investigation of an animal other than the play partner".
"OENV" : "olfactory investigation of the inanimate environment".
"OTH" : "other (any behaviours not falling into the above categories".

(For a full explanation of these categories, see section 3.2.3.1.3).

The abbreviations used for fig. 3.7 are as follows:

A1M : "the initiator moves away from the recipient".
A2M : "the recipient moves away from the initiator".
A1D : "the initiator is distracted by another animal".
A2D : "the recipient is distracted by another animal".
A1OG : "the initiator sniffs the inanimate environment".
A2OG : "the recipient sniffs the inanimate environment".
A1GM : "the initiator grooms himself".
A2GM : "the recipient grooms himself".
A1O2 : "the initiator sniffs the recipient".
A2O1 : "the recipient sniffs the recipient".
SEX : "sexual behaviours".
OTH : "other (any behaviours not falling into the above categories)".

(For a full explanation, see section 3.2.3.1.5).

FIG.3.3: OVERALL RELATIVE FREQUENCY OF DIFFERENT CLASSES OF ANTECEDENT, FOR INITIATORS OF PLAY (21-60 DAYS, MALES AND FEMALES COMBINED)

FIG.3.4: OVERALL RELATIVE FREQUENCY OF DIFFERENT CLASSES OF ANTECEDENT, FOR RECIPIENTS OF PLAY (21-60 DAYS, MALES AND FEMALES COMBINED)

animal different from that with which play was to occur, were all uncommmon precursors of play (each preceding approximately 4% of play-bouts).

For A2, essentially the same pattern was observed, except that eating and drinking, and self-grooming, were observed with slightly greater frequency, and sexual behaviour less often. The overall pattern, then, was for exploration (both of the inanimate and animate environments), play and locomotion to be frequent precursors of play; and for low-activity, maintenance activities (grooming, eating and drinking) and agonistic and sexual behaviours to precede play relatively infrequently.

3.3.6.2: Age-changes in the antecedents of play (males and females combined):

Table 3.15 shows age-changes in the relative frequency of the various antecedents of play for A1 and A2, combining the data for both sexes. There were few systematic age-changes in the relative frequencies of play's antecedents: the same general pattern described above was observed at all ages. However, there was a slight decrease with age in the frequency with which agonistic interactions were observed to precede play, for both A1 and A2 (from preceding over 6% of bouts between 21-30 days, to preceding less than 3% of bouts between 51-60 days). Another notable age-related change was the development of sexual activity as a precursor of play

TABLE 3.15: AGE-CHANGES IN ANTECEDENTS OF PLAY (MALES AND FEMALES COMBINED):

(Percentages are of the total number of play-bouts observed in the age-period concerned, combining the data for males and females).

(a) Antecedents of play for the initiator:

| | 21-30 | 31-40 | 41-50 | 51-60 |
|---|---|---|---|---|
| AGONISTIC BEHAVIOURS: | 6.7% (10) | 4.0% (7) | 3.0% (8) | 2.9% (3) |
| PLAY WITH SAME PARTNER: | 10.7% (16) | 13.1% (23) | 8.9% (24) | 5.8% (6) |
| PLAY WITH DIFFERENT PARTNER: | 19.3% (19) | 18.2% (32) | 18.5% (50) | 15.4% (16) |
| EATING OR DRINKING: | 0.0% (0) | 0.0% (0) | 0.4% (1) | 1.9% (2) |
| SELF-GROOMING: | 4.7% (7) | 2.3% (4) | 1.9% (5) | 1.0% (1) |
| ALLO-GROOMING: | 3.3% (5) | 1.7% (3) | 2.6% (7) | 0.0% (0) |
| LOCOMOTION: | 5.3% (8) | 10.8% (19) | 8.9% (24) | 10.6% (11) |
| SEXUAL BEHAVIOURS: | 0.7% (1) | 1.7% (3) | 10.0% (27) | 0.0% (0) |
| SNIFF PLAY-PARTNER: | 8.0% (12) | 5.7% (10) | 9.3% (25) | 13.5% (14) |
| SNIFF DIFFERENT ANIMAL: | 3.3% (5) | 2.3% (4) | 4.1% (11) | 5.8% (6) |
| SNIFF ENVIRONMENT: | 38.0% (57) | 39.8% (70) | 32.2% (87) | 43.3% (45) |
| OTHER: | 0.0% (0) | 0.6% (1) | 0.4% (1) | 0.0% (0) |

3.15(b): Antecedents of play for the recipient:

| | 21-30 | 31-40 | 41-50 | 51-60 |
|---|---|---|---|---|
| AGONISTIC BEHAVIOURS: | 6.0% (9) | 4.0% (7) | 2.6% (7) | 1.9% (2) |
| PLAY WITH SAME PARTNER: | 10.7% (16) | 13.6% (24) | 9.3% (25) | 5.8% (6) |
| PLAY WITH DIFFERENT PARTNER: | 11.3% (17) | 13.6% (24) | 16.7% (45) | 10.6% (11) |
| EATING OR DRINKING: | 3.3% (5) | 1.7% (3) | 2.6% (7) | 2.9% (3) |
| SELF-GROOMING: | 6.7% (10) | 6.8% (12) | 3.3% (9) | 5.8% (6) |
| ALLO-GROOMING: | 4.0% (6) | 0.6% (1) | 0.4% (1) | 1.0% (1) |
| LOCOMOTION: | 8.0% (12) | 8.0% (14) | 10.4% (28) | 5.8% (6) |
| SEXUAL BEHAVIOURS: | 2.7% (4) | 0.6% (1) | 2.2% (6) | 0.0% (0) |
| SNIFF PLAY-PARTNER: | 7.3% (11) | 9.1% (16) | 3.7% (10) | 9.6% (10) |
| SNIFF DIFFERENT ANIMAL: | 2.0% (3) | 0.6% (1) | 4.4% (12) | 4.8% (5) |
| SNIFF ENVIRONMENT: | 36.0% (54) | 41.5% (73) | 43.7% (118) | 51.9% (54) |
| OTHER: | 2.0% (3) | 0.0% (0) | 0.7% (2) | 0.0% (0) |

for A1. Although on an overall basis sexual activity preceded play only relatively infrequently, 10% of play-bouts recorded between 41-50 days were preceded by sexual activity on the part of the initiator of the bout.

3.3.6.3: Overall sex-differences in the antecedents of play (21-60 days):

Table 3.16 shows the relative frequencies of bout-antecedents, analysed according to the players' sex: ie, the antecedents for play by MA1, MA2, FA1 and FA2 (in this case, ignoring the sex of their partners). The overall pattern described above was shown by all sexes with only relatively minor fluctuations, probably attributable to the different numbers of bouts obtained for each category of interactant.

3.3.6.4: Age x Sex differences in the antecedents of play:

Table 3.17 shows age-changes in the relative frequencies of the different antecedents of play, for MA1, FA1, MA2 and FA2. There were no consistent age-related differences between any of these four classes of player. These data do show more clearly the development of sexual activity as a precursor of play, as described earlier. Sexual behaviour was a frequent antecedent of play only between 41-50 days, and then only in the case of initiators, not recipients. Note that during this period, female initiators were as likely as male initiators to be

TABLE 3.16: OVERALL SEX DIFFERENCES IN THE ANTECEDENTS OF PLAY (21-60 DAYS):

(Percentages are of the total number of bouts involving interactants of the sexes concerned, combining together the data from all age-periods).

(a) Initiators of play:

| | males | | females | |
|---|---|---|---|---|
| AGONISTIC BEHAVIOURS: | 4.3% | (18) | 3.5% | (10) |
| PLAY WITH SAME PARTNER: | 10.3% | (43) | 9.2% | (26) |
| PLAY WITH DIFFERENT PARTNER: | 17.3% | (72) | 19.4% | (55) |
| EATING OR DRINKING: | 0.0% | (0) | 1.1% | (3) |
| SELF-GROOMING: | 2.4% | (10) | 2.5% | (7) |
| ALLO-GROOMING: | 2.2% | (9) | 2.1% | (6) |
| LOCOMOTION: | 9.6% | (40) | 7.8% | (22) |
| SEXUAL BEHAVIOURS: | 4.8% | (20) | 3.9% | (11) |
| SNIFF PLAY-PARTNER: | 9.3% | (39) | 7.8% | (22) |
| SNIFF DIFFERENT ANIMAL: | 4.3% | (18) | 2.8% | (8) |
| SNIFF ENVIRONMENT: | 35.5% | (148) | 39.2% | (111) |
| OTHER: | 0.0% | (0) | 0.7% | (2) |
| TOTAL: | 100.0% | (417) | 100.0% | (283) |

(b) Recipients of play:

| | males | | females | |
|---|---|---|---|---|
| AGONISTIC BEHAVIOURS: | 5.0% | (17) | 2.2% | (8) |
| PLAY WITH SAME PARTNER: | 11.1% | (38) | 9.2% | (33) |
| PLAY WITH DIFFERENT PARTNER: | 14.6% | (50) | 13.2% | (47) |
| EATING OR DRINKING: | 2.3% | (8) | 2.8% | (10) |
| SELF-GROOMING: | 4.1% | (14) | 6.4% | (23) |
| ALLO-GROOMING: | 2.0% | (7) | 0.6% | (2) |
| LOCOMOTION: | 7.6% | (26) | 9.5% | (34) |
| SEXUAL BEHAVIOURS: | 1.8% | (6) | 1.4% | (5) |
| SNIFF PLAY-PARTNER: | 8.5% | (29) | 5.0% | (18) |
| SNIFF DIFFERENT ANIMAL: | 2.9% | (10) | 3.1% | (11) |
| SNIFF ENVIRONMENT: | 39.6% | (136) | 45.7% | (163) |
| OTHER: | 0.6% | (2) | 0.8% | (3) |
| TOTAL: | 100.1% | (343) | 99.9% | (357) |

TABLE 3.17: AGE-CHANGES IN SEX-DIFFERENCES IN ANTECEDENTS OF PLAY:

(Percentages are of the total number of play-bouts observed in the age-period concerned, involving the sex of interactant in question - regardless of the partner's sex)

(a) Male initiators:

| | 21-30 | 31-40 | 41-50 | 51-60 |
|---|---|---|---|---|
| AGONISTIC BEHAVIOURS: | 8.1% (7) | 3.9% (4) | 3.0% (5) | 3.3% (2) |
| PLAY WITH SAME PARTNER: | 9.3% (8) | 16.5% (17) | 7.8% (13) | 8.2% (5) |
| PLAY WITH DIFFERENT PARTNER: | 15.1% (13) | 17.5% (18) | 17.4% (29) | 19.7% (12) |
| EATING OR DRINKING: | 0.0% (0) | 0.0% (0) | 0.0% (0) | 0.0% (0) |
| SELF-GROOMING: | 3.5% (3) | 2.9% (3) | 2.4% (4) | 0.0% (0) |
| ALLO-GROOMING: | 2.3% (2) | 1.9% (2) | 3.0% (5) | 0.0% (0) |
| LOCOMOTION: | 5.8% (5) | 11.7% (12) | 10.8% (18) | 8.2% (5) |
| SEXUAL BEHAVIOURS: | 1.2% (1) | 1.9% (2) | 10.2% (17) | 0.0% (0) |
| SNIFF PLAY-PARTNER: | 9.3% (8) | 5.8% (6) | 10.2% (17) | 13.1% (8) |
| SNIFF DIFFERENT ANIMAL: | 3.5% (3) | 2.9% (3) | 4.2% (7) | 8.2% (5) |
| SNIFF THE ENVIRONMENT: | 41.9% (36) | 34.9% (36) | 31.1% (52) | 39.3% (24) |
| OTHER: | 0.0% (0) | 0.0% (0) | 0.0% (0) | 0.0% (0) |

(b) Female initiators:

| | 21-30 | 31-40 | 41-50 | 51-60 |
|---|---|---|---|---|
| AGONISTIC BEHAVIOURS: | 4.7% (3) | 4.1% (3) | 2.9% (3) | 2.3% (1) |
| PLAY WITH SAME PARTNER: | 12.5% (8) | 8.2% (6) | 10.7% (11) | 2.3% (1) |
| PLAY WITH DIFFERENT PARTNER: | 25.0% (16) | 19.2% (14) | 20.4% (21) | 9.3% (4) |
| EATING OR DRINKING: | 0.0% (0) | 0.0% (0) | 1.0% (1) | 4.7% (2) |
| SELF-GROOMING: | 6.3% (4) | 1.4% (1) | 1.0% (1) | 2.3% (1) |
| ALLO-GROOMING: | 4.7% (3) | 1.4% (1) | 1.9% (2) | 0.0% (0) |
| LOCOMOTION: | 4.7% (3) | 9.6% (7) | 5.8% (6) | 13.9% (6) |
| SEXUAL BEHAVIOURS: | 0.0% (0) | 1.4% (1) | 9.7% (10) | 0.0% (0) |
| SNIFF PLAY-PARTNER: | 6.3% (4) | 5.5% (4) | 7.8% (8) | 13.9% (6) |
| SNIFF DIFFERENT ANIMAL: | 3.1% (2) | 1.4% (1) | 3.9% (4) | 2.3% (1) |
| SNIFF THE ENVIRONMENT: | 32.8% (21) | 46.6% (34) | 34.0% (35) | 48.8% (21) |
| OTHER: | 0.0% (0) | 1.4% (1) | 1.0% (1) | 0.0% (0) |

(c) Male recipients:

| | 21-30 | 31-40 | 41-50 | 51-60 |
|---|---|---|---|---|
| AGONISTIC BEHAVIOURS: | 7.8% (6) | 4.2% (4) | 3.9% (5) | 5.0% (2) |
| PLAY WITH SAME PARTNER: | 11.7% (9) | 16.7% (16) | 9.2% (12) | 2.5% (1) |
| PLAY WITH DIFFERENT PARTNER: | 10.4% (8) | 10.4% (10) | 20.8% (27) | 12.5% (5) |
| EATING OR DRINKING: | 3.9% (3) | 1.0% (1) | 2.3% (3) | 2.5% (1) |
| SELF-GROOMING: | 1.3% (1) | 5.2% (5) | 3.9% (5) | 7.5% (3) |
| ALLO-GROOMING: | 5.2% (4) | 1.0% (1) | 0.8% (1) | 2.5% (1) |
| LOCOMOTION: | 7.8% (6) | 5.2% (5) | 10.0% (13) | 5.0% (2) |
| SEXUAL BEHAVIOURS: | 1.3% (1) | 0.0% (0) | 3.9% (5) | 0.0% (0) |
| SNIFF PLAY-PARTNER: | 9.1% (7) | 14.6% (14) | 3.1% (4) | 10.0% (4) |
| SNIFF DIFFERENT ANIMAL: | 2.6% (2) | 0.0% (0) | 5.4% (7) | 2.5% (1) |
| SNIFF THE ENVIRONMENT: | 37.7% (29) | 41.7% (40) | 36.1% (47) | 50.0% (20) |
| OTHER: | 1.3% (1) | 0.0% (0) | 0.8% (1) | 0.0% (0) |

(d) Female recipients:

| | 21-30 | 31-40 | 41-50 | 51-60 |
|---|---|---|---|---|
| AGONISTIC BEHAVIOURS: | 4.1% (3) | 3.8% (3) | 1.4% (2) | 0.0% (0) |
| PLAY WITH SAME PARTNER: | 9.6% (7) | 10.0% (8) | 9.3% (13) | 7.8% (5) |
| PLAY WITH DIFFERENT PARTNER: | 12.3% (9) | 17.5% (14) | 12.9% (18) | 9.4% (6) |
| EATING OR DRINKING: | 2.7% (2) | 2.5% (2) | 2.9% (4) | 3.1% (2) |
| SELF-GROOMING: | 12.3% (9) | 8.8% (7) | 2.9% (4) | 4.7% (3) |
| ALLO-GROOMING: | 2.7% (2) | 0.0% (0) | 0.0% (0) | 0.0% (0) |
| LOCOMOTION: | 8.2% (6) | 11.3% (9) | 10.7% (15) | 6.2% (4) |
| SEXUAL BEHAVIOURS: | 4.1% (3) | 1.2% (1) | 0.7% (1) | 0.0% (0) |
| SNIFF PLAY-PARTNER: | 5.5% (4) | 2.5% (2) | 4.3% (6) | 9.4% (6) |
| SNIFF DIFFERENT ANIMAL: | 1.4% (1) | 1.2% (1) | 3.6% (5) | 6.2% (4) |
| SNIFF THE ENVIRONMENT: | 34.3% (25) | 41.3% (33) | 50.7% (71) | 53.1% (34) |
| OTHER: | 2.7% (2) | 0.0% (0) | 0.7% (1) | 0.0% (0) |

involved in sexual activity immediately prior to play; however, it is unclear why initiators should be more likely than recipients to have engaged in some form of sexual activity before play.

Finally, these data reveal that the tendency for agonistic antecedents of play to decrease in relative frequency with age was a consistent feature of the behaviour of all categories of interactant.

3.3.6.5: Summary of the data on the antecedents of play:

In short, play was found to be most frequently preceded by active pursuits - exploration of the animate and inanimate environments, play with other animals and locomotion. More sedentary "maintenance" behaviours preceded play relatively infrequently, and agonistic and sexual behaviours were seen before play comparatively rarely. There were few age-changes in this overall pattern. Certainly there was no trend for play to be increasingly associated with agonistic behaviours with increasing age; in fact, agonistic precursors became less frequent as the subjects got older. These data do however reflect the marked rise in sexual activity shown by the pups between 41-50 days. It appears that play occurs between active, exploring or playing animals, rather than in any competitive or agonistic framework.

## 3.3.7: The consequences of play:

### 3.3.7.1: Overall consequences of play (21-60 days, males and females combined):

Taking the data for all age-periods and both sexes together, fig. 3.5 shows the relative frequencies with which different categories of activity by the initiator (A1) were observed to immediately follow play (ie, were seen to occur in the first three seconds directly after a play-bout was deemed to have ended). Fig. 3.6 shows the corresponding overall relative frequencies of behaviours following play in the case of the recipient animal (A2).

For A1, by far the most frequently occurring consequence of play was olfactory investigation of the inanimate environment; this followed nearly 40% of bouts. The next most common activity was play with a different partner, which occurred after 18% of bouts. Play with the same pup, and locomotion, each followed just under 10% of play-bouts. All other categories of consequence occurred with frequencies of less than 5%. The least frequently-observed consequence was agonistic behaviour, which followed only 2% of all bouts (14 out of 700).

This pattern of relative frequencies of the different consequences of play thus closely resembles that shown by play's antecedents, except that olfactory investigation of the play-partner preceded play more frequently than it

FIG.3.5: OVERALL RELATIVE FREQUENCY OF DIFFERENT CLASSES OF CONSEQUENCES, FOR INITIATORS OF PLAY (21-60 DAYS, MALES AND FEMALES COMBINED)

FIG.3.6: OVERALL RELATIVE FREQUENCY OF DIFFERENT CLASSES OF CONSEQUENCES, FOR RECIPIENTS OF PLAY (21-60 DAYS, MALES AND FEMALES COMBINED)

followed it, and that eating and drinking (almost never shown by A1 before a bout) followed play with a small but appreciable frequency. Levels of self-grooming also appear to be higher following play than before it.

The consequences of play for A2 showed an almost identical pattern to that shown by A1, except that playing with a different pup followed play less frequently for A2 than it did for A1.

3.3.7.2: Age-changes in the consequences of play:

Table 3.18 shows age-changes in the relative frequency of the various consequences of play for A1 and A2, combining the data for both sexes. These data reveal few systematic age-changes in the relative frequencies of activities following play: the same general pattern described above was observed at all ages, with olfactory investigation of the inanimate environment being by far the most common consequence of play, and playing with a different pup being the next most frequent.

The frequencies with which agonistic interactions followed play remained stable, and small, across all ages. It is clear therefore that, overall, play was not followed to any significant extent by aggression, and there was no trend for play to become increasingly associated with such behaviours as the interactants became older.

For A1, sexual behaviour reached its peak as a consequence of play between 41-50 days, when it followed nearly 7% of play-bouts. No clear trends were apparent in

TABLE 3.18: AGE-CHANGES IN CONSEQUENCES OF PLAY (MALES AND FEMALES COMBINED):

(All conventions are as for table 3.15)

(a) Consequences of play for initiators:

| | 21-30 | 31-40 | 41-50 | 51-60 |
|---|---|---|---|---|
| AGONISTIC BEHAVIOURS: | 1.3% (2) | 1.1% (2) | 2.2% (6) | 3.9% (4) |
| PLAY WITH THE SAME PARTNER: | 9.3% (14) | 13.6% (24) | 6.3% (17) | 4.8% (5) |
| PLAY WITH DIFFERENT PARTNER: | 17.3% (26) | 17.1% (30) | 21.1% (57) | 14.4% (15) |
| EATING OR DRINKING: | 4.7% (7) | 2.8% (5) | 2.6% (7) | 3.9% (4) |
| SELF-GROOMING: | 6.7% (10) | 2.8% (5) | 4.4% (12) | 9.6% (10) |
| ALLO-GROOMING: | 0.7% (1) | 0.6% (1) | 3.3% (9) | 3.9% (4) |
| LOCOMOTION: | 5.3% (8) | 9.1% (16) | 11.5% (31) | 10.6% (11) |
| SEXUAL BEHAVIOURS: | 1.3% (2) | 1.1% (2) | 6.7% (18) | 1.9% (2) |
| SNIFF PLAY-PARTNER: | 0.7% (1) | 4.6% (8) | 2.2% (6) | 3.9% (4) |
| SNIFF DIFFERENT ANIMAL: | 3.3% (5) | 6.8% (12) | 4.8% (13) | 3.9% (4) |
| SNIFF THE ENVIRONMENT: | 47.3% (71) | 38.6% (68) | 34.1% (92) | 38.5% (40) |
| OTHER: | 2.0% (3) | 1.7% (3) | 0.7% (2) | 1.0% (1) |

(b) Consequences of play for recipients:

| | 21-30 | 31-40 | 41-50 | 51-60 |
|---|---|---|---|---|
| AGONISTIC BEHAVIOURS: | 0.7% (1) | 1.7% (3) | 1.5% (4) | 1.9% (2) |
| PLAY WITH THE SAME PARTNER: | 9.3% (14) | 13.6% (24) | 5.9% (16) | 4.8% (5) |
| PLAY WITH DIFFERENT PARTNER: | 10.7% (16) | 11.9% (21) | 15.2% (41) | 7.7% ( 8) |
| EATING OR DRINKING: | 4.0% (6) | 3.4% (6) | 4.1% (11) | 1.9% (2) |
| SELF-GROOMING: | 6.7% (10) | 4.0% ( 7) | 4.4% (12) | 5.8% (6) |
| ALLO-GROOMING: | 2.0% (3) | 0.6% (1) | 1.5% (4) | 3.9% (4) |
| LOCOMOTION: | 6.7% (10) | 9.7% (17) | 11.9% (32) | 10.6% (11) |
| SEXUAL BEHAVIOURS: | 1.3% (2) | 1.1% (2) | 2.2% (6) | 1.9% (2) |
| SNIFF PLAY-PARTNER: | 2.7% ( 4) | 4.0% ( 7) | 3.3% ( 9) | 1.9% ( 2) |
| SNIFF DIFFERENT ANIMAL: | 4.7% (7) | 4.6% (8) | 6.7% (18) | 9.6% (10) |
| SNIFF THE ENVIRONMENT: | 48.7% (73) | 44.3% (78) | 42.6% (115) | 48.1% (50) |
| OTHER: | 2.7% (4) | 1.1% (2) | 0.7% (2) | 1.9% (2) |

the case of A2. Just as sexual behaviour was never a very common antecedent of play, so too it was clearly not a frequent consequence. The relative frequencies of all other categories of consequence showed no consistent age-related trends.

3.3.7.3: Sex-differences in the consequences of play:

Taking all ages together, Table 3.19 shows the relative frequencies of consequences of play, analysed according to whether the initiator or recipient was male or female (but taking no account of the sex of their partner).

Once again, as with the data on play's antecedents, the overall pattern described above was shown by all sexes of interactant, with fluctuations largely attributable to the different numbers of bouts obtained for each sex. One sex-related difference was that male initiators were more likely to show sexual behaviour after play (not necessarily with the play-partner) than were female initiators, male recipients or female recipients. This was, however, a small difference, male initiators following 5% of their play-bouts with sexual behaviour, as opposed to under 2% for the other three classes of player. Another difference suggested by inspection of table 3.19 is that initiators of play generally showed higher relative frequencies of playing with a different partner after a play-bout than did recipients; however, this was not related to the players' sex.

TABLE 3.19: OVERALL SEX DIFFERENCES IN THE CONSEQUENCES OF PLAY (21-60 DAYS):

(Percentages are of the total number of bouts involving the sex of interactant concerned, combining together the data from all age-periods).

(a) Initiators of play:

| | males | | females | |
|---|---|---|---|---|
| AGONISTIC BEHAVIOURS: | 1.9% | (8) | 2.1% | (6) |
| PLAY WITH THE SAME PARTNER: | 8.4% | (35) | 8.8% | (25) |
| PLAY WITH DIFFERENT PARTNER: | 20.4% | (85) | 15.2% | (43) |
| EATING OR DRINKING: | 2.9% | (12) | 3.9% | (11) |
| SELF-GROOMING: | 3.8% | (16) | 7.4% | (21) |
| ALLO-GROOMING: | 2.4% | (10) | 1.4% | (4) |
| LOCOMOTION: | 9.8% | (41) | 8.8% | (25) |
| SEXUAL BEHAVIOURS: | 5.0% | (21) | 1.1% | (3) |
| SNIFF PLAY-PARTNER: | 3.1% | (13) | 2.1% | (6) |
| SNIFF DIFFERENT ANIMAL: | 4.6% | (19) | 5.3% | (15) |
| SNIFF THE ENVIRONMENT: | 36.5% | (152) | 42.4% | (120) |
| OTHER: | 1.2% | (5) | 1.4% | (4) |
| TOTAL: | 100.0% | (417) | 99.9% | (283) |

(b) Recipients of play:

| | males | | females | |
|---|---|---|---|---|
| AGONISTIC BEHAVIOURS: | 1.5% | (5) | 1.4% | (5) |
| PLAY WITH THE SAME PARTNER: | 11.4% | (39) | 5.6% | (20) |
| PLAY WITH DIFFERENT PARTNER: | 12.8% | (44) | 11.8% | (42) |
| EATING OR DRINKING: | 3.2% | (11) | 3.9% | (14) |
| SELF-GROOMING: | 4.4% | (15) | 5.6% | (20) |
| ALLO-GROOMING: | 1.5% | (5) | 2.0% | (7) |
| LOCOMOTION: | 9.3% | (32) | 10.6% | (38) |
| SEXUAL BEHAVIOURS: | 1.7% | (6) | 1.7% | (6) |
| SNIFF PLAY-PARTNER: | 2.9% | (10) | 3.4% | (12) |
| SNIFF DIFFERENT ANIMAL: | 5.2% | (18) | 7.0% | (25) |
| SNIFF THE ENVIRONMENT: | 44.6% | (153) | 45.7% | (163) |
| OTHER: | 1.5% | (5) | 1.4% | (5) |
| TOTAL: | 100.0% | (343) | 100.0% | (357) |

3.3.7.4: Age x Sex differences in the consequences of play:

Table 3.20 shows the relative frequencies of the different categories of behaviour following play, for each combination of age and sex of interactant. There were no systematic trends apparent in these data, except that they show more precisely the relationship between play and the development of sexual activity. The data in table 3.20 suggest that sexual behaviour was a frequent consequence of play only for male initiators, between 41-50 days, when 10% of their bouts were followed by such behaviour.

3.3.7.5: Summary of data on the consequences of play:

To sum up, both A1 and A2 showed similar overall patterns of consequences of play, and these in turn were similar to the patterns of behaviours seen before play. By far the most common antecedent and consequence of play was exploration of the inanimate environment. Play with a different animal, and locomotion, also occurred frequently both before and after play. Olfactory investigation of the play-partner was seen to occur fairly often before play but to a lesser extent afterwards. Play thus took place within a milieu of social and non-social olfaction, play and activity. In contrast, low-activity, maintenance activities (grooming, eating and drinking) and agonistic and sexual behaviours were seen to precede and follow play

TABLE 3.20: AGE-CHANGES IN SEX-DIFFERENCES IN CONSEQUENCES OF PLAY:

(Percentages are of the total number of play-bouts observed in the age-period concerned, which involved the sex of interactant in question - regardless of the partner's sex).

(a) Male initiators:

| | 21-30 | 31-40 | 41-50 | 51-60 |
|---|---|---|---|---|
| AGONISTIC BEHAVIOURS: | 2.3% (2) | 1.0% (1) | 2.4% (4) | 1.6% (1) |
| PLAY WITH THE SAME PARTNER: | 8.1% (7) | 14.6% (15) | 5.4% (9) | 6.6% (4) |
| PLAY WITH DIFFERENT PARTNER: | 23.3% (20) | 19.4% (20) | 21.0% (35) | 16.4% (10) |
| EATING OR DRINKING: | 4.7% (4) | 1.9% (2) | 1.8% (3) | 4.9% (3) |
| SELF-GROOMING: | 3.5% (3) | 2.9% (3) | 3.6% (6) | 6.6% (4) |
| ALLO-GROOMING: | 0.0% (0) | 1.0% (1) | 4.2% (7) | 4.9% (3) |
| LOCOMOTION: | 4.7% (4) | 10.7% (11) | 11.4% (19) | 11.5% (7) |
| SEXUAL BEHAVIOURS: | 2.3% (2) | 1.0% (1) | 9.6% (16) | 3.3% (2) |
| SNIFF THE PLAY-PARTNER: | 1.2% (1) | 2.9% (3) | 3.6% (6) | 4.9% (3) |
| SNIFF DIFFERENT ANIMAL: | 4.7% (4) | 5.8% (6) | 4.2% (7) | 3.3% (2) |
| SNIFF THE ENVIRONMENT: | 43.0% (37) | 38.8% (40) | 31.7% (53) | 34.4% (21) |
| OTHER: | 2.3% (2) | 0.0% (0) | 1.2% (2) | 1.6% (1) |

3.20(b): Female initiators:

| | 21-30 | 31-40 | 41-50 | 51-60 |
|---|---|---|---|---|
| AGONISTIC BEHAVIOURS: | 0.0% (0) | 1.4% (1) | 1.9% (2) | 7.0% (3) |
| PLAY WITH THE SAME PARTNER: | 10.9% (7) | 12.3% (9) | 7.8% (8) | 2.3% (1) |
| PLAY WITH DIFFERENT PARTNER: | 9.4% (6) | 13.7% (10) | 21.4% (22) | 11.6% (5) |
| EATING OR DRINKING: | 4.7% (3) | 4.1% (3) | 3.9% (4) | 2.3% (1) |
| SELF-GROOMING: | 10.9% (7) | 2.7% (2) | 5.8% (6) | 13.9% (6) |
| ALLO-GROOMING: | 1.6% (1) | 0.0% (0) | 1.9% (2) | 2.3% (1) |
| LOCOMOTION: | 6.3% (4) | 6.9% (5) | 11.7% (12) | 9.3% (4) |
| SEXUAL BEHAVIOURS: | 0.0% (0) | 1.4% (1) | 1.9% (2) | 0.0% (0) |
| SNIFF THE PLAY-PARTNER: | 0.0% (0) | 6.9% (5) | 0.0% (0) | 2.3% (1) |
| SNIFF DIFFERENT ANIMAL: | 1.6% (1) | 8.2% (6) | 5.8% (6) | 4.7% (2) |
| SNIFF THE ENVIRONMENT: | 53.1% (34) | 38.4% (28) | 37.9% (39) | 44.2% (19) |
| OTHER: | 1.6% (1) | 4.1% (3) | 0.0% (0) | 0.0% (0) |

3.20(c): Male recipients:

| | 21-30 | 31-40 | 41-50 | 51-60 |
|---|---|---|---|---|
| AGONISTIC BEHAVIOURS: | 0.0% (0) | 1.0% (1) | 2.3% (3) | 2.5% (1) |
| PLAY WITH THE SAME PARTNER: | 14.3% (11) | 16.7% (16) | 8.5% (11) | 2.5% (1) |
| PLAY WITH DIFFERENT PARTNER: | 9.1% (7) | 11.5% (11) | 16.2% (21) | 12.5% (5) |
| EATING OR DRINKING: | 3.9% (3) | 2.1% (2) | 4.6% (6) | 0.0% (0) |
| SELF-GROOMING: | 5.2% (4) | 2.1% (2) | 4.6% (6) | 7.5% (3) |
| ALLO-GROOMING: | 1.3% (1) | 0.0% (0) | 0.8% (1) | 7.5% (3) |
| LOCOMOTION: | 6.5% (5) | 9.4% (9) | 12.3% (16) | 5.0% (2) |
| SEXUAL BEHAVIOURS: | 0.0% (0) | 0.0% (2) | 3.1% (4) | 0.0% (0) |
| SNIFF THE PLAY-PARTNER: | 2.6% (2) | 4.2% (4) | 2.3% (3) | 2.5% (1) |
| SNIFF DIFFERENT ANIMAL: | 2.6% (2) | 4.2% (4) | 5.4% (7) | 12.5% (5) |
| SNIFF THE ENVIRONMENT: | 51.9% (40) | 45.8% (44) | 38.5% (50) | 47.5% (19) |
| OTHER: | 2.6% (2) | 1.0% (1) | 1.5% (2) | 0.0% (0) |

3.20(d): Female recipients:

| | 21-30 | 31-40 | 41-50 | 51-60 |
|---|---|---|---|---|
| AGONISTIC BEHAVIOURS: | 1.4% (1) | 2.5% (2) | 0.7% (1) | 1.6% (1) |
| PLAY WITH THE SAME PARTNER: | 4.1% (3) | 10.0% (8) | 3.6% (5) | 6.3% (4) |
| PLAY WITH DIFFERENT PARTNER: | 12.3% (9) | 12.5% (10) | 14.3% (20) | 4.7% (3) |
| EATING OR DRINKING: | 4.1% (3) | 5.0% (4) | 3.6% (5) | 3.1% (2) |
| SELF-GROOMING: | 8.2% (6) | 6.3% (5) | 4.3% (6) | 4.7% (3) |
| ALLO-GROOMING: | 2.7% (2) | 1.2% (1) | 2.1% (3) | 1.6% (1) |
| LOCOMOTION: | 6.9% (5) | 10.0% (8) | 11.4% (16) | 14.1% (9) |
| SEXUAL BEHAVIOUR: | 2.7% (2) | 0.0% (0) | 1.4% (2) | 3.1% (2) |
| SNIFF THE PLAY PARTNER: | 2.7% (2) | 3.8% (3) | 4.3% (6) | 1.6% (1) |
| SNIFF DIFFERENT ANIMAL: | 6.9% (5) | 5.0% (4) | 7.9% (11) | 7.8% (5) |
| SNIFF THE ENVIRONMENT: | 45.2% (33) | 42.5% (34) | 46.4% (65) | 48.4% (31) |
| OTHER: | 2.7% (2) | 1.2% (1) | 0.0% (0) | 3.1% (2) |

relatively infrequently, although eating and drinking were seen more often after play than before it. Sexual behaviour was observed to follow 10% of play-bouts involving males between 41-50 days; as with the data on the antecedents of play, this reflects the high frequency of sexual behaviour during this age-period.

### 3.3.8: How play-bouts ended:

#### 3.3.8.1: Overall frequency of different bout-endings (21-60 days, males and females combined):

Fig. 3.7 shows the relative frequencies with which various categories of bout-ending were observed to occur, combining the data for both sexes and all age-periods.

The most common way in which a bout ended was for one of the interactants simply to move away from the other; 43% of bouts ended in this manner. A1 was as likely to move away from A2, as was A2 from A1; 23% of bouts were terminated by the former moving away, and 20% by the departure of the latter.

"Moving away" did not necessarily involve one of the interactants moving away completely from the other's vicinity (as is confirmed by the results in the Section on proximity in play, below): often a mere turning away of the terminating animal sufficed to end the bout. When this occurred, it constituted a play-signal which marked the end of the interaction, as clearly as the initial pounce served to signal the initiation of play. One (or sometimes

FIG.3.7: OVERALL RELATIVE FREQUENCY OF DIFFERENT WAYS IN WHICH PLAY ENDED
(21-60 DAYS, MALES AND FEMALES COMBINED)

both) of the players would turn away abruptly and then back again towards the partner, and play would "switch off" almost instantly.

The second most frequent way in which play ended was by one of the players becoming more involved with sniffing the surrounding inanimate environment (cage walls or floor) than with maintaining the play interaction. 26% of all bouts ended like this (17% terminated by A1, and 8% by A2). Usually, A1 stepped off his play partner, and began to sniff the ground nearby (or the wall, if play was occurring immediately next to it), apparently totally disregarding the animal with which he had just played and becoming unreceptive to any attempts by that animal to renew the play. A2 would end bouts either in the same way (if A2 was on top at the time); or, if A2 was laying on his back pinned down by A1 he might twist round to sniff the ground, A1 allowing him to get up without any hindrance. (Although the convention was adopted that only one of the animals could end the bout, just as only one was considered to begin it, this kind of behaviour emphasises the fact that play is essentially an interaction which both partners might mutually take some part in initiating and ending).

Third in order of frequency for ending play, was for either A1 or A2 to be distracted from playing with their present partner. This category accounted for 18% of all bout-endings. Distraction occurred either by a third animal breaking into the play-bout, so that the initiative

for terminating the encounter in a sense came from this other pup; or by the player himself breaking off play with his present partner in order to sniff, chase, follow, play or otherwise interact with a different animal who provided a distraction merely because of his presence nearby.

Small proportions of bouts (under 5% in all cases) were observed to be terminated by the remaining two categories of ending: self-grooming, and sniffing the play-partner. In both cases, A1 performed these behaviours more often than A2. In the case of self-grooming, what seemed to happen was that A1, laying over A2 and in the process of grooming him, came to transfer his efforts towards grooming himself. This allowed A2 to regain normal posture and move away unimpeded.

The termination of play by one of the players breaking off from play in order to sniff the play-partner, was in practice quite different from the kind of olfactory investigation performed within the play-bout itself, since it was accompanied by the sniffing animal moving away from ventral-ventral contact with his partner and generally failing to respond to any attempts by the other animal to maintain a playful type of interaction.

3.3.8.2: Age-differences in the frequency of bout-endings (males and females combined):

Table 3.21 shows how often the different categories of bout-endings were seen to occur in each age-period,

TABLE 3.21: AGE CHANGES IN HOW PLAY ENDED (M+F COMBINED):

(Percentages are of the total number of play-bouts observed in the age-period concerned, combining the data for males and females. "A1" = "initiator", "A2" = "recipient").

| Category of bout-ending: | Age-period: 21-30: | 31-40: | 41-50: | 51-60: |
|---|---|---|---|---|
| A1 MOVES AWAY: | 19.3% (29) | 21.0% (37) | 27.8% (75) | 20.2% (21) |
| A2 MOVES AWAY: | 28.7% (43) | 22.2% (39) | 14.8% (40) | 20.2% (21) |
| A1 IS DISTRACTED: | 10.8% (15) | 13.1% (23) | 14.1% (38) | 12.5% (13) |
| A2 IS DISTRACTED: | 3.3% (5) | 7.4% (13) | 5.9% (16) | 3.8% (4) |
| A1 SNIFFS GROUND: | 21.3% (32) | 17.6% (31) | 15.2% (41) | 16.4% (17) |
| A2 SNIFFS GROUND: | 10.0% (15) | 9.7% (17) | 7.8% (21) | 4.8% (5) |
| A1 SELF-GROOMS: | 2.7% (4) | 0.6% (1) | 3.7% (10) | 8.6% (9) |
| A2 SELF-GROOMS: | 1.3% (2) | 2.3% (4) | 2.2% (6) | 1.0% (1) |
| A1 SNIFFS A2: | 0.7% (1) | 2.8% (5) | 4.1% (11) | 6.7% (7) |
| A2 SNIFFS A1: | 0.0% (0) | 1.7% (3) | 0.4% (1) | 1.9% (2) |
| SEXUAL BEHAVIOUR: | 0.0% (0) | 0.0% (0) | 1.9% (5) | 0.0% (0) |
| OTHER: | 2.7% (4) | 1.7% (3) | 2.2% (6) | 3.8% (4) |

combining the data for males and females. With some fluctuations, the overall pattern described above was shown in all four age-periods - ie, the most common endings were firstly separation of the players, secondly breaking off from play to sniff the environment, and thirdly being distracted by a different animal. This analysis does however reveal two age-changes in bout-endings, which may possibly be related to each other. There was a steady increase with age in the frequency with which play ended by A1 sniffing A2; and sexual activities were seen to terminate play only during the 41-50 day age-period (and then only in less than 2% of bouts within that period).

3.3.8.3: Overall sex-differences in the frequency of bout-endings (21-60 days):

Table 3.22 shows the relative frequencies of the different categories of bout-endings, analysed according to the sexes of the animals involved - MA1/MA2, FA1/FA2, MA1/FA2, FA1/MA2. With minor variations, the overall pattern of bout-endings described previously was shown by all of these classes of interactant. There are some indications that play initiated by males was slightly more likely to be disrupted by sexual activity than was play initiated by females. Sniffing of the play-partner was more common as an ending of play-bouts inititated by the former than by the latter; and no play-bouts between females were terminated by sexual activity. These are very

TABLE 3.22: OVERALL SEX-DIFFERENCES IN HOW PLAY ENDED (21-60 DAYS):

(Percentages are of the total number of play-bouts involving the sexes of interactants concerned, combining together the data from all age-periods. "M" = male, "F" = female, "A1"=initiator, "A2"=recipient)

| Category of bout-ending: | Sexes of interactants: MA1-MA2 | FA1-FA2 | MA1-FA2 | FA1-MA2 |
|---|---|---|---|---|
| A1 MOVES AWAY: | 22.9% (41) | 19.3% (23) | 24.4% (58) | 24.4% (40) |
| A2 MOVES AWAY: | 22.4% (40) | 21.0% (25) | 21.0% (50) | 17.1% (28) |
| A1 IS DISTRACTED: | 10.1% (18) | 10.1% (12) | 16.0% (38) | 12.8% (21) |
| A2 IS DISTRACTED: | 8.4% (15) | 5.0% (6) | 5.0% (12) | 3.1% (5) |
| A1 SNIFFS GROUND: | 16.2% (29) | 20.2% (24) | 14.7% (35) | 20.1% (33) |
| A2 SNIFFS GROUND: | 7.8% (14) | 12.6% (15) | 5.0% (12) | 10.4% (17) |
| A1 SELF-GROOMS: | 1.7% (3) | 5.0% (6) | 5.0% (12) | 1.8% (3) |
| A2 SELF-GROOMS: | 1.1% (2) | 1.7% (2) | 0.8% (2) | 4.3% (7) |
| A1 SNIFFS A2: | 5.0% (9) | 2.5% (3) | 4.2% (10) | 1.8% (3) |
| A2 SNIFFS A1: | 0.0% (0) | 0.0% (0) | 0.8% (2) | 1.2% (2) |
| SEXUAL BEHAVIOUR: | 0.6% (1) | 0.0% (0) | 1.3% (3) | 0.6% (1) |
| OTHER: | 3.9% (7) | 2.5% (3) | 1.7% (4) | 2.4% (4) |

small differences, however, which may well be attributable to sampling error. The main conclusion is that there were no major sex-differences in how play ended.

3.3.8.4: Age x sex differences in the frequency of bout-endings:

Table 3.23 gives the relative frequencies of the various categories of bout-endings, for each permutation of age and sexes of interactants. There appear to be no systematic age-related sex-differences in how play ended, when one takes account of the different numbers of bouts observed for each age/sex category of player.

3.3.8.5: Summary of data on how play ended:

The overall picture given by these data is that play was in most cases terminated by physical separation of the interactants; secondarily, by involvement of one of the players in exploration of his immediate environment; and thirdly, by one of the players becoming distracted from play by another animal. Only comparatively minor age- and sex-differences were observed.

In all cases, A1 was responsible for ending more bouts than A2. Overall, A1 appeared to be responsible for ending 60% of all play-bouts. Since most play-bouts involve little reciprocity (see section 3.3.4 on role-reversals in play), this is obviously going to be the case: if the animal that initiates the interaction usually remains on top for the duration of that encounter, then it

TABLE 3.23: AGE-CHANGES IN SEX-DIFFERENCES IN HOW PLAY ENDED:

(Percentages are of the total number of play-bouts observed in the age-period concerned, which involved the sexes of interactants in question; other conventions as for table 3.21)

(a) 21-30 DAYS:

| | Sexes of interactants: | |
|---|---|---|
| Category of ending: | MA1-MA2: | FA1-FA2: |
| A1 MOVES AWAY: | 15.8% (6) | 20.0% (5) |
| A2 MOVES AWAY: | 26.3% (10) | 32.0% (8) |
| A1 IS DISTRACTED: | 13.2% (5) | 12.0% (3) |
| A2 IS DISTRACTED: | 5.3% (2) | 0.0% (0) |
| A1 SNIFFS GROUND: | 18.4% (7) | 16.0% (4) |
| A2 SNIFFS GROUND: | 7.9% (3) | 16.0% (4) |
| A1 SELF-GROOMS: | 2.6% (1) | 0.0% (0) |
| A2 SELF-GROOMS: | 2.6% (1) | 0.0% (0) |
| A1 SNIFFS A2: | 2.6% (1) | 0.0% (0) |
| A2 SNIFFS A1: | 0.0% (0) | 0.0% (0) |
| SEXUAL BEHAVIOUR: | 0.0% (0) | 0.0% (0) |
| OTHER: | 5.3% (2) | 4.0% (1) |

| Category of ending: | MA1-FA2: | FA1-MA2: |
|---|---|---|
| A1 MOVES AWAY: | 25.0% (12) | 15.4% (6) |
| A2 MOVES AWAY: | 29.2% (14) | 28.2% (11) |
| A1 IS DISTRACTED: | 10.4% (5) | 5.1% (2) |
| A2 IS DISTRACTED: | 6.3% (3) | 0.0% (0) |
| A1 SNIFFS GROUND: | 14.6% (7) | 35.9% (14) |
| A2 SNIFFS GROUND: | 10.4% (5) | 7.7% (3) |
| A1 SELF-GROOMS: | 4.2% (2) | 2.6% (1) |
| A2 SELF-GROOMS: | 0.0% (0) | 2.6% (1) |
| A1 SNIFFS A2: | 0.0% (0) | 0.0% (0) |
| A2 SNIFFS A1: | 0.0% (0) | 0.0% (0) |
| SEXUAL BEHAVIOUR: | 0.0% (0) | 0.0% (0) |
| OTHER: | 0.0% (0) | 2.6% (1) |

3.23(b): 31-40 DAYS:

| Category of ending: | Sexes of interactants: MA1-MA2: | | FA1-FA2: | |
|---|---|---|---|---|
| A1 MOVES AWAY: | 20.0% | (11) | 18.8% | (6) |
| A2 MOVES AWAY: | 27.3% | (15) | 15.6% | (5) |
| A1 IS DISTRACTED: | 5.5% | (3) | 12.5% | (4) |
| A2 IS DISTRACTED: | 10.9% | (6) | 9.4% | (3) |
| A1 SNIFFS GROUND: | 18.2% | (10) | 12.5% | (4) |
| A2 SNIFFS GROUND: | 10.9% | (6) | 15.6% | (5) |
| A1 SELF-GROOMS: | 0.0% | (0) | 0.0% | (0) |
| A2 SELF-GROOMS: | 1.8% | (1) | 3.1% | (1) |
| A1 SNIFFS A2: | 3.6% | (2) | 6.3% | (2) |
| A2 SNIFFS A1: | 0.0% | (0) | 0.0% | (0) |
| SEXUAL BEHAVIOUR: | 0.0% | (0) | 0.0% | (0) |
| OTHER: | 1.8% | (1) | 6.3% | (2) |

| Category of ending: | MA1-FA2: | | FA1-MA2: | |
|---|---|---|---|---|
| A1 MOVES AWAY: | 16.7% | (8) | 29.3% | (12) |
| A2 MOVES AWAY: | 25.0% | (12) | 17.1% | (7) |
| A1 IS DISTRACTED: | 20.8% | (10) | 14.6% | (6) |
| A2 IS DISTRACTED: | 8.3% | (4) | 0.0% | (0) |
| A1 SNIFFS GROUND: | 18.8% | (9) | 19.5% | (8) |
| A2 SNIFFS GROUND: | 4.2% | (2) | 9.8% | (4) |
| A1 SELF-GROOMS: | 2.1% | (1) | 0.0% | (0) |
| A2 SELF-GROOMS: | 0.0% | (0) | 4.9% | (2) |
| A1 SNIFFS A2: | 4.2% | (2) | 0.0% | (0) |
| A2 SNIFFS A1: | 0.0% | (0) | 2.4% | (1) |
| SEXUAL BEHAVIOUR: | 0.0% | (0) | 0.0% | (0) |
| OTHER: | 0.0% | (0) | 2.4% | (1) |

3.23(c): 41-50 DAYS:

| Category of ending: | Sexes of interactants: MA1-MA2: | | FA1-FA2: | |
|---|---|---|---|---|
| A1 MOVES AWAY: | 28.1% | (18) | 18.9% | (7) |
| A2 MOVES AWAY: | 20.3% | (13) | 10.8% | (4) |
| A1 IS DISTRACTED: | 12.5% | (8) | 10.8% | (4) |
| A2 IS DISTRACTED: | 9.4% | (6) | 8.1% | (3) |
| A1 SNIFFS GROUND: | 10.9% | (7) | 32.4% | (12) |
| A2 SNIFFS GROUND: | 6.3% | (4) | 10.8% | (4) |
| A1 SELF-GROOMS: | 1.6% | (1) | 5.4% | (2) |
| A2 SELF-GROOMS: | 0.0% | (0) | 2.7% | (1) |
| A1 SNIFFS A2: | 4.7% | (3) | 0.0% | (0) |
| A2 SNIFFS A1: | 0.0% | (0) | 0.0% | (0) |
| SEXUAL BEHAVIOUR: | 1.6% | (1) | 0.0% | (0) |
| OTHER: | 4.7% | (3) | 0.0% | (0) |

| Category of ending: | MA1-FA2: | | FA1-MA2: | |
|---|---|---|---|---|
| A1 MOVES AWAY: | 29.1% | (30) | 30.3% | (20) |
| A2 MOVES AWAY: | 14.6% | (15) | 12.1% | (8) |
| A1 IS DISTRACTED: | 16.5% | (17) | 13.6% | (9) |
| A2 IS DISTRACTED: | 4.9% | (5) | 3.0% | (2) |
| A1 SNIFFS GROUND: | 10.7% | (11) | 16.7% | (11) |
| A2 SNIFFS GROUND: | 3.9% | (4) | 13.6% | (9) |
| A1 SELF-GROOMS: | 6.8% | (7) | 0.0% | (0) |
| A2 SELF-GROOMS: | 1.9% | (2) | 4.6% | (3) |
| A1 SNIFFS A2: | 5.8% | (6) | 3.0% | (2) |
| A2 SNIFFS A1: | 1.0% | (1) | 0.0% | (0) |
| SEXUAL BEHAVIOUR: | 2.9% | (3) | 1.5% | (1) |
| OTHER: | 1.9% | (2) | 1.5% | (1) |

3.23(d): 51-60 DAYS:

| Category of ending: | Sexes of interactants: MA1-MA2: | | FA1-FA2: | |
|---|---|---|---|---|
| A1 MOVES AWAY: | 27.3% | (6) | 20.0% | (5) |
| A2 MOVES AWAY: | 9.1% | (2) | 32.0% | (8) |
| A1 IS DISTRACTED: | 9.1% | (2) | 4.0% | (1) |
| A2 IS DISTRACTED: | 4.6% | (1) | 0.0% | (0) |
| A1 SNIFFS GROUND: | 22.7% | (5) | 16.0% | (4) |
| A2 SNIFFS GROUND: | 4.6% | (1) | 8.0% | (2) |
| A1 SELF-GROOMS: | 4.6% | (1) | 16.0% | (4) |
| A2 SELF-GROOMS: | 0.0% | (0) | 0.0% | (0) |
| A1 SNIFFS A2: | 13.6% | (3) | 4.0% | (1) |
| A2 SNIFFS A1: | 0.0% | (0) | 0.0% | (0) |
| SEXUAL BEHAVIOUR: | 0.0% | (0) | 0.0% | (0) |
| OTHER: | 4.6% | (1) | 0.0% | (0) |

| Category of ending: | MA1-FA2: | | FA1-MA2: | |
|---|---|---|---|---|
| A1 MOVES AWAY: | 20.5% | (8) | 11.1% | (2) |
| A2 MOVES AWAY: | 23.1% | (9) | 11.1% | (2) |
| A1 IS DISTRACTED: | 15.4% | (6) | 22.2% | (4) |
| A2 IS DISTRACTED: | 0.0% | (0) | 16.7% | (3) |
| A1 SNIFFS GROUND: | 20.5% | (8) | 0.0% | (0) |
| A2 SNIFFS GROUND: | 2.6% | (1) | 5.6% | (1) |
| A1 SELF-GROOMS: | 5.1% | (2) | 11.1% | (2) |
| A2 SELF-GROOMS: | 0.0% | (0) | 5.6% | (1) |
| A1 SNIFFS A2: | 5.1% | (2) | 5.6% | (1) |
| A2 SNIFFS A1: | 2.6% | (1) | 5.6% | (1) |
| SEXUAL BEHAVIOUR: | 0.0% | (0) | 0.0% | (0) |
| OTHER: | 5.1% | (2) | 5.6% | (1) |

will be easier for him to terminate it than it will for the animal underneath because the latter has to extricate himself from the former's pinning before he can be seen to end the play-bout.

Those bouts where A2 was responsible for ending the play thus consist of those instances where A2 was actually in a position to end it: ie, they represent a combination of those bouts where A2 himself was on top at the end of the bout, and those bouts where A2 was allowed to right himself largely unhindered by A1. In the latter case, the play had probably effectively ended before the human observer had recognised the fact; play often ended by one or both of the partners simply "switching off" their "playfulness", and one got the feeling that what one was recording on this measure was not what was actually terminating the play but rather the first observable manifestation of the fact that play had ended.

## 3.3.9: Location of play-partners in the environment during play:

### 3.3.9.1: Proximity to the wall during play:

Informal observations suggested that the thigmotaxis shown by rats in non-playful activities was also maintained during playful interactions. In order to provide a quantitative estimate of whether rats do prefer to play near to what they might regard as protective cover, a record was taken for each play-bout of how far

FIG. 3.8: DIAGRAM OF THE ZONES USED FOR RECORDING THE LOCATION OF PLAY-BOUTS WITHIN THE CAGE:

(NB: not drawn to scale. For explanation see section 3.3.9.2)

from the nearest cage-wall the interactants were, while they were wrestling. This was scored as: within 10 cm of a wall; within 10 to 20 cm of a wall; and no proximity to a wall (over 20 cm away). (See fig. 3.8).

These observed frequencies were compared by Chi-squared tests to those expected if the players were located at random within the environment. In calculating the expected frequencies, account had to be taken of the different areas encompassed by each of these three zones: 64% of the cage floor area was encompassed by the inner zone (ie, over 20 cm from the wall), 17% by the middle zone, and 19% by the strip nearest the walls, so by chance one might expect the animals to be observed mainly within the central area.

3.3.9.1.1: Overall proximity of players to the wall (21-60 days, males and females combined):

Table 3.24(a) shows the overall frequency with which play was observed to occur in each of the three proximity zones just described, combining the data from all ages and both sexes.

There was a clear and highly significant preference for playing within 10 cm of the nearest wall. These data in fact underestimate the extent of the preference for cover during play, since many of the bouts scored under "no proximity" were located close to large bundles of nest-material, or within deep depressions excavated by the animals (not necessarily those which were playing) in

TABLE 3.24: PROXIMITY TO THE CAGE WALL DURING PLAY:

(a) OVERALL PROXIMITY TO CAGE WALL (21-60 DAYS, MALES AND FEMALES COMBINED):

(Percentages are of the total number of bouts observed, 700; raw data are in brackets. "O" = "observed", referring to the actual numbers of bouts occurring within each of the three proximity zones; "E" = "expected", the number of bouts which would be expected to occur within those zones if location of play within the environment were randomly-determined)

| | LEVEL OF PROXIMITY TO CAGE WALL | | | |
|---|---|---|---|---|
| | <10cm | 10-20cm | >20cm | Chi-Sq. (2 df) |
| O: | 70.7% (495) | 13.1% (92) | 16.1% (113) | 1241.92, |
| E: | 19.0% (133) | 17.0% (119) | 64.0% (448) | p<0.0001 |

(b) AGE-CHANGES IN PROXIMITY TO CAGE WALL (M+F COMBINED):

(Expressed as percentages of the total number of bouts in each age-period; raw totals in brackets).

| PROXIMITY TO WALL: | AGE-PERIOD: 21-30: | 31-40: | 41-50: | 51-60: |
|---|---|---|---|---|
| <10 cm: | 76.0% (114) | 65.9% (116) | 70.4% (190) | 72.1% (75) |
| 10-20 cm: | 13.3% (20) | 15.9% (28) | 12.6% (34) | 9.6% (10) |
| >20 cm: | 10.7% (16) | 18.2% (32) | 17.0% (46) | 18.3% (19) |

3.24(c): OVERALL SEX-DIFFERENCES IN PROXIMITY TO CAGE WALL (21-60 DAYS):

(Expressed as percentages of the total number of bouts recorded for each permutation of players' sexes: raw totals in brackets).

| PROXIMITY TO WALL: | SEXES OF PLAYERS MA1-MA2 | FA1-FA2 | MA1-FA2 | FA1-MA2 |
|---|---|---|---|---|
| <10 cm: | 67.6% (121) | 68.1% (81) | 71.8% (171) | 74.4% (122) |
| 10-20 cm: | 11.2% (20) | 17.6% (21) | 12.6% (30) | 12.8% (21) |
| >20 cm: | 21.2% (38) | 14.3% (17) | 15.5% (37) | 12.8% (21) |

the inner regions of the environment. The number of bouts occurring away from any cover at all was very small, suggesting that rats strongly prefer not to play in exposed areas - ie, that during play, they maintain the marked thigmotaxis that they display during more "serious" activities.

3.3.9.1.2: Age-differences in preference for cover during play (males and females combined):

Table 3.24(b) shows the proximity data described above, broken down by age but still combining the data for males and females. No consistent age-related trends were found: the same pattern, of preference for playing within 10 cm of cover, and avoidance of the centre of the environment, was shown at all ages. Clearly, increased body-size of the subjects (so that, relative to the animals, the environment becomes smaller) and increased familiarity with the environment with increasing age, do nothing to change these preferences.

3.3.9.1.3: Overall sex-differences in proximity to cover during play (21-60 days):

Taking all age-periods together, table 3.24(c) shows the frequency with which play occurred within each of the three zones described above, for each permutation of players' sexes (MM, FF, MF, FM). There were no consistent sex-differences in proximity to cover: again, play occurred much more frequently within 10 cm of a wall, than

elsewhere in the environment.

3.3.9.2: Location of play-bouts in the environment:

The floor of the environment was divided into nine areas of equal size, as shown by table 3.25. The location of each play-bout within this grid was recorded. The observed frequencies of play in each location were then compared to the expected frequencies obtained under the hypothesis that play occurred randomly around the perimeter of the cage.

Only the observed and expected scores for the eight peripheral regions of the environment were used in these calculations. Inclusion of the central area of the cage would merely reiterate the findings of the previous section that play was infrequently observed in the inner area, whereas the issue here is, given that play does occur around the periphery of the cage, whether or not it is more likely to occur at certain locations rather than others - for example, near areas containing food and water, so that play might be interpreted as being in some way related to defence of a resource.

Unfortunately data on this measure were collected only for 95 bouts from L1 (between days 41 and 60), and 92 bouts from L2 (between days 21-30, and 41-60), so a full age and sex analysis was not possible. Table 3.25 shows the observed and expected frequencies of play in each location, and the results of a Chi-Squared Goodness of

TABLE 3.25: OVERALL LOCATION OF PLAY IN THE ENVIRONMENT (21-60 DAYS, M+F COMBINED):

(Percentages are observed frequencies, as percentages of the total number of bouts for which data were obtained: N=187. All positions are with respect to the observer's seating position, which was closest to near-middle).

| | | | | | |
|---|---|---|---|---|---|
| Far left: | 16 (8.6%) | Far Middle: | 30 (16.0%) | Far right: | 15 (8.0%) |
| Middle left: | 11 (5.9%) | Middle: | 13 (6.9%) | Middle right: | 16 (8.6%) |
| Water-spouts: | 21 (11.2%) | Near middle: | 34 (18.2%) | Food-hopper: | 31 (16.6%) |

Expected frequency for all peripheral locations is 23.4.
Chi-Squared Goodness of Fit = 23.64, with 7 df: $p<0.01$.

Fit test on these, combining the data for the two litters. (Note that the observed frequencies of play in the centre of the cage are shown, even though they were not used in the Chi-Squared calculations).

Table 3.25 shows that play was not distributed randomly around the perimeter of the cage (Chi-squared = 24.64, 7 df; $p<0.01$). Without information on the location within the cage of non-play behaviours, these data are difficult to interpret. However, they offer little support for suggestions that play occurs primarily in areas of the environment containing resources. Although play took place fairly frequently in the vicinity of the food-hopper and water-spouts, it occurred equally often along the front of the cage. These data are more consistent with the interpretation that play occurred where the animals were most active - ie, away from the corners of the cage, where their nests tended to be.

3.3.9.3: Summary of data on location of play in the environment:

Young rats show a very marked avoidance of playing in the centre of the cage. Whatever the cause of this phenomenon, the net result is that play occurs close to physical cover and away from exposed areas. Within the various parts of the perimeter of the cage, subjects preferred to play in certain areas rather than others. However, these preferred areas did not correspond particularly closely to those regions of the cage which

contained potentially-contestable resources such as food or water. On the basis of the limited data available, rats appear to play where they are most active.

3.3.10: Who approached whom, before play began:

For each play-bout, a note was made of which of the two interactants approached the other. Observations fell into four categories, according to the players' behaviour in the three seconds immediately before play began:

(1) A1 approached A2;

(2) A2 approached A1;

(3) both animals were already in close proximity (bodies within 10 cm of each other);

(4) both animals approached each other simultaneously.

3.3.10.1: Overall frequency of categories of approach behavour (21-60 days, males and females combined):

Table 3.26 gives the overall frequencies with which each of these categories was observed to occur, combining the data for both sexes and all age-periods. Nearly half (46%) of all bouts were preceded by A1 approaching A2. The next most common category, accounting for 30% of all bouts, was for both pups to be close to each other already. 18% of bouts occurred after A2 approached A1. It was relatively uncommon for both partners to approach

TABLE 3.26: OVERALL FREQUENCIES OF CATEGORIES OF APPROACH BEHAVIOUR (21-60 DAYS, MALES AND FEMALES COMBINED):

(Percentages are of the total number of bouts for which there are data, ie 670; raw data in brackets)

| | | |
|---|---|---|
| A1 approached A2 | : | 46.0% (308) |
| A2 approached A1 | : | 18.4% (123) |
| Both approached | : | 5.2% (35) |
| Both already present | : | 30.4% (204) |
| No data | : | (30) |

TABLE 3.27: AGE-DIFFERENCES IN FREQUENCIES OF CATEGORIES OF APPROACH BEHAVIOUR (MALES AND FEMALES COMBINED):

(Percentages are of the total number of bouts in each age-period, for which there are data; raw data in brackets)

| | Age-period: | | | |
|---|---|---|---|---|
| Category of Approach: | 21-30: | 31-40: | 41-50: | 51-60: |
| A1 approached A2 : | 41.2% (56) | 46.1% (77) | 46.6% (123) | 50.5% (52) |
| A2 approached A1 : | 22.8% (31) | 16.8% (28) | 14.4% (38) | 25.2% (26) |
| Both approached : | 0.7% (1) | 4.8% (8) | 7.6% (20) | 5.8% (6) |
| Both already present: | 35.3% (48) | 32.3% (54) | 31.4% (83) | 18.5% (19) |
| No data : | (14) | (9) | (6) | (1) |

each other, only 5% of all bouts resulting from this type of encounter.

One implication of these results is that they reinforce the view suggested by the data on the location of play - namely, that play does not involve the defence of a resource site. If this were the case one might expect the category of A2 approaching A1 to be the most common, in the sense of a defender of a resource attacking an intruder; however, this is clearly not the case, since the great majority of bouts involve the initiator either moving towards the recipient, or else already being near to him.

3.3.10.2: Age-differences in the frequency of categories of approach behavour (males and females combined):

Table 3.27 shows the relative frequencies of the different categories of approach behaviour in each of the four age-periods, combining the data for both sexes. There is some slight indication of an age-related trend, in that with increasing age play was more frequently preceded by the initiator approaching the recipient. There was a corresponding decrease with age in the frequency with which play occured between two animals already in close proximity. This possibly underlies the subjective impression that with advancing age play tends to become less of a "spontaneous" phenomenon between two nearby animals.

TABLE 3.28: OVERALL SEX-DIFFERENCES IN FREQUENCIES OF CATEGORIES OF APPROACH BEHAVIOUR (21-60 DAYS):

(Percentages are of the total number of bouts for each permutation of players' sexes, for which there are data; raw data in brackets)

| Category of Approach: | MA1-MA2 | FA1-FA2 | MA1-FA2 | FA1-MA2 |
|---|---|---|---|---|
| A1 approached A2 : | 41.6% (72) | 50.5% (56) | 47.2% (108) | 45.9% (72) |
| A2 approached A1 : | 18.5% (32) | 17.1% (19) | 18.8% (43) | 18.5% (29) |
| Both approached : | 6.9% (12) | 4.5% (5) | 4.4% (10) | 5.1% (8) |
| Both already present: | 33.0% (57) | 27.9% (31) | 29.7% (68) | 30.6% (48) |
| No data : | (6) | (8) | (9) | (7) |

3.3.10.3: Overall sex-differences in the frequency of categories of approach behavour (21-60 days):

Table 3.28 shows the relative frequencies of the different categories of approach behaviour in MM, FF, MF and FM play, combining the data for all age-periods. There were no overall sex-differences in the relative frequencies of the different catgeories of approach behaviour, the same pattern being shown in each case as in section 3.3.11.1 above.

3.3.10.4: Age x sex differences in the frequency of categories of approach behavour:

Table 3.29 shows the relative frequencies of the different categories of approach behaviour in each of the four age-periods studied, broken down by sex of interactant. Allowing for the differing numbers of bouts obtained for each age/sex category, there appear to be no systematic departures from the overall pattern of approach behaviour described previously.

3.3.10.5: Summary of data on approach behaviour:

Nearly half of all play bouts were preceded by the initiator approaching the recipient; a third of all play took place between animals who were already in close proximity; and less than a fifth of all bouts were preceded by the recipient moving towards the initiator. These data again suggest that play does not involve

TABLE 3.29: AGE-CHANGES IN SEX-DIFFERENCES IN FREQUENCIES OF CATEGORIES OF APPROACH BEHAVIOUR:

(Percentages are of the total number of bouts in each age-period for each permutation of players' sexes, for which there are data; raw data in brackets)

(a) MA1-MA2:

| | AGE-PERIOD | | | |
|---|---|---|---|---|
| Type of approach: | 21-30: | 31-40: | 41-50: | 51-60: |
| A1 approached A2 : | 27.8% (10) | 47.2% (25) | 43.5% (27) | 45.5% (10) |
| A2 approached A1 : | 22.2% (8) | 17.0% (9) | 14.5% (9) | 27.3% (6) |
| Both approached : | 2.8% (1) | 3.8% (2) | 11.3% (7) | 9.1% (2) |
| Both already present: | 47.2% (17) | 32.1% (17) | 30.6% (19) | 18.2% (4) |
| No data : | (2) | (2) | (2) | (0) |

(b) FA1-FA2:

| | AGE-PERIOD | | | |
|---|---|---|---|---|
| Type of approach: | 21-30: | 31-40: | 41-50: | 51-60: |
| A1 approached A2 : | 52.4% (11) | 42.9% (12) | 51.4% (19) | 56.0% (14) |
| A2 approached A1 : | 23.8% (5) | 14.3% (4) | 8.1% (3) | 28.0% (7) |
| Both approached : | 0.0% (0) | 7.1% (2) | 5.4% (2) | 4.0% (1) |
| Both already present: | 23.8% (5) | 35.7% (10) | 35.1% (13) | 12.0% (3) |
| No data : | (4) | (4) | (0) | (0) |

3.29(c): MA1-FA2:

| Type of approach: | AGE-PERIOD 21-30: | 31-40: | 41-50: | 51-60: |
|---|---|---|---|---|
| A1 approached A2 : | 47.7% (21) | 44.7% (21) | 49.0% (49) | 44.7% (17) |
| A2 approached A1 : | 25.0% (11) | 17.0% (8) | 16.0% (16) | 21.1% (8) |
| Both approached : | 0.0% (0) | 6.4% (3) | 5.0% (5) | 5.3% (2) |
| Both already present: | 27.3% (12) | 31.9% (15) | 30.0% (30) | 28.9% (11) |
| No data : | (4) | (1) | (3) | (1) |

(d) FA1-MA2:

| Type of approach: | AGE-PERIOD 21-30: | 31-40: | 41-50: | 51-60: |
|---|---|---|---|---|
| A1 approached A2 : | 40.0% (14) | 48.7% (19) | 43.1% (28) | 61.1% (11) |
| A2 approached A1 : | 20.0% (7) | 17.9% (7) | 15.4% (10) | 27.8% (5) |
| Both approached : | 0.0% (0) | 2.6% (1) | 9.2% (6) | 5.6% (1) |
| Both already present: | 40.0% (14) | 30.8% (12) | 32.3% (21) | 5.6% (1) |
| No data : | (4) | (2) | (1) | (0) |

defence of a resource from an approaching animal by the animal who initiates the play.

### 3.3.11: Proximity of interactants before and after play:

For each play-bout, a note was made of the proximity of the interactants to each other in the three seconds before, and the three seconds after the bout. If the animals' bodies were within approximately 20 cm of each other, "close proximity" was scored; and if they were further apart than this, "no proximity" was recorded. The purpose of this was to obtain a crude estimate of (a) whether or not play occurred between animals which were close to each other in the first place; and (b) whether, after play, animals remained close together or separated. These measures might reveal that play brought previously-separated animals into close contact with each other and resulted then in them staying close together; or it might be that play was most likely to occur between animals which were close to each other anyway, but then led to them separating.

This measure was complementary to that of who approached whom, but the two scores do not correspond in any direct way: two animals could be in "close proximity" on this measure, but nevertheless, A1 could approach A2 or A2 approach A1.

3.3.11.1: Overall proximity of players, before and after play (21-60 days, males and females combined):

Table 3.30 shows the overall frequencies of players being in close proximity or not, both before and after bouts, combining the data for all ages and both sexes.

Binomial tests (converted to approximations to the normal distribution in view of the large N's involved) were performed to determine whether animals were more likely to be in close proximity to each other before play, or were not. A similar comparison was made between the frequencies of proximity and no proximity after play. 56% of all play bouts involved players being close to each other before play began, and 44% were preceded by no proximity between them; thus, on an overall basis, play was significantly more likely to occur between individuals who were already in close proximity ("z" = 3.213, N = 700, $p<0.005$). Similarly, 58% of bouts were followed by the interactants remaining near to each other, and 42% were followed by no proximity, so that players were significantly more likely to remain in close proximity than they were to separate ("z" = 4.120, N = 700, $p<0.001$).

When proximity before and after each bout is taken into account, there were four possible permutations: proximity before and after; no proximity before or after; proximity before but not after; and no proximity before but proximity after. Table 3.30 shows that the most frequent of these was proximity both before and after a

TABLE 3.30: OVERALL FREQUENCY OF PROXIMITY BETWEEN PLAYERS, BEFORE AND AFTER PLAY (21-60 DAYS, M+F COMBINED):

( Percentages are of the total number of bouts observed, N= 700. "P" = close proximity; "NP" = no proximity).

| | | |
|---|---|---|
| Proximity before, and no proximity after: | 38.1% | (267) |
| No proximity before, and no proximity after: | 24.1% | (169) |
| Proximity before, and no proximity after: | 18.0% | (126) |
| No proximity before, and proximity after: | 19.7% | (138) |
| Total no. bouts with proximity before: | 56.1% | (393) |
| Total no. bouts with no proximity before: | 43.9% | (307) |

Binomial test: prob(P) = prob(NP): $z = -3.213$, $p<0.005$

| | | |
|---|---|---|
| Total no. bouts with proximity after: | 57.9% | (405) |
| Total no. bouts with no proximity after: | 42.1% | (295) |

Binomial test: prob(P) = prob(NP): $z = -4.120$, $p<0.001$

bout; 38% of bouts fell into this category (Chi-squared = 70.11, 3 df; $p<0.001$).

3.3.11.2: Overall sex-differences in proximity of players, before and after play (21-60 days):

Table 3.31 shows the relative frequencies of the proximity measures described above, analysed according to the participants' sexes, but summing the data over all age-periods. These data suggest that there were some sex-differences in the proximity measures. In the case of play-bouts involving female recipients (ie, FA1-FA2 and MA1-FA2 play), the interactants were as likely to be apart from each other before or after play, as they were to be together. In contrast, when play involved a male recipient, the players were more likely to be in close proximity before and after play than they were to be apart, in a ratio of 60:40 in favour of remaining close together. In other words, male recipients were more likely to be involved in play with an animal near to them, and were more likely to remain close to that animal once the play had ended.

In all cases, the most commonly observed permutation of proximity scores was proximity both before and after play; however, in the case of play involving a female recipient, the "no proximity before or after" category occurred almost equally frequently.

TABLE 3.31: OVERALL SEX-DIFFERENCES IN THE FREQUENCY OF PROXIMITY BETWEEN PLAYERS, BEFORE AND AFTER PLAY (21-60 DAYS):

(Percentages are of the total number of bouts performed by each permutation of players' sexes. "P" = close proximity; "NP" = no proximity).

| | SEXES OF PLAYERS | | | |
|---|---|---|---|---|
| Proximity: | MA1-MA2 | FA1-FA2 | MA1-FA2 | FA1-MA2 |
| P before, P after : | 41.9% (75) | 33.6% (40) | 34.0% (81) | 43.3% (71) |
| NP before, NP after: | 21.2% (38) | 31.1% (37) | 26.5% (63) | 18.9% (31) |
| P before, NP after : | 17.9% (32) | 16.0% (19) | 20.2% (48) | 16.5% (27) |
| NP before, P after : | 19.0% (34) | 19.3% (23) | 19.3% (46) | 21.3% (35) |
| Total: | 100.0% (179) | 100.0% (119) | 100.0% (238) | 100.0% (164) |

| | MA1-MA2 | FA1-FA2 | MA1-FA2 | FA1-MA2 |
|---|---|---|---|---|
| Total P before: | 59.8% (107) | 49.6% (59) | 54.2% (129) | 59.8% (98) |
| Total NP before: | 40.2% (72) | 50.4% (60) | 45.8% (109) | 40.2% (66) |
| Total P after: | 60.9% (109) | 52.9% (63) | 53.4% (127) | 64.6% (106) |
| Total NP after: | 39.1% (70) | 47.1% (56) | 46.6% (111) | 35.4% (58) |

3.3.11.3: Age-changes in proximity of players (males and females combined):

Table 3.32 shows the data on the proximity of players before and after play, broken down by age but combining the data for both sexes of interactant. There were no consistent age-changes in the proximity measure, except that in the final age-period play was more likely to occur between animals who were not close to each other beforehand. In the first three age-periods, play was more likely to occur between pups who were close together than between animals who were not near to each other (in a ratio of 60:40 in favour of the former category). In the final age-period the opposite pattern was shown, with approximately 60% of bouts occurring between animals who were not close to each other, and 40% between animals in close proximity. The frequency with which animals remained close together or separated after play had ended, remained very consistent across age-periods; in all cases, players were more likely to remain in close proximity than they were to separate.

3.3.11.4: Age-related sex-differences in proximity of players:

Table 3.33 shows the data on the proximity of players before and after play, analysed by age and sex. These figures reveal that there were few consistent age-related sex-differences in proximity between the interactants. Possible exceptions are found in the case of play between

TABLE 3.32: OVERALL AGE-CHANGES IN THE FREQUENCY OF PROXIMITY BETWEEN PLAYERS, BEFORE AND AFTER PLAY (M+F COMBINED):

(Percentages are of the total number of bouts observed in each age-period. "P" = close proximity; "NP" = no proximity).

| | AGE-PERIOD | | | |
|---|---|---|---|---|
| Proximity: | 21-30 | 31-40 | 41-50 | 51-60 |
| P before, P after : | 36.0% (54) | 42.6% (75) | 41.5% (112) | 25.0% (26) |
| NP before, NP after: | 22.7% (34) | 25.0% (44) | 21.1% (57) | 32.7% (34) |
| P before, NP after : | 21.3% (32) | 13.6% (24) | 20.0% (54) | 15.4% (16) |
| NP before, P after : | 20.0% (30) | 18.8% (33) | 17.4% (47) | 26.9% (28) |
| Total: | 100.0% (150) | 100.0% (176) | 100.0% (270) | 100.0% (104) |

| | 21-30 | 31-40 | 41-50 | 51-60 |
|---|---|---|---|---|
| Total P before: | 57.3% (86) | 56.3% (99) | 61.5% (166) | 40.4% (42) |
| Total NP before: | 42.7% (64) | 43.7% (77) | 38.5% (104) | 59.6% (62) |
| Total P after: | 56.0% (84) | 57.4% (101) | 58.9% (159) | 58.6% (61) |
| Total NP after: | 44.0% (66) | 42.6% (75) | 41.1% (111) | 35.4% (43) |

males, and in play initiated by females with males.

In the former instance, with increasing age, there was a decrease in the total frequency with which players were in close proximity to each other before the bout began, from 66% to 41% of bouts; ie, as the animals got older, play was more likely to be observed between animals who were not near to each other, than between adjacent male pups. There were no age-related changes in the proximity of male pups after play had ceased, however; in all four age-periods, approximately 60% of male-male bouts ended with the interactants remaining close to each other.

In the case of FA1-MA2 play, the pattern of proximity before and after play showed marked changes in the final age-period. Between 21-50 days, approximately 60% of bouts were accompanied by the players being in close proximity before the play began. However, between 51-60 days, this dropped to only 28% of bouts; ie, play between female initiators and male recipients was much more likely to occur between animals who were not near to each other beforehand. After the play had finished, for the first three age-periods the most frequently seen outcome was for the interactants to remain close to each other; however, in the final age-period players were as likely to move apart as they were to stay together.

The overall conclusion is that there were few age-related sex differences in the proximity of players before or after play.

TABLE 3.33: AGE-CHANGES IN SEX-DIFFERENCES IN THE FREQUENCY OF PROXIMITY BETWEEN PLAYERS, BEFORE AND AFTER PLAY:

(Percentages are of the total number of bouts observed in each age-period, for each permutation of players' sexes. "P" = close proximity; "NP" = no proximity. "M" = male; "F" = female; "A1" = initiator; "A2" = recipient of play).

(a) MA1-MA2:

| | AGE-PERIOD | | | |
|---|---|---|---|---|
| Type of approach: | 21-30 | 31-40 | 41-50 | 51-60 |
| P before, P after : | 47.4% (18) | 41.8% (23) | 43.8% (28) | 27.3% (6) |
| NP before, NP after: | 15.8% (6) | 23.6% (13) | 21.9% (14) | 22.7% (5) |
| P before, NP after : | 18.4% (7) | 20.0% (11) | 17.2% (11) | 13.6% (3) |
| NP before, P after : | 18.4% (7) | 14.5% (8) | 17.2% (11) | 36.4% (8) |
| Total: | 100.0% (38) | 99.9% (55) | 100.0% (64) | 100.0% (22) |
| Total P before: | 65.8% (25) | 61.8% (34) | 60.9% (39) | 40.9% (9) |
| Total NP before: | 34.2% (13) | 38.2% (21) | 39.1% (25) | 59.1% (13) |
| Total P after: | 65.8% (25) | 56.4% (31) | 60.9% (39) | 63.6% (14) |
| Total NP after: | 34.2% (13) | 43.6% (24) | 39.1% (25) | 36.4% (8) |

3.33(b): FA1-FA2:

| Type of approach: | AGE-PERIOD 21-30 | 31-40 | 41-50 | 51-60 |
|---|---|---|---|---|
| P before, P after : | 20.0% (5) | 34.4% (11) | 45.9% (17) | 28.0% (7) |
| NP before, NP after: | 36.0% (9) | 28.1% (9) | 21.6% (8) | 44.0% (11) |
| P before, NP after : | 24.0% (6) | 15.6% (5) | 10.8% (4) | 16.0% (4) |
| NP before, P after : | 20.0% (5) | 21.9% (7) | 21.6% (8) | 12.0% (3) |
| Total: | 100.0% (25) | 99.9% (32) | 99.9% (37) | 100.0% (25) |
| Total P before: | 44.0% (11) | 50.0% (16) | 56.8% (21) | 44.0% (11) |
| Total NP before: | 56.0% (14) | 50.0% (16) | 43.2% (16) | 56.0% (14) |
| Total P after: | 40.0% (10) | 56.3% (18) | 67.6% (25) | 40.0% (10) |
| Total NP after: | 60.0% (15) | 43.7% (14) | 32.4% (12) | 60.0% (15) |

33.3(c): MA1-FA2:

| Type of approach: | AGE-PERIOD 21-30 | 31-40 | 41-50 | 51-60 |
|---|---|---|---|---|
| P before, P after : | 27.1% (13) | 41.7% (20) | 35.9% (37) | 28.2% (11) |
| NP before, NP after: | 27.1% (13) | 35.4% (17) | 20.4% (21) | 30.8% (12) |
| P before, NP after : | 27.1% (13) | 8.3% (4) | 24.3% (25) | 15.4% (6) |
| NP before, P after : | 18.7% (9) | 14.6% (7) | 19.4% (20) | 25.6% (10) |
| Total: | 100.0% (48) | 100.0% (48) | 100.0% (103) | 100.0% (39) |
| Total P before: | 54.2% (26) | 50.0% (24) | 60.2% (62) | 43.6% (17) |
| Total NP before: | 45.8% (22) | 50.0% (24) | 39.8% (41) | 56.4% (22) |
| Total P after: | 45.8% (22) | 56.3% (27) | 55.3% (57) | 53.9% (21) |
| Total NP after: | 54.2% (26) | 43.7% (21) | 44.7% (46) | 46.1% (18) |

3.33(d): FA1-MA2:

| Type of approach: | AGE-PERIOD 21-30 | 31-40 | 41-50 | 51-60 |
|---|---|---|---|---|
| P before, P after : | 46.1% (18) | 51.2% (21) | 45.5% (30) | 11.1% (2) |
| NP before, NP after: | 15.4% (6) | 12.2% (5) | 21.2% (14) | 33.3% (6) |
| P before, NP after : | 15.4% (6) | 9.8% (4) | 21.2% (14) | 16.7% (3) |
| NP before, P after : | 23.1% (9) | 26.8% (11) | 12.1% (8) | 38.9% (7) |
| Total: | 100.0% (39) | 100.0% (41) | 100.0% (66) | 100.0% (18) |
| Total P before: | 61.5% (24) | 61.0% (25) | 66.7% (44) | 27.8% (5) |
| Total NP before: | 38.5% (15) | 39.0% (16) | 33.3% (22) | 72.2% (13) |
| Total P after: | 69.2% (27) | 78.1% (32) | 57.6% (38) | 50.0% (9) |
| Total NP after: | 30.8% (12) | 21.9% (9) | 42.4% (28) | 50.0% (9) |

3.3.11.5: Summary of data on proximity of players:

Overall, a significant majority of play-bouts (56%) were preceded by the interactants being in close proximity to each other. Players were also significantly more likely to remain near to each other after play had ended, than to move far apart. Nearly 40% of play bouts were both preceded and followed by close proximity.

Play involving male recipients (regardless of the sex of the initiator) tended to involve the two players being close to each other before and after play. In contrast, for play involving a female recipient, the categories of "proximity before and after", and "no proximity before and after", occurred with almost equal frequency. However, these were relatively minor departures from the overall pattern, which do not support any suggestions that female rats are more likely to avoid the animal with which they have just played.

In the last age period, play was more likely to occur between animals who were not close to each other beforehand. There were, however, no age changes in proximity after play; this suggests that, although the

most frequent means of terminating play seems to be for one of the players to move away from the other (see section 3.3.8), in most cases this moving away does not constitute a very marked separation of the animals concerned. Play does not lead to the play partners subsequently avoiding each other, and there are no tendencies for it to do so with increasing age - as one might expect if play became "rougher" with age.

## 3.3.12: DISCUSSION:

### 3.3.12.1: Overall summary of the results of this section:

#### 3.3.12.1.1: The frequency of play:

These data, obtained by rather different means to those in chapter two, nevertheless show a broadly similar ontogenetic trend to those reported in that chapter. The inverted-"U" -shaped frequency distribution of play was more coarsely sampled in the present studies, firstly because they involved the use of only four age-periods (rather than eight, as in chapter two), and secondly because the frequency of play was measured only indirectly, in terms of the ease with which suitable bouts could be selected for analysis. Nevertheless, the bulk of play appeared to occur between 31-50 days, as in the studies reported in chapter two.

The major sex difference found in play was for males

to be involved in more play-bouts than females. This was apparently because males initiated play with each other and with females more frequently than would be expected by chance. This difference was consistent over time.

The other analyses described in this chapter revealed remarkably few sex- or age-differences in play.

3.3.12.1.2: The duration of play:

Play was found to have an overall median duration of approximately 11 seconds, although this figure concealed a wide variation in bout length. Bout-termination was apparently randomly-determined; the majority of play-bouts were under 20 seconds long, but there was no particular "cut-off" point at which play was more likely to end. Bouts between males tended to last longer than those involving females. No age-differences were found in the duration of play, overall; however, in the first two age-periods, play between males lasted significantly longer than play involving females.

Fagen (1974, 1981) has suggested that if play has any benefits, then it is in the interests of players to guard against "cheating" by their partner. There are many forms that "cheating" could take. However, given that play-wrestling involves the interactants in positional advantage-seeking (Aldis, 1975), it might be that whatever benefit is obtained from play is obtained by the animal who is pinning, rather than the animal who is being pinned. This is, of course, a major assumption to make; it is quite conceivable that any benefit from play is derived

from being pinned rather than pinning, or that both animals derive benefits from play regardless of the roles which they happen to adopt. But, if being the "pinner" were the sought-after role, then cheating might consist of failing to allow the partner his "fair share" of pinning experience within a play-bout.

Evidence on this point comes from the analyses described in this chapter, of what proportion of the bout was spent by each of the interactants in the "on-top" position, and how often the players reversed roles between pinning and being pinned. These show that, within any given play-bout, there was typically very little reciprocity between the interactants; most bouts involved the intiator remaining on top of his partner for about two-thirds of the encounter, and two-thirds of all bouts involved no role reversals whatsoever. In short, a pup who initiated play tended to remain on top for most of the interaction: the recipient achieved near-total "domination" in only 4 bouts out of the total of 700 observed.

There were statistically significant correlations between the duration of bouts, the percentage of time each interactant was on top, and the mumber of role reversals which took place within a bout; however, these correlations were uniformly low, suggesting that players were not particularly sensitive to asymmetries in on-top relationships which occurred within any one particular bout. The small size of these correlations implies that

the majority of variation in bout length must have been associated with factors other than the degree of asymmetry within a bout.

Moreover, a practical point is that the very animal which might be "suffering" from the asymmetry (ie, the individual being pinned down) was usually in no position to do anything about it. The data on how bouts ended show that in more than half of the observed bouts, it was the initiator who determined how long a bout lasted - and yet he was the one who was presumably benefiting from the asymmetry (if such benefits exist).

There was some indication that females initiating play with males were less likely to maintain their initial on-top position for the duration of the encounter (a fact which possibly explains the relative infrequency of play initiated by females with males). There was also some evidence of a tendency for play (other than that initiated by females with males) to become less reciprocal, more "one-sided", with age. However, the overall conclusion from these investigations was that there was little evidence for any marked age or sex-differences in this feature of play - mainly because play was a highly asymmetrical encounter from the outset.

Taken in conjunction with the results of chapter two, which showed that all littermates fairly equally frequently engaged both in pinning others and in being pinned themselves, these data suggest that if young rats do guard against "cheating", then it is not by ensuring

* The data on individual differences in the frequency of "on-top" behaviour in social play, reported in chapter two (section 2.3.4.2), suggest that reciprocity <u>across</u> bouts – as opposed to <u>within</u> bouts – does in fact occur in rats, at least during the period studied.

that they alternate roles within a bout, but rather by alternating roles across bouts: ie, if "cheating" is avoided, then it is by engaging in numerous interactions and ensuring that over time, roughly as many separate bouts involve pinning as involve being pinned - even though any particular bout is itself highly asymmetrical (for or against that individual's benefit).*

Such a phenomenon, of numerous individually asymmetrical but comparatively brief encounters, would be in accordance with the way by which a reciprocally altruistic behaviour can evolve - ie, by means of numerous encounters, each in itself low in cost, but occurring between individuals who repeatedly interact with each other and keep account of the outcomes of previous interactions (Trivers 1972; Fagen 1974, 1981).

3.3.12.1.3: The context of play:

The main value of the results from the analyses of play's antecedents, consequences and manner of ending, and from the measures of proximity and location, is to show the relationship of play to other behaviours, emphasising its links with activity and exploration and showing clearly how different play is from agonistic behaviours.

Caution has to be exercised in interpreting these results, due to the lack of an adequate baseline against which to evaluate them. The relative frequencies with which various behaviours were observed to precede and follow play in the studies described in this chapter, have

to be assessed in the light of the relative frequencies of those activities in the animals' behavioural repertoire in general

Some insight may be given by a comparison of the contextual data given in this chapter, with the results of the time-sampling studies in chapter two - as long as due allowance is made for the procedural differences between the two sets of studies. Sleeping and maternal behaviour aside, the most frequent activities shown by the subjects in chapter two were eating and drinking (comprising 12% of all behaviour sampled), self-grooming (11%) and olfactory investigation of the inanimate environment (10%). Amongst non-play social behaviours, allo-grooming was most common (28% of all social behaviour), followed by social olfaction (23%) and agonistic activities of one form or another (17%).

On the basis of these data from chapter two, therefore, one might expect the relative frequencies of these behaviours to be reflected in the relative frequencies with which they preceded or followed play. However, the picture presented by the data in the current chapter is somewhat different.

Play was preceded by similar events for both the initiator and the recipient. The most frequent precursor by far was olfactory investigation of the environment - as might be expected on the basis of the findings of chapter two. The next most common were playing with a different partner (reflecting the fact that play-bouts tend to occur

in sessions rather than in isolation); locomotion; and olfactory investigation of the play partner. In other words, play was associated with exploration, both of the animate and inanimate environments (insofar as these can be meaningfully distinguished) and activity. Sedentary, maintenance behaviours (grooming, eating and drinking) and agonistic and sexual behaviours preceded play relatively infrequently - and yet, with the exception of sexual behaviour, all of these latter activities feature prominently in the young rat's behavioural repertoire.

The consequences of play revealed a similar pattern: olfactory investigation of the inanimate environment figured prominently, followed by playing with a different pup, locomotion, and playing with the same partner Again, eating, drinking, grooming, sex and agonistic actvities followed play only rarely. Agonistic behaviours, in particular, were very rarely associated with play; only 14 out of 700 play bouts (2%) were followed by agonistic or competitive activities: and yet these activities comprised 17% of the social behaviour of the subjects in chapter two.

Thus the consequences of play were similar to its precursors, except that olfactory investigation of the play-partner preceded play more frequently than it followed it, and that levels of self-grooming were higher following play than before it (which is hardly surprising, considering the ruffling of fur caused by vigorous rough and tumble). Play is thus occurring within a milieu of

activity, much of which consists of active exploration of the environment.

The lack of allogrooming before and after play, and the fact that olfactory investigation of the play-partner was less common after play than before it, hint at two major features of play: firstly that potentially it is able to provide a great deal of olfactory information about the interactant, and secondly that play is a major source of allogrooming. This is not to say that allogrooming and the acquisition of olfactory information are functions of play, but they are certainly major features of it.

The data on events preceding and following play also show how little association play has with agonistic activities. This is especially so when one considers that the categories of "agonistic" antecedents and consequences included activities which might well be considered only potentially "agonistic" or merely "competitive" - such as food-stealing, or jostling with another animal for access to some olfactorily-interesting spot on the cage wall or floor. Even using such a broad definition of agonistic behaviour, such behaviours occurred before or after a very small proportion of bouts. Furthermore there were no trends for agonistic precursors and sequelae to increase with age, even though the animals were in other circumstances becoming less tolerant of each other: in fact, there was a trend for agonistic antecedents to decline in frequency as pups matured.

Further emphasis of the lack of association between play and agonistic activities comes from the data on how play-bouts ended. Although most play-bouts were terminated by physical separation of the interactants, this was not by the animal underneath fleeing; as mentioned above, in at least half of the observed bouts, play was ended by the animal on top simply moving away from his partner. There were cases in which the recipient of the play ran away (often into the nest, and into the pile of resting pups, which was apparently an effective way of avoiding a pursuer), but more often than not play was simply "switched off": it became apparent that one or both of the pups had simply lost interest in the encounter, and moving away - in many cases amounting to litle more than a turning away of the head from the partner - effectively acted as a play signal that the interaction was to be considered finished.

The data on the proximity of the pups before and after play, and who approached whom before play occurred, also imply that play is essentially non-agonistic, whatever its superficial appearance. Most bouts involved the animals being in close proximity before and after. Just over half of all bouts involved the interactants being near to each other before play began; and nearly 60% of bouts were followed by the players remaining in close proximity to each other.

It appears that play had little effect on the proximity of pups either before or after it; it certainly

did not lead to immediate separation of the interactants in the same way as would adult fighting. Similarly, if play were linked to defence of resources (such as the food-hopper, water-spouts or incipient nesting-sites) one might expect it to have occurred more often in these sites than in other parts of the environment, and to be initiated by the animal who was already there rather than by the "intruder". However, this was found not to be the case. Although certain areas of the environment appeared to be preferred for play, these were not necessarily areas containing resources; and the single largest category of approach behaviour was for the initiator to approach the recipient, rather than for the intitiator to lay in wait for an "intruder".

3.3.12.2: Methodological criticisms of these studies:

The studies described in this chapter are open to various methodological criticisms. Some of these are concerned with the way in which bouts were selected for analysis, while others are to do with the analysis itself.

3.3.12.2.1: The restriction of analysis to exclusively dyadic interactions:

The validity of the results described in this chapter was possibly affected by the decision to analyse only exclusively dyadic play bouts. By confining attention to play between pairs, certain features of play may have been completely overlooked in the present studies; for example,

Humphreys (1982) looked at the size of play-groups in the laboratory rat, and claimed that they decreased with age, so that play increasingly became a dyadic phenomenon. It is conceivable that play between animals within larger groups might differ in various respects from play between pairs, for example in the number of role reversals occurring and in the overall duration of bouts, etc.

In this chapter, the main reason for confining analyses to play occurring between pairs of pups was primarily one of convenience; it proved much easier to make accurate measurements of the temporal and contextual features of dyadic interactions than of bouts involving three or more pups.

There is, however, also some justification for this policy in the nature of the play itself. Aldis (1975) and Symons (1978) have argued that play-wrestling is essentially a dyadic phenomenon, and that play within larger groups should really be thought of in terms of a number of successive, fleeting interactions between pairs of animals. The present author shares this view, and considers that group play in the rat is better considered in terms of the individual component interactions. However, the nature of play within groups should be investigated further; until then, the possibility remains that the restriction of analysis to dyadic play might somehow have biassed the data described in this chapter - or, at least, that the picture of rat play presented here is an incomplete one, in that it applies

only to a certain class of playful interaction.

3.3.12.2.2: The problems of defining a play-"bout":

In the present chapter, a "bout" of play was defined as beginning with an intitial pounce and ending with the cessation of contact between the two interactants for more than three seconds. These criteria were based on prior observations of rat play (mainly in the course of performing the studies described in chapter two), but are open to the criticisms that they are ad hoc and arbitrary. Obviously, a different set of criteria by which to establish the "boundaries" of instances of play would have yielded different data - not just in the case of the temporal measures, but also possibly in terms of the apparent context within which play occurred.

It is perhaps easier to defend the choice of criteria by which play was considered to have commenced, than the criteria by which it was deemed to have ended. The initial pounce seemed to represent a "play signal". It cannot be said that this pounce is observed solely in the context of initiating social play, since, in the form of one or more high "stotting" leaps, it was often observed to be performed by an active animal who was nowhere near another pup. It may thus represent in some instances an appetitive behaviour, showing that the performer is in a "playful mood"; or it may simply reflect a state of high arousal in the animal concerned, a condition during which social play is likely to occur (as appears to be the

case in the ferret - Sen Gupta, personal communication). However, although not all pounces were followed by playful wrestling, all instances of rough and tumble appeared to be preceded by a pounce, so that the use of this behaviour as a starting point for play-bouts seems justified on more than purely arbitrary grounds.

As far as the choice of criteria for deciding that play has ended are concerned, all that can be said is that a three-second cut-off point appeared to work well in practice, generally corroborating subjective impressions of when play had ended as opposed to being momentarily disrupted. Chalmers and Locke-Haydon (1981) have devised a more objective means of determining when play has ended in captive marmosets, by examining the nature of the inter-bout intervals. Unfortunately their paper did not come to the attention of the present author until the current studies were completed. However, a technique similar to theirs could readily be applied to the study of rat play, and would provide a sounder basis for deciding when play has ceased than that used in the present work.

3.3.12.2.3: Problems of context:

As mentioned in section 3.3.12.1.3, one problem with the analyses of play's context as reported in this chapter, is the lack of a baseline against which to evaluate them. For example, it could be argued that it is hardly surprising that most play occurs in a context of olfactory activity, since the studies in chapter two

suggest that this is what rats do much of the time anyway. While the contextual data do provide some indication of the milieu within which play occured - sufficient to show that the context was neither agonistic nor sedentary - they tell only half the story. A similar criticism applies to the analyses of where play occurred within the cage.

Ideally, what are required are analyses of the relative frequencies with which various behaviours precede and follow other social behaviours, especially agonistic ones - preferably in young animals rather than adult ones, although this might be difficult given the very low frequencies of juvenile agonistic behaviours (which is the reason why a contextual comparison between play and aggression was not performed here). Without these data as a comparison, the informativeness of the contextual analyses in this chapter is greatly limited, and future work should be directed at correcting this omission.

### 3.3.13: CONCLUSION:

Two main points emerge from the analyses described in this chapter.

Firstly, the most striking feature of the results of this chapter is that they show that any age- or sex-differences in rat play are primarily quantitative in nature, rather than qualitative. Although there were some differences between males and females in the relative frequency with which they were observed to play, they differed remarkably little in the nature of the play

itself or the context within which it occurred. The same applies to age-changes in play, which were confined to how much play occurred, rather than any systematic variations in the nature of the play itself.

This lack of consistent age-differences in play (other than in terms of frequency) is somewhat surprising when one considers that within the period in which rats play there are two major milestones of development - weaning, and the development of sexual maturity. The effects of enforced weaning at 21 days may well have disrupted any changes in play which are associated with weaning, and in retrospect this aspect of the procedure was a serious mistake. Nevertheless, one might have expected the development of sexual behaviour to have been reflected in play, but this was not the case. Though sexual behaviour increased in frequency as an antecedent of play from 30 days of age onwards (but mainly at 41-50 days), it was always a relatively minor precursor of play, especially when one considers its frequency in the general behaviour of young rats at this time.

The second major point to be made from these data is that they emphasise somewhat different aspects of play to those normally focussed upon - partly because they investigate different aspects of the behaviour itself than those which have been examined so far (ie, in the case of the studies by Poole and Fish (1975, 1976) and Meaney and Stewart (1981), the morphology of the behaviour-patterns themselves).

Poole and Fish (1975, 1976) stress the similarities between "play-fighting" and adult aggression: "Play-fighting may... be regarded as a mixture of low level aggressive and defensive behaviour accompanied by extravagant and energetic movements" and "social play is for the most part playful aggression." (Poole and Fish 1975).

Meaney and Stewart (1981) also emphasise play's relationship to aggression: "Despite the difference between the play-fighting of juveniles and the agonistic encounters of adults, most of the behaviour patterns involved in aggression among rats first emerge within the context of play-fighting". The latter authors also stress the relationship between play and the development of sexual behaviour.

The data presented in this chapter suggest an alternative view of play, which gets away from fixation on its superficial resemblance to adult fighting and emphasises instead play's close relationship to exploration of the environment, both social and inanimate. Play is a major source of olfactory information about one's peers, occurring within a milieu of olfactory investigation of the surroundings. Play may also represent a prime oportunity for allogrooming.

The contextual data, in particular, emphasise the inappropriateness of a "juvenile aggression" model as a wholly satisfactory description of play, suggesting instead a view of play as a strongly affiliative,

interactive process which is information-gathering (and possibly also information-generating) in nature.

To sum up, the analyses of this chapter suggest that social play in the rat is one which in many ways is very stereotyped, both between the sexes and over time. These findings are compatible with those of previous researchers since they deal with rather different aspects of the phenomenon to those hitherto investigated; however they suggest a different conception of play to that usually stressed, implying that play is an amicable behaviour with greater affinities to exploration than aggresssion.

In the following section, experiments will be described which attempted to focus more closely on some of the features involved in the immediate causation of play, as suggested by the conception of play inspired by the observational studies of this and the preceding chapter.

# CHAPTER FOUR: EXPERIMENTAL STUDIES OF SOCIAL PLAY:

## 4.1: INTRODUCTION TO EXPERIMENTAL STUDIES OF SOCIAL PLAY:

The following three studies used experimental rather than observational methods, in order to deal with a few of the many questions arising from the previous chapters' data. The previous two sections have produced the following observations.

(1) Play is motivationally distinct from other behaviours occurring during the same period in ontogeny. In particular, play appears to have little in common with aggressive behaviours, and some affinities with amicable behaviours such as social olfaction and allo-grooming.

(2) The initiation of play seems somehow to be related to exploration of the inanimate environment. Environmental change appears to be a frequent precursor of social play, although much of the evidence for this conclusion is admittedly anecdotal, based on informal observations made while the previously-described studies were in progress.

The three experiments to be described in this chapter sought to clarify these conclusions to some extent. As with the rest of this thesis, the aim was to explore the idea that social play in the rat has a motivational system distinct from that underlying other social behaviours, inasmuch as it is differentially - and specifically- affected by environmental manipulations such as social deprivation, food-deprivation, and changes in the

inanimate environment. Following on from this, these experiments will also be used to show that play is not related to aggression, by demonstrating that play has no relationship to territoriality-induced aggression, one of the most common sources of intra-specific aggression in the rat (Chivers 1982).

## 4.2: EXPERIMENT ONE: THE EFFECTS OF SOCIAL DEPRIVATION ON LEVELS OF SOCIAL PLAY:

### 4.2.1: Introduction:

The effects of social deprivation on subsequent levels of social play have already been described at some length in the section on the causation of play, in Chapter One (section 1.3). The studies described there (eg by Einon et al., 1978, Panksepp and Beatty 1980, Panksepp 1981) show that removal of the opportunity to engage in social or exercise play can result in a subsequent increase in the amount of play shown, compared to the levels of play shown by undisturbed animals - a "rebound" effect.

There are, however, a number of points which remain unresolved. Firstly, there are some methodological improvements which could be made. There is scope for a study in which rats are as normally reared as possible, before the experimental manipulations begin, so that there is minimal disruption of their normal social development. For example, Panksepp's rats were abruptly weaned at 18 days,which is only a day or so after they are even capable of surviving independently from the mother. Particularly in those experiments which charted an increase in play with age from day 18 onwards, at least part of this increase might be spurious due to confounding true maturation of play with recovery from the trauma of the

initial handling, separation from the mother, and introduction into a new environment (the home cage).

Sufficient observation of the animals must be made before it can be determined whether any rebound effect recorded represents an actual quantitative increase in the amount of play shown, or merely a redistribution, into one short period immediately following the end of deprivation, of all the play which would otherwise have occurred that day but on a wider time-scale. This is a question which Panksepp's experiments have failed to resolve due to the brevity of his observation periods.

More important than either of these points however, especially in view of the conception of play suggested by the earlier studies of this thesis, is that none of the previous play-deprivation studies has shown conclusively that it is play-deprivation per se that leads to a subsequent increase in play, rather than general social deprivation. There have as yet been no attempts to address this problem by manipulating the quality of the social experience itself within this paradigm. This is especially relevant to the present thesis, where two suggestions that have been repeatedly made, are (a) that play has a distinctive motivational basis; and (b) that allo-grooming and social olfaction are notable correlates of play activity. The demonstration of a rebound effect might be further evidence in favour of the view that play has its own motivation; however, the question remains of whether or not the other social behaviours with which play is so

closely associated, can compensate for a lack of specifically-playful experience.

In an attempt to examine these issues, an experiment was devised to test the following two hypotheses:

(1) Short-term (20-hour) play deprivation should lead to a subsequent marked increase in play when the animals are again allowed access to each other.

(2) A condition in which there is almost total social isolation should lead to a greater "rebound" effect than a condition in which there is deprivation solely of play, since in the latter state the animals have the opportunity for alternative forms of contact behaviour which might to some extent compensate for the lack of play.

If the effects of deprivation persist for longer than 24 hours, then these two experimental groups (ie, animals experiencing 20 hours' total social deprivation, and animals receiving 20 hours' partial social deprivation) should show more play than control subjects who have experienced no such deprivation, when compared to the latter on non-deprivation days which immediately follow the deprivation days. If the effects of deprivation can be compensated for within 24 hours after deprivation has ceased, then experimental animals should show similar levels of play to those of the controls on these non-deprivation days.

A close examination will be made of the effects of time of observation on recorded levels of play, with the expectation that the amount of observed play will decline

progressively with increasing time after the end of deprivation.

4.2.2: Method:

The main independent variable was the presence or absence of varying degrees of social contact. Rats were housed in pairs and subjected to one of the following treatments.

(1) Condition A:

Members of a pair had uninterrupted access to each other throughout the experiment. These pairs constituted a control group, designed to provide a baseline level against which to compare the two experimental groups.

(2) Condition B:

Members of a pair were physically separated from each other by means of a wire partition, on days 2, 4 and 6 of the experiment. On days 1, 3, 5 and 7, each pair had unrestricted access to each other, as for condition A. The wire partition was designed to prevent only gross physical contact (and hence play behaviour): visual, tactual and olfactory contact, grooming and (to some extent) huddling together were still possible either through or by laying against the wire. Thus social contact other than play was disrupted as little as possible during the periods of deprivation.

(3) Condition C:

This was identical to condition B except that the partition was made of transparent plastic, rather than

wire. This was intended to eliminate all physical contact between the two animals while still permitting olfactory communication (underneath the partition) and visual access. This condition was included in an attempt to assess the effects of more extensive social deprivation upon subsequent levels of play, and to separate out the effects of social isolation from the effects of play deprivation.

A second independent variable manipulated was the time of observation within the animals' diurnal rhythm. Each pair of subjects was observed at exactly the same times on each day of the experiment, in order to record their behaviour at roughly the same point in their activity cycle on different days (This was made possible by using video-filming of all subjects simultaneously).

Panksepp (1981) gives no details of exactly when he looked at his animals, and yet this could well be crucial information for a potential replicator; informal observations made in the course of the studies reported in the first two chapters of this thesis, suggested that there may well be marked diurnal differences in the distribution of play in rats.

Three separate 20-hour deprivation periods were used, mainly in an attempt to obtain as much data as possible on an inherently variable process. However, if the effects of deprivation on play persist for longer than the interval between two deprivation periods, then there might well be a cumulative effect of play-deprivation over days of

testing which would be detected by this means.

The dependent variable chosen was the total duration of play between each pair of subjects, in each observation session.

4.2.2.1: Subjects:

36 juvenile male hooded rats (PVG strain) were used, taken from nine different litters. The mothers were multiparous, and had themselves been raised and maintained on the same reversed-light schedule as used for their pups (12 hours light from 10.00 pm to 10.00 am, and 12 hours darkness from 10.00 am to 10.00 pm).

4.2.2.2: Apparatus:

For the first 30 days of life, each litter was raised with its mother in a standard white plastic breeding cage (North Kent Plastics RB1, 48 cm long x 35 cm wide x 18 cm deep). From days 30 to 41, littermates were housed in pairs, each pair being placed in one of the ten compartments of the apparatus depicted in figure 4.2.1.

This was a purpose-built cage, measuring 150 cm long x 60 cm wide x 30 cm deep, with smooth opaque walls, a transparent perspex lid, and a wire-mesh floor, 5cm beneath which was suspended a sawdust-filled soil tray. Within this cage, each compartment was approximately 60 cm x 15 cm x 30 cm, and was readily divisible into sub-compartments (each 30 cm x 30 cm x 15 cm) by slotting in a central partition (30 cm high and 15 cm wide) of

**FIG. 4.2.1: DIAGRAM OF THE OBSERVATION CAGE USED IN EXPERIMENT ONE:**

either wire mesh or perspex. The wire mesh of the cage floor and central partitions consisted of galvanised wire with spaces between the bars of 25 mm x 10 mm.

Water-bottles were located at both ends of each compartment, their spouts projecting downwards into the cage from a centrally-located hole in the cage wall, 7.5 cm from the floor. Food pellets (S.D.S. rat and maintenance diet number 1, in expanded form) were distributed over the floor of the cage, for easy ad-lib feeding.

Illumination of both the rearing cages and the experimental cage during the dark phase was by a 40-watt red tungsten light, suspended approximately one and a half metres above the lid of the experimental cage. Daytime lighting was provided by the room's fluorescent strip-lighting.

The animals' play-bouts were timed to the nearest half-second with a Campden Instruments electronic timer, model CI565.

4.2.2.3: Procedure:

Three pairs of animals were tested at a time. Up to the beginning of the experiment, all animals were left completely undisturbed from the day of birth until day 30, except for replenishing food and water. At day 30, two approximately equal-sized pups were selected from each litter. Each pair was randomly assigned to one of the compartments in the experimental cage. Pairs had no access

to each other, except perhaps for ultrasonic communication and general olfaction.

4.2.2.3.1: Conditions of observation:

Each pair was randomly assigned to one of the three conditions A, B or C, for the duration of the experiment. Pairs were then left undisturbed from day 31 to 35, in order to allow them to recover from the effects of handling, and adjust to maternal separation and the novelty of their new environment.

On each day from day 36 to day 42, subjects were observed for a total of 2 hours per pair: the first hour after the onset of darkness (experimental time 00.00 to 01.00) and the third hour after darkness (time 02.00 to 03.00). Each of these hours was divided into three 20-minute sessions for the purposes of subsequent analysis.

The first day of the experiment (day 36 of age) represented a "baseline", on which play in each of the three conditions was measured; at this point, all subjects had received similar experiences, and these observations were intended to establish that pairs in different conditions were roughly comparable in their levels of play before any group-specific manipulations were carried out.

On days 38, 40, and 42 (days 3, 5, and 7 of the experiment proper), the animals were not interfered with in any way, prior to observation: these were the

## OUTLINE OF EXPERIMENTAL PROCEDURE FOR EXPERIMENT ONE:

SUBJECTS' AGE (DAYS)

| | 30 | 31-35 | 36 | 37 | 38 | 39 | 40 | 41 | 42 |
|---|---|---|---|---|---|---|---|---|---|
| A | WEANING OF SUBJECTS, AND RANDOM | UNDISTURBED HOUSING | BASELINE MEASURE- | CONTINUOUS HOUSING IN PAIRS | | | | | |
| EXPERIMENTAL CONDITION: B | ASSIGNMENT OF PAIRS TO EACH EXPERIM-ENTAL | IN PAIRS, IN THE TEST | MENT OF PLAY IN ALL | PDD 1 | NDD 1 | PDD 2 | NDD 2 | PDD 3 | NDD 3 |
| C | CONDITION, A, B, OR C. HOUSING IN TEST CAGE. | CAGE. | PAIRS. | PDD 1 | NDD 1 | PDD 2 | NDD 2 | PDD 3 | NDD 3 |

(PDD = "POST-DEPRIVATION DAY"; NDD = "NO-DEPRIVATION DAY" - SEE PP. 454-455)

## PROCEDURE ON EACH PDD:-

## PROCEDURE ON EACH NDD:-

UNRESTRICTED ACCESS OF PAIR-MEMBERS TO EACH OTHER (IN ALL CONDITIONS) SINCE 10.00 AM ON PRECEDING DAY).

OBSERVATION OF ALL SUBJECTS FOR ONE HOUR

OBSERVATION OF ALL S's FOR ONE HOUR

FOR SUBJECTS IN CONDITION A, UNRESTRICTED ACCESS AS BEFORE; FOR SUBJECTS IN CONDITIONS B AND C, PARTITIONS WERE PLACED IN THEIR CAGES AT 2.00 PM, THUS ISOLATING PAIR-MEMBERS FROM EACH OTHER. PARTITIONS REMAINED IN PLACE UNTIL 10.AM ON FOLLOWING DAY.

"non-deprivation days" (NDD's) on which unrestricted social contact between pair-members was possible. At 2.00 pm on these days, the appropriate partitions were interposed between the pair members of conditions B and C, and these were left in position for 20 hours, until 10.00 am the following day.

On days 37, 39 and 41 (ie, days 2, 4 and 6 of the experiment), the partitions were removed at 10.00 am, immediately following the onset of darkness, and the animals were then observed at the same times as on the NDD's. Days 2, 4 and 6 were therefore the "post-deprivation days" (PDD's) for subjects under conditions B and C. The animals were then left together until 2.00 pm on the following day (ie, an NDD), at which time the partitions were again placed in the compartments.

Thus, on NDD's, the observation periods came after 24 hours of unrestricted access to each other (for all groups), and on PDD's observations were made after 20 hours of restricted access (in the case of groups B and C). All observations were filmed on video.

4.2.2.3.2: Definition of "play" for this experiment:

As with the studies in chapter 3, play was considered to commence with the initial pounce of one animal on the other, and to end with the complete cessation of contact between the two animals, one rat turning away from the other. Chasing was not considered to be part of the play

bout, unless the animals were in actual physical contact.

Each play bout was measured to the nearest 0.5 second, and these times were summed for each session.

## 4.2.3: Results:

### 4.2.3.1: Overall duration of play:

Table 4.2.1 shows the mean grand total amounts of play recorded for each group, combining the data from all observation sessions on all days of the experiment.

A comparison of the three groups by means of a Kruskal-Wallis test revealed that they differed significantly in the total duration of play performed ("H" = 11.79 with 2 df; $p<0.01$). However, there was no significant difference between the overall amounts of play shown by groups B and C, over the whole of the experiment (Mann-Whitney "U" = 12, N1=6, N2=6; $p>.10$). Inspection of table 4.2.1 shows that subjects in groups B and C differed little from each other, but that both groups showed more play than subjects in group A, the control group.

Tables 4.2.2 and 4.2.3 show the overall mean amount of play observed for each condition, combining the data for all observation periods but summing separately for post-deprivation days (PDD's) and non-deprivation days (NDD's).

Overall, subjects in all three conditions showed an increase in play on post-deprivation days, compared to

**TABLE 4.2.1: THE MEAN GRAND TOTAL AMOUNT OF PLAY OBSERVED IN EACH GROUP:**

(Means refer to the mean total number of seconds of play per pair of rats, combining the data from all days - baseline, no-deprivation and post-deprivation - and all observation sessions. Standard deviations are in brackets. N=6 per group).

| Condition : | A | B | C |
|---|---|---|---|
| Mean total amount of play (seconds): | 1141.0 (535.3) | 2635.3 (660.4) | 2131.7 (180.6) |

Kruskal- Wallis "H" = 11.79, 2 df, N = 6 pairs per group; $p<0.01$.

Mann-Whitney "U", for conditions B versus C, = 12, N1 = 6, N2 = 6; $p>.10$.

TABLE 4.2.2: THE MEAN TOTAL AMOUNT OF PLAY OBSERVED IN EACH GROUP, ON ALL THREE NO-DEPRIVATION DAYS COMBINED:

("Mean amount" of play refers to the mean total number of seconds of play observed for each pair of rats, over the three NDD's. Standard deviations are in brackets. N=6 per group).

| Condition: | A | B | C |
|---|---|---|---|
| Mean total amount of play (seconds): | 498.7 (245.4) | 707.0 (264.9) | 599.0 (328.6) |

Kruskal- Wallis "H" = 1.68, 2 df, N = 6 pairs per group: p>.10.

Mann-Whitney "U", for conditions B versus C, = 16, N1 = 6, N2 = 6; p>.10.

TABLE 4.2.3: THE MEAN TOTAL AMOUNT OF PLAY OBSERVED IN EACH GROUP, ON ALL THREE POST-DEPRIVATION DAYS COMBINED:

("Mean amount" of play refers to the mean total number of seconds of play observed for each pair of rats, over the three PDD's. Standard deviations are in brackets. N=6 per group).

| Condition: | A | B | C |
|---|---|---|---|
| Mean total amount of play (seconds): | 642.3 (416.5) | 1928.3 (498.3) | 1532.7 (186.2) |

Kruskal- Wallis "H" = 11.79, 2 df, N = 6 pairs per group: p<0.01.

Mann-Whitney "U", for conditions B versus C, = 12, N1 = 6, N2 = 6; p>.10.

non-deprivation days. However, this increase was much more marked for conditions B and C than for A. Subjects under condition B played nearly three times more than those in condition A, but only slightly more than those in condition C. Condition C animals played nearly two and a half times more than those in condition A.

Kruskal-Wallis tests performed on these data revealed that there were no significant differences between the three conditions on NDD's ("H" = 1.68, with 2 df; $p>.10$) but that the three groups differed significantly on PDD's ("H" = 11.79, 2 df; $p<0.01$). A Mann-Whitney test comparing the amounts of play shown on PDD's by subjects in conditions B and C, found no significant difference between them ("U" = 16, N1=6, N2=6; $p>.10$). Related "t"-tests, comparing the amount of play on NDD's to the amount of play on PDD's for each condition, showed that the apparent increase in play shown by subjects in condition A was not statistically significant ("t" = 0.827, 5 df; $p>.10$). However, subjects in conditions B and C both showed signficant increases in play on PDD's compared to NDD's ("t" = 6.674, 5 df, $p<0.001$, for condition B; and "t" = 4.550, 5 df, $P<0.005$, for condition C).

Taken together, these results suggest that deprivation of social contact leads to a marked rise in the amount of play shown, when the deprived animals are again allowed to interact socially - such that, taken over the whole of the period for which observations

**TABLE 4.2.4: MEDIAN TOTAL AMOUNT OF PLAY PERFORMED IN EACH OBSERVATION SESSION:**

(Medians are of the total amount of play in seconds which was observed in each of the six 20-minute observation sessions made daily on each of the 6 pairs of subjects in each condition, A, B or C. Observation periods are collapsed across days of a condition: ie, this table shows the median amount of play observed in session one, combined across all three post-deprivation days; the median amount of play seen in session two, across all three post-deprivation days; etc. Bracketed figures are ranges. "H" = results of Kruskal-Wallis tests on the column of figures above the appropriate value of "H", with 2 df in each case. "U" = results of Mann-Whitney tests, with N1=6, N2=6, comparing B and C in the column above. All tests are two-tailed. For full details of observation-periods, see text).

(a) Post-deprivation days:

| | Observation period | | | | | |
|---|---|---|---|---|---|---|
| | 1st | 2nd | 3rd | 4th | 5th | 6th |
| A: | 54 | 2 | 0 | 127 | 24 | 21 |
| | (0- ) | (0- ) | (0- ) | (0- ) | (0- ) | (0- ) |
| | (251) | (141) | (257) | (531) | (135) | (302) |
| B: | 750 | 589 | 274 | 75 | 28 | 73 |
| | (601-) | (511-) | (0- ) | (0- ) | (18-) | (72-) |
| | (755) | (815) | (775) | (126) | (221) | (102) |
| C: | 645 | 276 | 220 | 94 | 0 | 112 |
| | (610-) | (235-) | (182-) | (0- ) | (0- ) | (0- ) |
| | (765) | (593) | (289) | (137) | ( 46) | (394) |
| | *** | *** | | | | |
| "H": | 11.52 | 12.54 | 3.56 | 1.68 | 2.99 | 0.75 |
| "U": | 16 | 8 | 16 | 14 | 8 | 12 |

(b) No-deprivation days:

| | Observation period | | | | | |
|---|---|---|---|---|---|---|
| | 1st | 2nd | 3rd | 4th | 5th | 6th |
| A: | 141 | 11 | 11 | 93 | 0 | 108 |
| | (102-) | (0- ) | (0- ) | (10-) | (0- ) | (2- ) |
| | (506) | ( 18) | ( 51) | (166) | (154) | (123) |
| B: | 30 | 11 | 6 | 25 | 237 | 81 |
| | (0- ) | (0- ) | (0- ) | (0- ) | (212-) | (67-) |
| | (200) | ( 75) | (261) | (459) | (363) | ( 86) |
| C: | 162 | 135 | 0 | 9 | 92 | 100 |
| | (23-) | (26-) | (0- ) | (0- ) | (90-) | (42-) |
| | (296) | (249) | (201) | ( 10) | (158) | (204) |
| | | *** | | * | *** | |
| "H": | 2.46 | 9.41 | 0.67 | 5.62 | 12.76 | 1.31 |
| | | ** | | | **** | |
| "U": | 12 | 4 | 12 | 10 | 0 | 12 |

"*" = p<0.05: "**" = p<0.02: "***" = p<0.01:
"****" = p<0.001

were made, deprived animals showed more than double the amount of play displayed by non-deprived controls. This effect is in addition to a slight, non-significant, increase in play apparently produced by mere disturbance alone (as shown by condition A on PDD's).* There appears to be no difference between the effects of partial deprivation (as in condition B) and full deprivation (as in condition C).

4.2.3.2: Effects of time of observation:

Table 4.2.4 shows the median amount of play shown by each of the three groups on PDD's and NDD's, broken down according to the time of observation (ie, into six 20-minute sessions, three in the first hour after darkness and three in the second). Data were summed across all three PDD's combined, and all three NDD's combined, in order to arrive at these figures.

Figures 4.2.2 and 4.2.3 depict the medians graphically. (For the purpose of clarity of presentation, the ranges have been omitted from these graphs; however, as can be seen from table 4.2.4, they were very large).

For each 20-minute period, a Kruskal-Wallis test was performed to determine whether there was any significant difference between the three groups in terms of the amount of play shown. In addition, for each 20-minute period, a Mann-Whitney test was carried out between the scores of animals in conditions B and C. The results of these tests

* This disturbance was caused by the removal of the wire and perspex cage-dividers from the compartments of animals experiencing release from deprivation under conditions B and C, and any noise made by the experimenter while he was doing this.

FIG.4.2.2: EXPERIMENT ONE - MEDIAN AMOUNT OF PLAY IN EACH OBSERVATION SESSION, ON POST-DEPRIVATION DAYS:

FIG.4.2.3: EXPERIMENT ONE - MEDIAN AMOUNT OF PLAY IN EACH OBSERVATION SESSION, ON NON-DEPRIVATION DAYS:

are also shown in table 4.2.4.

4.2.3.2.1: Effects of time of observation, on PDD's:

These data show that the increase in the total duration of play shown on PDD's by subjects in conditions B and C, was confined to the first two 20-minute periods immediately after deprivation was lifted (For the first 20 minutes, "H" = 11.52; and for the second 20 minutes, "H" = 12.54; both with 2 df, and $p<0.01$). There were no significant differences between the three groups in the remaining four time-periods. These effects are shown clearly in fig.4.2.2.

No significant differences were found on the Mann-Whitney tests between the total amounts of play recorded for conditions B and C in any time-period on PDD's. As with the results of the overall tests between conditions B and C, this implies that these two groups did not differ from each other in their responses to deprivation.

4.2.3.2.2: Effects of time of observation, on NDD's:

Fig. 4.2.3 shows that there were no systematic effects of time of observation on NDD's. The three groups did, however, differ significantly in the amount of play shown in three time-periods: the second, fourth and fifth 20-minute sessions ("H" = 9.41, $p<0.01$; 5.62, $p<0.05$; and 12.76, $p<0.001$, respectively: all with 2 df). Mann-Whitney tests further revealed that in the second and

fifth sessions, conditions B and C differed significantly from each other ("U" = 4, $p<0.02$, and "U" = 0, $p<0.001$, respectively; N1=6, N2=6 in both cases).

These differences followed no clear pattern, however; in the second 20-minute period, animals in group C showed more play than animals in group B, but in the fifth observation session this situation was reversed, and B showed the most play. This suggests that there were some differences between the three groups (and between B and C in particular) in the timing of their play on NDD's, but since there were no significant overall differences between the three conditions on NDD's, these results are difficult to interpret.

4.2.3.3: Effects of day of observation on the amount of play shown:

Fig. 4.2.4 shows the median amount of play shown on each day of the experiment (including the first, baseline, day) by subjects in each of the three conditions, combining the data for all observation-periods on a given day. The daily medians displayed in this graph (together with their associated ranges) are displayed in table 4.2.5. Fig. 4.2.4 shows clearly how animals in groups B and C responded to deprivation by playing more than subjects in group A. It also reveals that there was no tendency for subjects in groups B and C to show increased levels of play as the experiment progressed, either over all three NDD's or all three PDD's. In other words, there

FIG.4.2.4: EXPERIMENT ONE - MEDIAN TOTAL AMOUNT OF PLAY PER DAY:

TABLE 4.2.5: MEDIAN TOTAL AMOUNT OF PLAY PERFORMED ON EACH DAY OF THE SOCIAL DEPRIVATION EXPERIMENT:

(Medians are of total amount of play in seconds, obtained from the six 20-minute observation sessions made daily on each of the 6 pairs of subjects in each condition, A, B or C: ranges in brackets. "B/L" = "baseline"; "PDD" = "post-deprivation day"; "NDD" = "no-deprivation day").

Day of Experiment:

| | B/L | PDD-1 | NDD-1 | PDD-2 | NDD-2 | PDD-3 | NDD-3 |
|---|---|---|---|---|---|---|---|
| A: | 140 | 255 | 109 | 360 | 88 | 240 | 242 |
| | (62-) | (106-) | (192-) | (0- ) | (85-) | (0- ) | (145-) |
| | (180) | (305) | (297) | (399) | ( 95) | (262) | (416) |
| B: | 113 | 607 | 243 | 774 | 111 | 560 | 200 |
| | (91-) | (598-) | (36-) | (161-) | (0- ) | (519-) | (177-) |
| | (207) | (878) | (849) | (855) | (172) | (833) | (333) |
| C: | 167 | 605 | 265 | 516 | 101 | 442 | 272 |
| | (0- ) | (422-) | (114-) | (337-) | (78-) | (240-) | (11-) |
| | (515) | (671) | (295) | (813) | (158) | (552) | (513) |

is no evidence for a cumulative effect of deprivation on levels of play in these two groups, at least not within the observation periods used in this study.

### 4.2.4: Discussion:

The main finding of this experiment is that deprivation of full physical contact with a conspecific (deprivation which includes play) sufficed to produce an immediate and very marked increase in play when deprivation ceased. This occured whether the deprivation was of all social interaction or merely of vigorous physical contact. Interestingly, the mere incidental disturbance of control animals who did not experience deprivation, also led to an increase in play. Although this latter result failed to reach statistical significance, it does suggest that one should be careful in interpreting the effects of any deprivation conditions on baseline play levels, unless undisturbed controls are included in the design.

The effects of deprivation were short-lived in the sense that the most dramatic increase in play persisted only for 40 minutes or so from the time at which the animals were released from deprivation. Even so, this was enough to ensure that groups B and C showed a net increase in play over the whole of the experiment, compared to group A. The effect of deprivation does not appear to be cumulative, however, since the third day of deprivation produced no more play than the second or first, as might

be expected to occur if the interval between deprivation periods was too short for whatever "need" motivates play to be satiated within it.

These results confirm the existence of the rebound effect already found as a consequence of total social isolation in the rat by Panksepp and Beatty (1980) and Panksepp (1981); taken in conjunction with Baldwin and Baldwin's (1974) findings on the squirrel monkey, and Smith and Hagan's (1980) results from nursery-school children, it appears that there is evidence for a rebound effect on levels of play behaviour which is caused specifically by prior play deprivation.

It is interesting to compare these studies and the results of the present experiment, on the extent to which deprivation increased play levels compared to baseline levels of play preceding deprivation. Baldwin and Baldwin (1974), using enforced foraging to deprive monkeys of play, found a maximal increase of only 50% in post-deprivation play levels compared to pre-deprivation levels. Panksepp and Beatty (1980), using three days of total social isolation as a technique for play deprivation, reported a tenfold increase for "pinning" of one animal by the other, and a trebling of "together time" at 21 days. In the present experiment, animals in conditions B and C showed over twice as much play as those in group A, over the whole of the experiment.

The size of the effect of deprivation on play does not seem to be correlated in any simple way with the

nature of the deprivation: Baldwin and Baldwin (1974) obtained less of a rebound effect than was found in either the present experiment or Panksepp's studies. One possible explanation for this is that in the Baldwins' studies there were opportunities for extended non-play social contact which may have been able in some way to compensate for the lack of play. This would be in accordance with Baldwin and Baldwin's (1974) suggestion that there may be alternative ways to achieve normal social development if play is not an available strategy. Yet in the experiment reported here, the group with opportunities for alternative social contact (condition B) played as much after deprivation as the group with no social contact (condition C).

It may be that, while social deprivation is an adequate technique for eliciting a rebound effect, deprivation of play alone is just as effective (a suggestion supported by the findings of Einon, Morgan and Kibbler 1978, and Humphreys and Einon 1981). The very high levels of play obtained by Panksepp and Beatty could have been due to the length of the deprivation period used (three days as opposed to a mere 20 hours here). However, the difficulties in equating these studies, due to the use of diverse deprivation techniques on different subject-species at diffrent observation times, make it pointless to speculate too much on the sources of the differences between them. For example, because Panksepp and Beatty (1980) and Panksepp (1981) looked at their

animals only for the first five minutes immediately after deprivation ended, they saw the maximum amount of play that they were likely to see for the next three hours. In the present experiment, most post-deprivation play occurred within 5-10 minutes of the deprived animals regaining access to each other, and so the rates of play per minute for the first and last five minutes of a session would give very different impressions of what was going on. One implication of this is that, with as short an observation session such as that used by Panksepp it becomes critical to know exactly when the animals were observed.

Using a sufficiently long observation period also enables some statements to be made concerning whether the rebound effect represents a genuine increase in play, or merely a redistribution, a "piling up" of play in one time-period at the expense of play at some other time. If the rebound effect were to have any adaptive function, then one might expect play deprivation to produce a genuine quantitative increase in play, as this would to some extent "make good" the loss. A redistribution would achieve less, although it might ensure that as much play as possible was obtained before the recurrence of whatever adverse conditions previously prevented play.

Either way, the presence of a rebound effect would suggest that there is an adaptive regulatory mechanism governing the occurrence of play and ensuring that as far as possible the animal obtains its optimal level of play.

The data from this experiment suggest that, at least within the time-periods studied, there is a quantitative increase in how much play occured after deprivation, rather than a redistribution effect with earlier high levels of play being followed by lower than normal ones. This increase was apparently confined to the first hour after deprivation had ended; and yet there appear to have been no cumulative effects of deprivation, over the whole of the experiment.

In considering these results, one should bear in mind that observations were made only for two hours per day; it would be unwise to make too strong inferences about how much play occurred in any of the three groups outside of the period covered. If these findings are valid, however, they suggest that one hour of play per day may suffice to satisfy whatever "need" for play exists - a conclusion which fits in well with Einon et al's (1978) claim that animals provided with as little as one hour of predominantly playful social contact per day, between days 25 and 45, show little evidence of the cognitive impairments displayed by animals who are totally isolated during that period. However, to settle this issue fully would really require post-deprivation observation on the scale of that by Muller-Schwarze (1968) and Chepko (1971).

There are a number of problems with the present experiment which should be mentioned at this point. As with previous studies, this experiment still fails to show

conclusively that, of all the things which were being witheld by restriction of social contact, it was play which was the critical factor in producing the rebound effect. Certainly, the fact that play levels rose in the control subjects of this experiment, who were subjected to nothing other than a transitory disturbance, would suggest that play deprivation is not the only factor in such experiments which gives rise to an increase in play. In the present experiment, condition B represented an attempt to deprive the subjects of play rather than anything else; but although they had fairly good social access to each other (for example, spending much of their time sniffing and pawing at each other through the wire, climbing on it and sleeping next to it so that they were both in contact) they were still being deprived not just of play but also of activities including mutual grooming and competition for access to food, water and places to sniff.

A potentially serious problem with the present experiment is that as it was performed by one experimenter there was the possibility of biassing the results in accordance with prior expectations. To some extent, to be aware of the problem is to be able to guard against it; but two precautions were taken against possible bias. Firstly, durations were "rounded down" rather than to the nearest figure so as to counter any unconscious tendency to linger on the timer button when observing subjects under deprivation conditions. Secondly, on post-deprivation days, the partitions were removed during

the first observation session rather than before it, thus shortening the sessions in which bias was most likely to occur by approximately ten to twenty seconds. Ideally, however, experiments of this kind should be run totally under "blind" conditions, with the observer completely unaware of what condition the animals were under.

Given that a rebound effect does occur, the questions remain of why it should occur and what implications its existence has. At first sight, it would seem to provide evidence for Spencer's "surplus energy" theory, deprivation preventing the release of energy in play with the result that this energy builds up and is all discharged in as little time as possible at the earliest opportunity. However, quite apart from their being no known physiological basis for such a theory, a "suplus energy" explanation is not very useful - it merely describes what is observed to occur, in different terms.

Baldwin and Baldwin (1974) suggest that the rebound effect is explicable in terms of a reinforcement theory of play. They propose that play has a reinforcing value which is enhanced by deprivation, so that when the subjects are again able to play, they initially find play more reinforcing. After a while satiation sets in, and play becomes less reinforcing. There is other, independent, evidence that play can serve as a reinforcer: for example, Humphreys and Einon (1981) found that rats would learn a maze in order to play. Baldwin and Baldwin may be correct, but if novelty is involved it must be novelty specific to

play: the relative unfamiliarity per se of a playmate does not seem to be a factor, since otherwise play would not have increased in the Baldwins' own experiment, since their subjects otherwise had free social access to each other. And in the present experiment, subjects in condition C would have been expected to play more than those in condition B, as the transparent partition of the former condition would conceivably have made pair-members more unfamiliar to each other than would the wire partition of the latter group.

An explanation in terms of the exercise theory of play (Brownlee 1951; Fagen 1981) would explain these findings, if it is allowed that the exercise which occurs in play is of a special, more vigorous kind than that provided by climbing on the wire for long periods of time, in condition B of this experiment.

Whatever the explanation for why the rebound effect occurs, it suggests that there is an endogenous, homeostatic regulatory mechanism that is somehow able to assess how much play has occurred and - by comparison of this figure with an expected figure - how much play should take place in order to attain optimal levels of play and thereby optimal levels of whatever the benefits are that play provides. This homeostatic mechanism must be fairly sensitive if it can detect a lack of play over 20 hours and make good the loss.

Field anecdotes (eg, Krott and Krott 1963, Fagen 1981) suggest that the rebound effect is not just a

laboratory artifact, but something which may well occur in the wild. It is easy to imagine how such a regulatory mechanism would be adaptive in a natural environment: for example, it would make good any losses of play in ontogeny due to illness, poor weather and food-shortage, and so ensure that an animal managed to obtain as many of play's benefits as possible within the constraints imposed upon him. A regulatory mechanism such as this would help to prevent "cheating" by play-partners, in the sense of one animal obtaining benefit from play while denying those benefits to his partner, since an individual who repeatedly failed to benefit from play with a particular peer would eventually be in a state of mild play deprivation and so be driven to obtain more satisfactory social contact elsewhere. Such a mechanism would in short best exploit whatever opportunities arose to play.

## 4.3: EXPERIMENT TWO: THE EFFECTS OF ENVIRONMENTAL CHANGE ON LEVELS OF SOCIAL PLAY, AND THE DEVELOPMENT OF STABLE "ON-TOP" RELATIONSHIPS BETWEEN PAIRED INDIVIDUALS:

### 4.3.1: Introduction:

This experiment deals with two issues raised by the previous studies described in this thesis. For the purposes of clarity, these two questions will be discussed separately, although data from this experiment was used to examine both of them. The following section deals with the first issue, the effects of environmental change on levels of social play. Section 4.3.3 will deal with the second topic, the question of whether stable "on-top" relationships develop between pairs of animals over repeated play encounters.

### 4.3.2: The effects on play of environmental change:

#### 4.3.2.1: Introduction:

The results of Experiment One suggest that mere disturbance may be sufficient to elicit play from young rats. Mention has already been made in Section 1.3 of numerous studies on other species, reporting increases in playfulness apparently in response to diverse variations in the environment, such as sudden changes in

the weather or being moved to a different cage. It may be, therefore, that environmental change elicits play. This possibility was investigated in the following experiment, which set out to determine whether introducing environmental change (a novel object) into the otherwise fairly impoverished environment of captive young rats, resulted in increased levels of social play.

4.3.2.2: Method:

One problem in increasing the novelty-value of an animal's environment is deciding upon the appropriate level of novelty: too great a degree of environmental change might result in neophobic responses by the subjects, and so produce an apparent depression of play until the environment was determined still to be "safe". Within the design of this experiment, therefore, an attempt was made to allow ample opportunities for familiarity with the object to occur, by observing on successive days to see if play was enhanced once the object was familiar enough to be "safe" but still relatively novel.

Because levels of play are potentially so variable between subjects, a repeated-measures design was used. However, this in itself might fail to control for the effects of extraneous environmental influences on the levels of play observed, so the amount of play shown by undisturbed controls was measured on the same days as observations were made on the experimental subjects.

Specifically, each unit of the experiment involved collecting data from two pairs of animals. One pair were the experimental subjects, presented with a novel object, while the other pair acted as controls who experienced no environmental change. The controls then became the experimentals, and the former experimentals were used as controls. Thus for each pair of pairs, the response of each pair to the introduction and removal of a novel object was measured, while the other pair provided data on undisrupted levels of play.

In contrast to the previous experiment, in which duration of play was used as the dependent variable, in this experiment play was measured in terms of the number of separate ventral-ventral pinnings performed by each animal towards his partner, following the example of Panksepp and Beatty (1980), and Panksepp (1981). (This was in order to make the results more directly comparable to these authors', for use in dealing with the second issue that this experiment was designed to address, the question of whether stable "on top" relationships develop between paired individuals). Since Panksepp and Beatty (1980) found a 0.89 correlation between the duration and pinning, the results obtained in this experiment should be directly comparable to those obtained in the earlier studies in this thesis, despite the use of a different dependent variable.

4.3.2.2.1: Subjects:

Eight pairs of male PVG rats were used, aged 21 days at the beginning of the experiment.

4.3.2.2.2: Apparatus:

Two novel objects were used: a house brick, and a red cricket-ball. Subjects were housed in pairs in purpose-built observation cages. These measured 25 cm high x 77 cm wide x 45 cm deep , with back and side walls made of aluminium sheet and a removable perspex front measuring 20 cm high x 77 cm wide. A food-hopper and two water-bottles were located on the right-hand wall of the cage. The roof of the cage was constructed of galvanized wire mesh (1 x 2.5 cm size), and the floor was made of sheet metal and covered with sawdust to a depth of approximately 2 cm. Subjects were fed on S.D.S rat and mouse maintenance diet number 1 in solid pellet form; both food and water were available ad lib.

Subjects were housed in a large experimental room containing other animals but at some distance from them. The room was maintained on a reversed daylight schedule (12 hours' light/ 12 hours' darkness) using a conventional on-off timer to control the lights. Illumination during the light phase was by three 40-watt fluorescent lights on the ceiling of the test room. During the dark phase of the cycle, the room was lit by a 40-watt red lamp, positioned approximately one metre away from the front of the cage and directed so as to provide enough shadowless illumination for the observer to be able to see the

players clearly throughout the experiment.

Each test session was recorded on videotape, and analysed subsequently. This was to minimise the possibility of unconscious biassing of the results, which could have occurred if the observer was seated in front of the animals and recording their behaviour "live".

4.3.2.2.3: Procedure:

All subjects were raised in normal mixed-sex litter groups with their mothers until weaning at 21 days. At this time, they were placed in the experimental cages, one pair in each cage, in which they remained until 65 days of age. Each pair consisted of male littermates of approximately equal size.

The subjects were tested two pairs at a time. One pair was randomly chosen to be the experimental subjects, and the other pair constituted controls. Subjects were observed for one hour per day, immediately after the lights went off. The basic procedure was as follows:

(a) Day One: Baseline (B/L) - all subjects were observed undisturbed for one hour, to obtain data on their normal levels of play and to establish that the experimental and control pairs initially played at comparable levels.

(b) Day Two: Introduction of novel object (O) - the fronts of the cages of the experimental pairs were opened, and the novel object placed at centre-front in the cage. The first four pairs tested received a cricket ball as the

## OUTLINE OF PROCEDURE FOR EXPERIMENT TWO:

(a) CONDITION IN WHICH A BALL WAS USED AS THE NOVEL OBJECT:

| | AGE (DAYS) 21 | 22 - 27 | 28 | 29 | 30 | 31 | 32 | 33 | E+C SWITCH 34 - 39 | 51 - 65 |
|---|---|---|---|---|---|---|---|---|---|---|
| EXPERIMENTALS | ALL SUBJECTS WEANED AT 21 DAYS AND | OBSERVED BUT UNDISTURBED HOUSING IN PAIRS, | B/L | O | A1 | A2 | OR | B2 | THE SEQUENCE BETWEEN DAYS 28-33 WAS REPEATED, WITH | OBSERVATIONS MADE ON UNDISTURBED PAIRS IN BOTH |
| CONTROLS | RANDOMLY ASSIGNED IN PAIRS TO E OR C CONDITIONS | FOR ALL SUBJECTS | UNDISTURBED; OBSERVED FOR ONE HOUR ON EACH OF THESE DAYS. | | | | | | THE FORMER EXPERIMENTAL PAIRS ACTING AS CONTROLS FOR THE FORMER CONTROL SS. | GROUPS. (NO OBSERVATIONS ON DAYS 59 AND 61). |

(b) CONDITION IN WHICH A BRICK WAS USED AS THE NOVEL OBJECT:

| 21 - 24 | 25 - 29 | 30 | 31 | 32 | 33 | 34 | 35 | E+C SWITCH 38 - 43 | 51 - 65 |
|---|---|---|---|---|---|---|---|---|---|
| ALL SUBJECTS WEANED AT 21 DAYS AND RANDOMLY | OBSERVED, BUT UNDISTURBED HOUSING IN | B/L | O | A1 | A2 | OR | B2 | THE SEQUENCE BETWEEN DAYS 30-35 WAS REPEATED, WITH THE FORMER | OBSERVATIONS MADE ON UNDIST-URBED PAIRS IN BOTH GROUPS. |
| ASSIGNED IN PAIRS TO E OR C CONDITIONS. (LEFT UNDISTURBED FROM 21-24 DAYS) | PAIRS, FOR ALL SUBJECTS | UNDISTURBED; OBSERVED FOR ONE HOUR ON EACH OF THESE DAYS. | | | | | | EXPERIMENTAL PAIRS ACTING AS CONTROLS FOR THE FORMER CONTROL S'S. | (NO OBSERVATIONS ON DAYS 55, 57, 59, 60, 62-64). |

## PROCEDURE ON OBSERVATION DAYS:

12.00 PM (LIGHTS-OFF)

1. EXPERIMENTAL SUBJECTS:-

(a) ON DAYS B/L, B2, A1 + A2:- OBSERVED FOR ONE HOUR.

(b) ON DAY OR:- OBJECT REMOVED FROM CAGE; OBSERVED FOR ONE HOUR.

(c) ON DAY O:- OBJECT PLACED IN CAGE; SUBJECTS OBSERVED FOR ONE HOUR.

2. CONTROL SUBJECTS:-

OBSERVED FOR ONE HOUR.

UNOBSERVED, UNRESTRICTED ACCESS OF SUBJECT-PAIRS TO EACH OTHER, UNTIL 12.00 PM ON FOLLOWING DAY.

novel object, while later pairs received a house-brick. The object was placed in the cage as the lights went out, and the hour's observation followed immediately.

(c) Day Three: First day of acclimatisation to the novel object for experimental subjects (A1) - all subjects were observed for one hour, after the object had been present in the cage of the experimental subjects for 24 hours.

(d) Day Four: Second day of acclimatisation to the novel object for experimental subjects (A2) - all subjects were observed for one hour.

(e) Day Five: Object-removal (OR) - The object was removed from the experimental subjects' cage as the lights went out, and the hour's observation followed immediately.

(f) Day Six: Baseline (B2) - all subjects were observed undisturbed for one hour.

This procedure was then repeated for the control subjects, the former experimental subjects acting as their controls.

These manipulations occurred at the following ages.

In the case of the studies involving use of a brick as the novel object, all subjects were observed without interference from days 25 to 29. The novel-object manipulations (ie, the treatments described under (a) to (f) above) were performed between 30 and 35 days of age, and then again (with the former experimental subjects as the controls and vice versa) between days 38 and 43. All subjects' undisturbed levels of play were then

recorded on days 51 to 54, 56, 58, 61 and 65.

For the subjects who were presented with a ball as a novel object, a broadly similar procedure was followed, except for three things: firstly, the novel-object experiment was begun on day 28 rather than day 30; secondly, no observations on undisturbed levels of play were made before this; and finally, observations on the undisturbed animals were made on every day from 51 to 65 days, except for days 59 and 61.

### 4.3.2.3: Results:

As no differences existed between using the ball or the brick as the novel object, the results of these two procedures will be combined in this section.

Fig. 4.3.1 shows the median number of pins observed on each of the six days of the experiment, for both the experimental and control conditions. Table 4.3.1 presents the medians and their associated ranges (which have been omitted from fig.4.3.1 for clarity), and the results of Mann-Whitney tests comparing experimental and control subjects on each day.

From fig. 4.3.1, it would appear that the effect of introducing the novel object (and of removing it) was to suppress play on those particular days, and possibly lead to an increase in play on the first day immediately following the object's introduction. However, there was a large amount of variance in pinning scores, both within

FIG.4.3.1: EXPERIMENT TWO - MEDIAN NUMBER OF PINNINGS OBSERVED ON EACH DAY OF THE EXPERIMENT

**TABLE 4.3.1: MEDIAN TOTAL AMOUNT OF PLAY PERFORMED IN EACH OBSERVATION SESSION:**

(Medians are of the total number of pins per pair of subjects per observation session, shown for when subjects were under experimental conditions and when they acted as controls. Bracketed figures are ranges. "U" = results of Mann-Whitney tests, with N1=8, N2=8, comparing experimentals and controls in the column above. All tests are two-tailed. "E" refers to subjects when they were experiencing the experimental conditions; and "C" refers to them when they were acting as controls. "BL" = baseline; "OI" = day on which the novel object was first introduced; "H1" and "H2" refer to the first and second days after OI; and "OR" refers to the day on which the object was removed).

| | Day of experiment | | | | | |
|---|---|---|---|---|---|---|
| | BL | OI | H1 | H2 | OR | BL |
| E: | 10.5 (0-23) | 6.5 (0-20) | 21.5 (0-59) | 19.5 (3-38) | 4.5 (1-10) | 14.0 (1-33) |
| C: | 14.5 (5-28) | 18.5 (0-30) | 22.5 (0-26) | 14.0 (3-33) | 14.5 (9-30) | 10.5 (4-21) |
| "U": | 20 | 16.5 | 30 | 29 | 2.5*** | 29 |

"***" = $p<0.01$

and across days, and all but one of the Mann-Whitney tests found no significant differences between experimental subjects and their controls. The exception was on the day when the object was removed from the experimentals' cage; this resulted in a significant reduction in play between experimental subjects, compared to controls ("U" = 2.5, N1=8, N2=8; $p<0.01$).

Wilcoxon tests were performed to compare within-subject pinning levels on different days of the experiment, when those subjects were under the experimental conditions. These revealed no significant difference between levels of pinning on the initial baseline day and the day on which the object was introduced ("W" = 10, N=8, $p>.10$). However, there were significant differences in pinning levels for experimental subjects between the day of object-introduction and the following acclimatisation day ("W" = 3, $p<0.05$); between the second acclimatization day and the following object-removal day ("W" = 1, $p<0.02$); and between the object-removal day and the final baseline day ("W" = 1, $p<0.02$). days ($p<0.01$), but this was common to both experimentals and controls.

These results suggest that the introduction of change into these young rats' environment resulted not in an increase in play, but rather a suppression of it ,on the days on which the objects were presented or removed.

4.3.2.4: Discussion:

The results from this experiment fail to support the hypothesis that increasing the degree of novelty in the environment of young rats would increase their levels of play. If anything, introduction or removal of the novel object appeared to suppress play, rather than enhance it.

The main difficulty in testing this hypothesis is in deciding on what might be the optimum time to observe the animals. Too soon after the object's introduction might result in apparently-depressed levels of play if the subjects spent the observation-period either being wary due to the disturbance or else exploring the new object. Conversely of course, observations made some considerable time after the object was placed in the cage, would fail to reveal any effect because the object's novelty would have worn off.

This may be the explanation for the results of the present experiment. The hour's observation immediately after placing the novel object in the cage, may reflect the animals' behaviour during the initial suppressive phase of the object's effects; and the hour's observation 24 and 48 hours afterwards, may have recorded their behaviour after the object had ceased to be novel. If environmental change does enhance play in rats (a point which could be clarified by further experiments, using a wider range of observation-times) then it is only after the source of the change has been thoroughly

investigated. If this is indeed the case, then this would be a highly adaptive response, preventing play from occurring in conditions which are potentially hazardous to the players. This interpretation fits in with other researhers' suggestions that play occurs only in a "relaxed field" (Bally 1945), when animals are not in stressful conditions.

An alternative strategy to that adopted in this experiment would have been to isolate the animals between observation sessions, as in the experiments described in 4.2 and 4.4. This procedure, however, was deliberately avoided for two reasons. Firstly, it was thought that the tendency for rat pups to play more, following isolation, might interfere with any effects of the novel object. Although subjects receiving a novel object and a play-partner might play more than subjects supplied only with a play-partner, given the high levels of play produced simply by isolation, the outcome would more probably be a "ceiling" effect. In a sense, this would also be a different experiment, contrasting the response of the control subjects to a novel, animate object (a playmate), to the reaction of the experimental subjects to a playmate plus an novel inanimate object. Secondly, the data on individual differences in pinning-levels required to test the second hypothesis would not have been obtained from normal animals but from isolates who differed from those of Panksepp (1981) only in the degree of isolation suffered (23 hours a day

isolation, as opposed to 5 minutes of social experience every four days).

## 4.3.3: The development of stable "on top" relationships in social play between paired animals:

### 4.3.3.1: Introduction:

This section deals with the second issue described in section 4.3.1: the issue of whether stable "on top" relationships develop between paired individuals over the course of repeated encounters.

In experiment two, described in the previous section, the opportunity was taken to record the number of pinnings performed by each member of a pair, in order to obtain further data on the development of any asymmetries in "on-top" behaviour in play. The previous studies described in this thesis raise a question which these data on asymmetries on pinning might be used to investigate. As mentioned in chapters 2 and 3, Panksepp (1981) claims that stable "dominance" relationships develop between pairs of rats with increasing age - "dominance" being defined in terms of one of the pair consistently adopting the "on-top" role in play, consistently pinning down his partner. (Panksepp provides no justification for his interpretation of pinning as a reflection of "dominance" relationships, an interpretation which seems to be derived

from an overly simplistic notion of play as direct practice for adult agonistic behaviours. In the present work, "on-top" behaviour will be described as such, without the use of labels as unwarrantedly interpretative as "dominance").

Panksepp's conclusions were based on data obtained from studies of the pinning behaviour of total isolates paired together in a strange cage for 5 minutes every four days from 20 days of age (except in the case of his "ontogeny probes", who did not begin this treatment until 40 days of age). The effect of this treatment on the "on-top" relationships observed is unclear, since although Panksepp also observed continuously socially-housed pairs of rats he did not report their pinning levels, claiming that they showed too little play for analysis to be worthwhile and that anyway the social animals would have had ample opportunity to develop social relationships outside of the test environment.

In view of the extensive claims made by Panksepp on the basis of the data from his isolate rats, the applicability of his findings to more normally-raised animals is an important issue. As mentioned earlier, the observational studies reported in chapters 2 and 3 of this thesis did not confirm Panksepp's claims, finding no evidence for the establishment over time of stable "on-top" relationships in play. There are at least two possible reasons for this discrepancy. One is that stable on-top relationships do not develop in normally-raised

litters; the other is that on-top relationships do develop in normally-raised animals, but only when they are in pairs rather than larger groups.

The data obtained on pinning in experiment two may clarify this issue. Subjects in this experiment (as opposed to those in experiments one and three in this chapter) were housed together in pairs for the whole of the period during which they were under scrutiny. If no marked asymmetries in on-top behaviour develop in the present study, then this implies that Panksepp's results are the outcome of isolation-induced aberrations in social behaviour, rather than the effect of being housed in pairs.

4.3.3.2: Method:

The procedural details of this experiment have already been given, in section 4.3.2.2. Data on the number of pins performed by each subject were obtained on a number of occasions from 25 to 65 days of age - ie, up to the age at which play has virtually ceased, and beyond the age (55 days) by which Meaney and Stewart (1981) claim that stable "dominance" relationships have developed.

4.3.3.3: Results:

In this section, the results of the two experimental procedures performed will be reported separately to some extent, since they involved observing the subjects on different days of age. A further complication is that on

different days, different pairs of subjects were undergoing different treatments (ie, in the sense of being presented with an object, having that object removed, or not being disturbed, etc.). Variations in the absolute numbers of pinnings by any particular pair of animals on any particular day are therefore probably not very meaningful: however, since there is little reason to suspect that the experimental manipulations would affect one member of a pair more than the other (at least in terms of their predisposition to pin or be pinned), differences between play-partners in the relative frequency with which they pinned or were themselves pinned, are probably reasonably accurate.

Table 4.3.2 shows the number of pinnings performed by each member of each pair of subjects, and the results of binomial tests on these frequencies both for all days combined, and for each of four age-periods - 26-35, 36-45, 46-55 and 56-65 days respectively. Grouping of the data in this way was necessary in order to obtain large enough numbers of bouts to make meaningful comparisons between the two partners in each pair: even so, (especially in the case of subjects experiencing the brick as their novel object) relatively few pinnings were observed after 46 days of age.

These results show that marked asymmetry in the number of pinnings performed by each partner of a pair was relatively uncommon: taking all days together, only two pairs showed significant departures from the 50:50 ratio

TABLE 4.3.2: AGE-CHANGES IN NUMBER OF PINNINGS SHOWN BY EACH PAIR OF SUBJECTS:

("N" = number of observation-sessions per pair, in the age-period concerned).

(a) Pairs receiving ball as novel object:

(Percentages are of the total number of pinnings in that age-period; number of pins per subject is in brackets. "Pr." = "pair; "P1" and "P2" are the members of a pair).

| Ageblock: | 26-35 (N=6) | 36-45 (N=6) | 46-55 (N=5) | 56-65 (N=8) | OVERALL (N=25) |
|---|---|---|---|---|---|
| Pr.1, P1: | 40.7% (55) | 44.2% (23) | 38.5% (10) | 66.7% (20) | 44.4% (108) |
| Pr.1, P2: | 59.3% (80) | 55.8% (29) | 61.5% (16) | 33.3% (10) | 55.6% (135) |
| Pr.2, P1: | 49.1% (57) | 55.3% (47) | 76.9% (20) | 56.3% (9) | 54.7% (133) |
| Pr.2, P2: | 50.9% (59) | 44.7% (38) | 23.1% (6) | 43.7% (7) | 45.3% (110) |
| Pr.3, P1: | 44.9% (40) | 31.4% (11) | 46.7% (14) | 60.8% (31) | 46.8% (96) |
| Pr.3, P2: | 55.1% (49) | 68.6% (24) | 53.3% (16) | 39.2% (20) | 53.2% (109) |
| Pr.4, P1: | 40.8% (31) | 48.2% (40) | 38.5% (15) | 41.4% (12) | 43.2% (90) |
| Pr.4, P2: | 59.2% (45) | 51.8% (43) | 61.5% (24) | 58.6% (17) | 56.8% (129) |

Binomial tests (converted to "z"-scores for N>25 where appropriate) on data above:

| | 26-35 | 36-45 | 46-55 | 56-65 | OVERALL |
|---|---|---|---|---|---|
| Pr. 1, P1: | -2.066* | -0.693 | -0.981 | -1.643 | -1.668 |
| Pr. 2, P1: | -0.093 | -0.868 | -2.550** | -0.804 | -1.411 |
| Pr. 3, P2: | -0.655 | -2.028* | -0.183 | -1.400 | -0.838 |
| Pr. 4, P1: | -1.491 | -0.220 | -1.281 | -0.743 | -1.991* |

(* = $p<0.05$; ** = $p<0.02$; *** = $p<0.01$: all tests are two-tailed).

(b) Pairs receiving brick as novel object:

(Percentages are of the total number of pinnings in an age-period; number of pins per subject is in brackets).

| Ageblock: | 26-35 (N=10) | 36-45 (N=6) | 46-55 (N=4) | 56-65 (N=4) | OVERALL (N=24) |
|---|---|---|---|---|---|
| Pr.1, P1: | 54.6% | 36.3% | 0.0% | 66.7% | 49.6% |
| | (83) | (37) | (0) | (3) | (143) |
| Pr.1, P2: | 45.4% | 63.7% | 100.0% | 33.3% | 50.4% |
| | (69) | (65) | (1) | (1) | (141) |
| Pr.2, P1: | 47.3% | 36.4% | 62.5% | 50.0% | 44.4% |
| | (86) | (40) | (15) | (1) | (150) |
| Pr.2, P2: | 52.7% | 63.6% | 37.5% | 50.0% | 55.6% |
| | (96) | (70) | (9) | (1) | (188) |
| Pr.3, P1: | 47.0% | 42.6% | 45.5% | 77.8% | 46.5% |
| | (70) | (26) | (5) | (7) | (125) |
| Pr.3, P2: | 53.0% | 57.4% | 54.5% | 22.2% | 53.5% |
| | (79) | (35) | (6) | (2) | (144) |
| Pr.4, P1: | 41.6% | 51.6% | 50.0% | 66.6% | 43.8% |
| | (47) | (16) | (8) | (4) | (84) |
| Pr.4, P2: | 58.4% | 48.4% | 50.0% | 33.3% | 56.2% |
| | (66) | (15) | (8) | (2) | (108) |

Binomial tests (converted to "z"-scores for N>25 where appropriate) on above data:

| Age-period: | 26-35 | 36-45 | 46-55 | 56-65 | OVERALL |
|---|---|---|---|---|---|
| Pr.1, P1: | -0.435 | -2.673*** | - | - | -0.059 |
| Pr.2, P1: | -0.667 | -2.765*** | -0.303 | - | -2.013* |
| Pr.3, P2: | -0.665 | -1.024 | -1.000 | -0.180 | -1.097 |
| Pr.4, P1: | -1.693 | -0.000 | -1.196 | -0.688 | -1.659 |

(* = p<0.05; ** = p<0.02; *** = p<0.01: all tests are two-tailed).

of pinnings which each animal would be expected to show by chance. In the case of one of these pairs (pair 4 of the "ball" experiment) there was no significant departure from expected frequencies of pinning by either partner in any of the four ageblocks, when they were considered individually; and the other pair's (pair 2 of the "brick" experiment) significant result appears to be derived predominantly from a marked asymmetry in pinning between days 36-45. Pair 1 of the "brick" experiment, and pair 3 of the "ball" experiment also showed unequal levels of pinning at this age. The other two significant results were displayed by pairs 1 and 2 of the "ball" experiment, at 26-35 days; and 46-55 days respectively. Three of these tests (including the two overall tests) were significant only at the .05 level of significance, and the other three were significant at the .02 level: considering that a total of 37 binomial tests were performed on this data, some of these results may well be due to Type I error. In only one pair was one individual observed to be on top more than the other, in all four age-periods (pair 4 of the "ball" experiment). The overall conclusion is that there is no evidence of statistically-significant age-related increases in asymmetry in on-top relationships between pair-members.

4.3.3.4: Discussion:

This experiment found no evidence that stable "on-top" relationships develop between paired animals

with increasing age. These data thus confirm the observations reported in chapters 2 and 3, and are further evidence against Panksepp's (1981) claims that play leads to the formation of "dominance" relationships between individuals.

There are a number of possible reasons for the differences between differences between Panksepp's (1981) study and the experiment reported here, and the only way to decide conclusively whether or not there are differences in pinning behaviour between severely-isolated rats and more normally-raised animals would be to compare the behaviour of social and playing-isolate animals within the same experiment, keeping all other factors constant. However, the possibility that Panksepp's results are a manifestation of aberrant behaviour in his isolates is the most plausible explanation for the observed differences in pinning-levels.

In the absence of any information on whether or not Panksepp's socially-housed animals showed the same kind of behavioural trends (one would suspect that they did not, since the data were not presented in his report) it is quite possible that his observed asymmetries in pinning behaviour were the response of socially maladjusted animals to the presence of a conspecific. While the subjects of the present study can hardly be described as having been reared under "normal" social conditions (ie, mixed-sex social groups), they were at least subjected to less drastic deprivations than Panksepp

employed.

As with the other studies in this thesis, the results reported here emphasise the reciprocity in the play-relationships of young rats, rather than any asymmetries in them. Furthermore, they would suggest that strong caution should be exercised in extrapolating from the behaviour of isolates to that of social animals, in the field of play research as in any other social behaviour. Panksepp (1981) claims that "social play can be efficiently studied" by using prolonged isolation to raise play-levels; that his procedures "...can help us make substantial progress..." in understanding play; and draws the conclusion from his results that "one function of play may be to establish stable social relationships". He further asserts that "...through social deprivation, we can amplify play so that brief observation periods suffice for a substantial sample of the behaviour". These claims may or may not be correct; but the results from the present experiment suggest that Panksepp's claims are at best premature; and that it may be highly misleading to opt for experimental convenience by employing methods to artificially increase play-levels on demand, without thoroughly investigating the possible consequences of such techniques.

## 4.4: THE EFFECTS OF FOOD DEPRIVATION ON LEVELS OF SOCIAL PLAY:

### 4.4.1: Introduction:

In contrast to the previous experiments, which have focussed on the elicitation of play by means of social deprivation (Experiment One) and introduction of change into the environment (Experiment Two), this experiment looks at the suppression of play by means of food deprivation. The experiments of Baldwin and Baldwin (1974), in which captive squirrel monkeys were used to simulate conditions of food shortage apparently commonplace in the natural environment (Baldwin and Baldwin 1974; Southwick, 1967; Hall 1963) have already been discussed at length in section 1.4. The Baldwins expressed surprise at the persistence of play under circumstances of severe food deprivation, and noted a "rebound" effect when deprivation ceased.

This experiment attempts to replicate the Baldwins' results, using rats. If similar effects occur, then this is possibly evidence that social play in squirrel monkeys and rats have certain features in common and may represent the same process in different species. Obviously, a reduction in the amount of play shown as a response to starvation is of very little interest in itself; but if rats show a "rebound" effect when deprivation stops then this suggests that the motivational mechanisms governing the performance of play in rat and monkey might have

something in common.

One way in which the experiment to be described here differs from that of the Baldwins', is that subjects were not housed in social groups Instead, each subject was housed in isolation except for one hours contact with another individual (always the same animal) each day. This was done for two reasons: firstly, it ensured that all play which occurred was observed - if social contact were unrestricted, it could always be argued that food-deprivation was not depressing play, but merely redistributing it. Secondly, given that experiment one has shown how powerful the drive to play is when opportunities for play are withheld, it might be interesting to see how strong this drive is under conditions of food-deprivation: ie, is the motivation to play following social isolation, strong enough to overcome the effects of food-deprivation? If the energetic costs of play are signficant, and animals are tuned to drop play from their behavioural repertoire if it becomes too "costly", energetically, as has been suggested by Fagen (1981), then one might expect food-deprivation to abolish play regardless of whether or not opportunities for play present themselves.

In the present experiment, all social behaviours occurring between the two animals of each pair were recorded, during the observation session. In this way it was hoped to discover whether any depressive effects of food-deprivation are specific to play or affect all social

behaviours equally; or, alternatively, whether, if only play is suppressed by food-deprivation, other behaviours - such as allo-grooming - increase in frequency, perhaps in some way obtaining experiences normally provided by play but rendered too "expensive" to obtain that way. In this way, the present experiment examines the issue of whether play has a distinctive motivational basis, from another angle to that explored in section 4.2.

Finally, a record was taken of which animal performed the social behaviours. In each pair, one animal was designated the "resident" and the other the "intruder". The "intruder" was always placed into the "resident"'s cage for their mutual daily 30 minutes of social experience. If play is in any way related to agonistic behaviour (ie, resource-defence) then more play should be performed by the resident towards the intruder than vice versa, and this tendency should become more pronounced the more extreme the food deprivation becomes (ie, should increase with increased value of the resources at stake). If play is entirely unrelated to resource defence, whether of territory and/or food, then increased deprivation should not lead to one of the animals performing more social behaviours than the other.

### 4.4.2: Method:

A repeated-measures design with matched controls was used, similar to that of Experiment Two, except that (a) controls did not subsequently become the experimental

subjects and vice versa, and (b) pairs were not housed together continuously, but received only one hour per day of social contact with each other.

Pinning was used as the dependent variable, to enable the results of this experiment to be compared directly to those of experiment two and to those of Panksepp (1981).

4.4.2.1: Subjects:

16 pairs of male PVG rats were used, aged 30 days at the beginning of the experiment.

4.4.2.2: Apparatus:

For each of the 16 pairs, one rat was housed in a standard plastic cage (North Kent Plastics, RB1) with wire top containing a water bottle, and the other rat was housed in one of the purpose-built metal cages described in the Method Section of Experiment Two. In both cases, subjects were kept on sawdust, and food (S.D.S. rat and mouse maintenance diet number 1, in small pelleted form) was placed on the floor of the cage. Subjects were housed in the same room, and under the same lighting regimen, as in Experiment Two, except that the lights went on and off at 11 o'clock rather than 12. Each test session was videotaped, and records of behaviour made fron the tape under "blind" conditions, ie with the observer unaware of what deprivation condition subjects were in at any particular time.

4.4.2.3: Procedure:

All subjects were raised in normal mixed-sex litter groups with their mothers until weaning at 21 days. The

mothers were then removed, and the subjects retained with their littermates until the Experiment began at 30 days. Pairs of males were then selected, roughly matched for size. Pairs were randomly allocated to the experimental and control conditions. Subjects were tested in two batches of six pairs (three experimental and three control, in each case) and one batch of four pairs (two experimental and two control).

Subjects were observed for 30 minutes per day, following total social isolation from each other and any other conspecifics since the end of the previous day's session (ie, following 23 hours' isolation). As mentioned previously, in each pair one animal was the "intruder" and the other the "resident", and the "intruder" was always placed in the "resident"'s cage and removed from it back to his own cage at the end of the test session. Subjects were given one hour of contact with each other per day, but only the first 30 minutes of this period were observed.

For each pair, observations were made under four conditions:

<u>(a) Day One: Baseline (BL):</u> all subjects were observed after 24 hour's social isolation, to establish that experimental and control pairs played at comparable levels. At 3 pm on this day, subjects in the experimental group were food-deprived.

<u>(b) Day Two: Food Deprivation (FD):</u> subjects in the experimental group were placed together in their pairs,

## OUTLINE OF PROCEDURE IN EXPERIMENT THREE:

(a) PART ONE:

AGE (DAYS)

| | 21 | 21 - 29 | 30 | 31 | 32 | 33 | 34 | 35 |
|---|---|---|---|---|---|---|---|---|
| EXPERIMENTAL | WEANING; MOTHER REMOVED | CONTINUOUS, UNOBSERVED HOUSING OF | RANDOM ALLOCATION OF S's | B/L | FD1 | FD2 | R1 | R2 |
| | | | | 1 HOUR OF SOCIAL CONTACT BETWEEN PAIR-MEMBERS ON EACH OF THESE DAYS. | | | | |
| CONTROL | FROM LITTERS | PUPS IN THEIR ORIGINAL LITTER GROUPS | TO PAIRS, THEN SOCIAL ISOLATION | 1 HOUR OF SOCIAL CONTACT BETWEEN PAIR-MEMBERS ON EACH OF THESE DAYS. | | | | |

B/L: ONE HOUR OF SOCIAL CONTACT AFTER 23 HOUR'S SOCIAL ISOLATION.

FD1: 1 HOUR'S SOCIAL CONTACT AFTER 23 HOUR'S SOCIAL ISOLATION, DURING WHICH S's EXPERIENCED 20 HOUR'S FOOD-DEPRIVATION.

FD2: 1 HOUR'S SOCIAL CONTACT, AFTER 23 HOUR'S SOCIAL ISOLATION. SUBJECTS HAD BY THEN EXPERIENCED 44 HOUR'S FOOD-DEPRIVATION.

R1: 1 HOUR'S SOCIAL CONTACT, AFTER 23 HOUR'S SOCIAL ISOLATION, AND 20 HOURS OF AD-LIB FEEDING.

R2: 1 HOUR'S SOCIAL CONTACT, AFTER 23 HOUR'S SOCIAL ISOLATION, AND 44 HOURS OF AD-LIB FEEDING.

SUBJECTS IN PART TWO RECEIVED THE SAME TREATMENT EXCEPT THAT FD2 WAS OMITTED.

## PROCEDURE ON EACH DAY:-

11.00 AM — 12.00 PM — 3.00 PM

ROOM-LIGHTS OFF:

SUBJECTS PLACED IN PAIRS, AND BEHAVIOUR RECORDED FOR THE FIRST 30 MINUTES OF THE HOUR.

SUBJECTS ISOLATED, UNTIL 11.00 AM ON THE FOLLOWING DAY.

(a) ON B/L DAY, FOOD-DEPRIVATION BEGAN

(b) ON FD2 (FOR SUBJ IN PART ONE) OR FD1 (FOR SUBJ IN PART TWO), AD FEEDING WAS REINTRODUCED.

still under conditions of food deprivation, and social behaviour in experimentals and controls recorded. Thus subjects in both the experimental and control pairs were observed after 23 hours' social isolation, but the experimental subjects had endured in addition 20 hours without food. Experimental subjects received food pellets in their cages immediately after the end of this session, and were on ad lib feeding from then on.

(c) Day Three: Recovery One (R1): levels of social behaviour were recorded in experimentals and controls, following 23 hours' social isolation.

(d) Day Four: Recovery Two (R2): levels of social behaviour were recorded in experimentals and controls, after 23 hours' isolation..

The first batch of six pairs tested differed from this procedure in that they had a second day of food-deprivation immediately following the first. The effects of over 40 hours without food on 30 day-old rats are so severe, however, that this was not repeated, although the results from this manipulation will be described.

To sum up, six pairs of rats received two days of food-deprivation, followed by two recovery days; and the remaining ten pairs experienced only one day without food, followed by two recovery days. The former group will henceforth be described as "part one" of the study, and the latter as "part two".

## 4.4.3: Results:

### 4.4.3.1: Effects of food-deprivation on social behviours:

#### 4.4.3.1.1: Effects of food-deprivation on play:

Figure 4.4.1(a) shows the mean number of pinnings performed by the experimental and control subjects on each day of Part One of the experiment. Fig. 4.4.1(b) depicts the corresponding data for subjects in Part Two of the experiment.

Table 4.4.1 shows the results of mixed-design ANOVA's (with food-deprivation as the independent factor and day of treatment as the repeated measure) on the number of pinnings, for Parts One and Two of the experiment. The results were similar in both cases.

In Part One of the experiment, there was a significant effect of day of treatment ($p<0.02$, two-tailed); a significant interaction between group (ie, food-deprived versus not food-deprived) and day of treatment ($p<0.02$, two-tailed); and no significant difference between the groups overall. Part Two showed similar results, with the effects of day of treatment and the interaction between day and group both significant at $p<0.0001$. Inspection of Figs. 4.4.1(a,b) suggests the following interpretation.

Control subjects showed fairly constant levels of play on all days of the experiment. On the initial

FIG.4.4.1(a): EXPERIMENT THREE (PART ONE): MEAN NUMBER OF PINNINGS PERFORMED ON EACH DAY OF THE EXPERIMENT:

FIG.4.4.1(b): EXPERIMENT THREE (PART TWO): MEAN NUMBER OF PINNINGS PERFORMED ON EACH DAY OF THE EXPERIMENT:

(VERTICAL ERROR-BARS ON FIGS. 4.4.1 TO 4.4.7 SHOW THE MEAN, PLUS AND MINUS ONE STANDARD DEVIATION)

TABLE 4.4.1: RESULTS OF ANOVAS ON THE EFFECTS OF FOOD DEPRIVATION ON PLAY, IN EXPERIMENT THREE:

(a) EFFECTS OF FOOD-DEPRIVATION ON PLAY (NUMBER OF PINS) IN PART ONE:

| Source of variance | SS | DF | MS | F | p |
|---|---|---|---|---|---|
| Deprivation / no deprivation (A) | : 1687.50 | 1 | 1687.50 | 7.435 | ns |
| Error AS | : 907.87 | 4 | 226.97 | | |
| Day of treatment (B): | : 2786.47 | 4 | 696.62 | 6.771 | p<0.005 |
| Interaction A*B | : 1937.00 | 4 | 484.25 | 4.707 | p<0.02 |
| Error B*AS | : 1646.13 | 16 | 102.88 | | |
| Total | : 8964.97 | 29 | | | |

(b) EFFECTS OF FOOD-DEPRIVATION ON PLAY (NUMBER OF PINS) IN PART TWO:

| Source of variance | SS | DF | MS | F | p |
|---|---|---|---|---|---|
| Deprivation / no deprivation (A) | : 1010.02 | 1 | 1010.02 | 4.027 | ns |
| Error AS | : 2006.50 | 8 | 250.81 | | |
| Day of treatment (B) | : 3005.48 | 3 | 1001.83 | 12.864 | p<0.0001 |
| Interaction A*B | : 3543.67 | 3 | 1181.22 | 15.167 | p<0.0001 |
| Error B*AS | : 1869.10 | 24 | 77.88 | | |
| Total: | :11434.77 | 39 | | | |

baseline day, the experimental subjects showed levels of play comparable to those of the controls; however, 20 hours' food-deprivation resulted in a dramatic drop in the number of pinnings displayed by the experimental subjects, both in contrast to their own performance on the previous day and in comparison to the behaviour of the controls on the same day. In the case of the experimental subjects in Part One, the second day of food deprivation led to a further drop in observed levels of pinning. In the first observation session after food-deprivation ceased (which came after 20 hours of ad-lib feeding), experimental subjects in both Parts showed a return to frequencies of pinning that were comparable both to their own baseline levels and to the levels of play shown by their controls on the same day.

In both Parts of the experiment, the amount of play shown by experimental subjects on the first day after food-deprivation had ceased, was higher than that observed on the baseline day: however, "t"-tests comparing the levels of pinning in experimental subjects on these two days were not significant for either Part of the experiment ("t"= 1.387 with 2 df for Part One; "t"= 0.854 with 4 df for Part Two; $p>0.05$, one-tailed, in both cases). Thus there is no evidence to suggest that the lack of play caused by food-deprivation led to a subsequent "rebound" effect.

4.4.3.1.2: Effects of food-deprivation on allo-grooming:

Figs. 4.4.2(a) and (b) show the mean number of individually distinguishable allo-grooming sessions performed by experimental and control subjects on each day, in Parts One and Two of the experiment respectively. Table 4.4.2 reports the results of ANOVA's on these data.

In the case of allo-grooming, the results differ for the two parts of the experiment.

In part one, there was a significant effect of day of treatment ($p<0.02$), but not of group or of the interaction between day and group. This suggests that there was no effect of food-deprivation on levels of allo-grooming, and examination of fig. 4.4.2(a) confirms this. The control group showed a gradual increase in the frequency of allo-grooming over the course of the experiment, while the experimental group displayed a similar but more variable pattern. The latter group exhibited a decrease in allo-grooming in the first observation-period after the cessation of deprivation, but only to the same mean level of grooming as they had shown on the first day of the experiment.

In part two, there was a significant effect of day of treatment as in part one ($p<0.005$), but also a significant interaction between day of treatment and group ($p<0.005$). Examination of fig. 4.4.2(b) reveals that the levels of allo-grooming shown by experimental subjects on the food-deprivation day were markedly lower than on the other

FIG.4.4.2(a): EXPERIMENT THREE (PART ONE): MEAN NUMBER OF ALLO-GROOMING EPISODES PERFORMED ON EACH DAY OF THE EXPERIMENT:

FIG.4.4.2(b): EXPERIMENT THREE (PART TWO): MEAN NUMBER OF ALLO-GROOMING EPISODES PERFORMED ON EACH DAY OF THE EXPERIMENT:

TABLE 4.4.2: RESULTS OF ANOVAS ON THE EFFECTS OF FOOD-DEPRIVATION ON ALLO-GROOMING, IN EXPERIMENT THREE:

(a) EFFECTS OF FOOD-DEPRIVATION ON ALLO-GROOMING (NUMBER OF SEPARATE BOUTS) IN PART ONE:

| Source of variance | SS | DF | MS | F | p |
|---|---|---|---|---|---|
| Deprivation / no deprivation (A) : | 24.30 | 1 | 24.30 | 0.92 | ns |
| Error AS : | 105.60 | 4 | 26.40 | | |
| Day of treatment (B): | 77.20 | 4 | 19.30 | 4.26 | p<0.02 |
| Interaction A*B : | 11.20 | 4 | 2.80 | 0.62 | ns |
| Error B*AS : | 72.40 | 16 | 4.52 | | |
| Total: : | 290.70 | 29 | | | |

(b) EFFECTS OF FOOD-DEPRIVATION ON ALLO-GROOMING (NUMBER OF SEPARATE BOUTS) IN PART TWO:

| Source of variance | SS | DF | MS | F | p |
|---|---|---|---|---|---|
| Deprivation / no deprivation (A) : | 1.60 | 1 | 1.60 | 0.033 | ns |
| Error AS : | 384.80 | 8 | 48.10 | | |
| Day of treatment (B): | 186.70 | 3 | 62.23 | 5.548 | p<0.005 |
| Interaction A*B : | 125.60 | 3 | 41.87 | 3.732 | p<0.025 |
| Error B*AS : | 269.20 | 24 | 11.22 | | |
| Total: : | 967.90 | 39 | | | |

days of the experiment; in contrast, the control subjects showed a consistent increase in allo-grooming over the course of the experiment.

The effects of food-deprivation on allo-grooming are thus not as clear-cut as they are in the case of play. In part one of the experiment, food-deprivation appears to have had no effect on allo-grooming, whereas in part two the consequences of deprivation appear to have been similar to those on play.

4.4.3.1.3: The effects of food-deprivation on social olfaction:

Figs. 4.4.3 (a,b) show the mean number of sniffs of the partner performed by experimental and control subjects on each day, in Parts One and Two of the experiment respectively. Table 4.4.3 reports the results of ANOVA's on these data.

Again, as with allo-grooming, the results differ for the two parts of the experiment. In part one, there were significant effects of day of treatment ($p<0.005$) and of the interaction between group and day of treatment ($p<0.05$). Inspection of fig. 4.4.3(a) suggests that the day of treatment effect stems from the steep decline over successive days in olfactory investigation of the partner, shown by both experimental and control subjects. The interaction presumably results from the fact that levels of olfaction were elevated in the experimental group on food-deprivation days and depressed on the first

FIG.4.4.3(a): EXPERIMENT THREE (PART ONE): MEAN NUMBER OF SOCIAL SNIFFS PERFORMED ON EACH DAY OF THE EXPERIMENT:

FIG.4.4.3(b): EXPERIMENT THREE (PART TWO): MEAN NUMBER OF SOCIAL SNIFFS PERFORMED ON EACH DAY OF THE EXPERIMENT:

TABLE 4.4.3: RESULTS OF ANOVAS ON THE EFFECTS OF FOOD-DEPRIVATION ON SOCIAL OLFACTION IN EXPERIMENT THREE:

(a) EFFECTS OF FOOD-DEPRIVATION ON SOCIAL OLFACTION (NUMBER OF INDIVIDUAL SNIFFS) IN PART ONE:

| Source of variance | | SS | DF | MS | F | p |
|---|---|---|---|---|---|---|
| Deprivation / no deprivation (A) | : | 128.13 | 1 | 128.13 | 4.224 | ns |
| Error AS | : | 121.33 | 4 | 30.33 | | |
| Day of treatment (B) | : | 492.47 | 4 | 123.12 | 6.39 | $p<0.005$ |
| Interaction A*B | : | 241.53 | 4 | 60.38 | 3.14 | $p<0.05$ |
| Error B*AS | : | 308.00 | 16 | 19.25 | | |
| Total: | : | 1291.47 | 29 | | | |

(b) EFFECTS OF FOOD-DEPRIVATION ON SOCIAL OLFACTION (NUMBER OF INDIVIDUAL SNIFFS) IN PART TWO:

| Source of variance | | SS | DF | MS | F | p |
|---|---|---|---|---|---|---|
| Deprivation / no deprivation (A) | : | 6.40 | 1 | 6.40 | 0.164 | ns |
| Error AS | | 311.70 | 8 | 38.96 | | |
| Day of treatment (B) | : | 150.50 | 3 | 50.17 | 2.486 | ns |
| Interaction A*B | : | 24.20 | 3 | 8.07 | 0.399 | ns |
| Error B*AS | : | 484.30 | 24 | 20.18 | | |
| Total: | | 977.10 | 39 | | | |

post-deprivation day, relative to controls.

In the case of subjects in part two, there were no significant changes in olfaction, either between or within groups, although examination of fig. 4.4.3(b) suggests that there may have been a trend for social olfaction to decline in all subjects, over successive days of the experiment.

The overall conclusion is therefore that food-deprivation had no clear effects on levels of social olfaction, at least not to the extent of producing a marked drop in such behaviour on deprivation days.

4.4.3.2: The effects of food-deprivation on the behaviour of the "resident" and the "intruder":

This section investigates firstly whether being the "resident" or "intruder" of a pair affected behaviour, regardless of which experimental condition the subjects were in; and secondly, whether food-deprivation further influenced their behaviour, such that food-deprived residents and intruders behaved differently to their non-food-deprived counterparts.

4.4.3.2.1: The effects of the "resident"/"intruder" variable on play:

For each pair of subjects, a binomial test (converted to "z"-scores for N>25) was performed to determine whether the two partners pinned each other with equal frequency. The number of pins by each pair, and the

results of the binomial tests, are shown in Table 4.4.4.

In part one of the experiment, only two of the six pairs of subjects showed significant inequalities in their levels of pinning: one of these pairs came from the experimental group, and the other from the control group. In both cases, the resident member of each pair pinned his partner more frequently than he himself was pinned. In each of the remaining four pairs, it was the intruder who pinned most, though in none of these cases did this even approach statistical significance.

The subjects in part two of the experiment showed a somewhat different pattern. Four out of the five pairs of controls showed a marked asymmetry in pinning levels, whereas only one of the five experimental pairs did so. Of these four pairs of controls, two pairs displayed a preponderance of pinnings by the resident member of the pair, while in the other two pairs it was the intruder who was on top most frequently. In the case of the one experimental pair showing signficantly-unequal levels of pinning, it was the resident who pinned most often. In two of the remaining pairs of experimental subjects, the intruder pinned most; one pair showed more pins by the resident; and one pair showed almost exactly equal numbers of pins by its members.

Taking the results of the two parts of the study together, it is clear that the resident/intruder factor did not determine which member of a pair pinned the most. Only 7 out of 16 pairs showed a significant

**TABLE 4.4.4: RELATIVE FREQUENCY OF PINNING BY "RESIDENTS" AND "INTRUDERS":**

("z-score" refers to the result of the binomial test, using the normal approximation to the binomial for N>25; "p" refers to the probability of obtaining that score, under the null hypothesis that both players pin with equal frequency; all tests are two-tailed)

**(a) PART ONE:**

**Experimental subjects:**

| | Total no. of pins: | Number of pins by resident: | Number of pins by intruder: | z-score: | p: |
|---|---|---|---|---|---|
| PAIR 1: | 126 | 106 | 20 | -7.572 | <0.00001 |
| PAIR 2: | 108 | 46 | 62 | -1.443 | 0.150 |
| PAIR 3: | 184 | 88 | 96 | -0.516 | 0.603 |

**Control subjects:**

| | Total no. of pins: | Number of pins by resident: | Number of pins by intruder: | z-score: | p: |
|---|---|---|---|---|---|
| PAIR 4: | 184 | 161 | 23 | -8.984 | <0.00001 |
| PAIR 5: | 228 | 111 | 117 | -0.331 | 0.741 |
| PAIR 6: | 231 | 114 | 117 | -0.132 | 0.897 |

**(B) PART TWO:**

**Experimental subjects:**

| | Total no. of pins: | Number of pins by resident: | Number of pins by intruder: | z-score: | p: |
|---|---|---|---|---|---|
| PAIR 1: | 175 | 136 | 39 | -7.257 | <0.00001 |
| PAIR 2: | 215 | 106 | 109 | -0.136 | 0.889 |
| PAIR 3: | 179 | 90 | 89 | 0.000 | 1.000 |
| PAIR 4: | 158 | 69 | 89 | -1.512 | 0.131 |
| PAIR 5: | 114 | 65 | 49 | -1.405 | 0.162 |

**Control subjects:**

| | Total no. of pins: | Number of pins by resident: | Number of pins by intruder: | z-score: | p: |
|---|---|---|---|---|---|
| PAIR 6: | 241 | 184 | 57 | -8.116 | <0.00001 |
| PAIR 7: | 201 | 74 | 127 | -3.668 | 0.0002 |
| PAIR 8: | 229 | 75 | 154 | -5.154 | 0.0001 |
| PAIR 9: | 190 | 119 | 71 | -3.410 | 0.0006 |
| PAIR 10: | 181 | 88 | 93 | -0.297 | 0.764 |

asymmetry in pinning levels, and in only 4 of these pairs was it the resident who pinned most. Furthermore, this was true whether or not food-deprivation was involved: only 2 of the 8 experimental pairs showed asymmetries in pinning frequencies (although in both of these it was the resident who pinned most).

The analysis above shows only that there were no overall within-pair asymmetries in pinning levels that could be related to the resident/intruder variable: however, residents might still be pinning more frequently than their partners (or vice-versa) on certain days. For example, although food-deprivation might lead to a relative increase in the one-sidedness of pinning in post-deprivation observation-sessions, this could be obscured by an examination of overall pinning levels, because the absolute frequency of pinning would be less on those days. In other words, there might be marked asymmetries in pinning only when the situation became critical, which were thus confined to post-deprivation days. To test this hypothesis, an ANOVA was carried out on the number of pins performed each day by the resident of each pair, expressed as a percentage of the daily total number of pins observed for that pair. Thus, if food-deprivation led to less reciprocity in pinning, the percentage of pinning shown by the resident would vary, regardless of the absolute number of pins shown.

The results of this analysis are shown in Table 4.4.5. The mean percentages of the daily totals of pins

TABLE 4.4.5: RESULTS OF ANOVAS ON EFFECTS OF FOOD-DEPRIVATION ON PINNING BY "RESIDENTS" AND "INTRUDERS":

(a) EFFECTS OF FOOD-DEPRIVATION ON THE PERCENTAGE OF THE DAILY FREQUENCY OF PINNING PERFORMED BY THE RESIDENT OF EACH PAIR IN PART ONE:

| Source of variance | | SS | DF | MS | F | p |
|---|---|---|---|---|---|---|
| Deprivation / no deprivation (A) | : | 7.73 | 1 | 7.73 | 0.003 | ns |
| Error AS | : | 11140.86 | 4 | 2785.21 | | |
| Day of treatment (B) | : | 2586.79 | 4 | 646.70 | 3.632 | $p<0.05$ |
| Interaction A*B | : | 3106.27 | 4 | 776.57 | 4.361 | $p<0.025$ |
| Error B*AS | : | 2848.79 | 16 | 178.05 | | |
| Total | : | 19690.44 | 29 | | | |

(b) EFFECTS OF FOOD-DEPRIVATION ON THE PERCENTAGE OF THE DAILY FREQUENCY OF PINNING PERFORMED BY THE RESIDENT OF EACH PAIR IN PART TWO:

| Source of variance | | SS | DF | MS | F | p |
|---|---|---|---|---|---|---|
| Deprivation / no deprivation (A) | : | 211.19 | 1 | 211.19 | 0.189 | ns |
| Error AS | : | 8911.66 | 8 | 1113.96 | | |
| Day of treatment (B) | : | 4.85 | 3 | 1.62 | 0.019 | ns |
| Interaction A*B | : | 320.86 | 3 | 106.95 | 1.282 | ns |
| Error B*AS | : | 2002.29 | 24 | 83.43 | | |
| Total | : | 11450.84 | 39 | | | |

FIG.4.4.4(a): EXPERIMENT THREE (PART ONE): MEAN PERCENTAGE OF DAILY TOTAL OF PINNINGS PERFORMED BY 'RESIDENTS' IN EXPERIMENTAL AND CONTROL CONDITIONS:

FIG.4.4.4(b): EXPERIMENT THREE (PART TWO): MEAN PERCENTAGE OF DAILY TOTAL OF PINNINGS PERFORMED BY 'RESIDENTS' IN EXPERIMENTAL AND CONTROL CONDITIONS:

that were performed by the resident subjects, both in the control and experimental conditions, are displayed graphically in Figs. 4.4.4(a) and 4.4.4(b), for parts one and two of the experiment respectively.

In the case of subjects in part one of the experiment, the ANOVA revealed a significant difference between the food-deprived and control groups ($p<0.05$) and a significant interaction between group and day of treatment ($p<0.025$). Examination of fig. 4.4.4(a) shows that whereas the relative percentages of pinning by residents remained fairly constant in the case of the control pairs, this was not so for the experimental subjects: the relative frequency of pinning by residents in the food-deprived group decreased over the course of the experiment. (This decline appears more dramatic than it actually was: note the enormous variation on day two of food-deprivation, which arises as a consequence of converting into percentages small absolute frequencies of pinning - play on this day was almost negligible in this part of the experiment).

The corresponding ANOVA for part two of the experiment showed no significant differences between the groups in any way, and examination of fig. 4.4.4(b) suggests that the relative frequencies of pinning by residents in both groups were remarkably constant over days.

The overall conclusion must therefore be that food-deprivation did not lead to increased asymmetry in

levels of pinning by either the resident or the intruder. There appears to have been some effect on the relative frequencies of pinning by residents in the food-deprived condition of part one of the experiment, but this was in the direction of of a decrease in pinning. In any case, this result must be treated with caution as it is based on a small sample of pins from severely food-deprived animals.

4.4.3.2.2: The effects of the "resident"/"intruder" variable on allo-grooming:

Table 4.4.6 shows the numbers of individually distinguishable allo-grooming bouts performed by each member of each pair of subjects, and the results of binomial tests on these frequencies, testing the hypothesis that the partners groomed each other equally frequently.

In the case of part one of the experiment, 5 out of 6 pairs showed higher levels of allo-grooming by the resident of the intruder than vice versa; however, this was only significantly so in the case of two pairs. One of these pairs came from the experimental group, and the other from the control group.

The same pattern was shown by subjects in both groups of part two of the experiment: 8 of the 10 pairs showed a preponderance of allo-grooming by the resident partner of the pair, although this attained statistical significance only in the case of two pairs - both from the experimental

TABLE 4.4.6: RELATIVE FREQUENCY OF ALLO-GROOMING BY "RESIDENTS" AND "INTRUDERS":

("z-score" refers to the result of the binomial test, using the normal approximation to the binomial for N>25; "p" refers to the probability of obtaining that score, under the null hypothesis that both players groom with equal frequency; all tests are two-tailed)

(A) PART ONE:

Experimental subjects:

| | Total no. of grooms: | Number of grooms by resident: | Number of grooms by intruder: | z-score: | p: |
|---|---|---|---|---|---|
| PAIR 1: | 17 | 11 | 6 | -0.970 | 0.332 |
| PAIR 2: | 14 | 13 | 1 | -2.940 | 0.003 |
| PAIR 3: | 32 | 20 | 12 | -1.237 | 0.215 |

Control subjects:

| | Total no. of grooms: | Number of grooms by resident: | Number of grooms by intruder: | z-score: | p: |
|---|---|---|---|---|---|
| PAIR 4: | 21 | 18 | 3 | -3.055 | 0.002 |
| PAIR 5: | 45 | 29 | 16 | -1.789 | 0.073 |
| PAIR 6: | 24 | 12 | 12 | 0.000 | 0.500 |

(B) PART TWO:

Experimental subjects:

| | Total no. of grooms: | Number of grooms by resident: | Number of grooms by intruder: | z-score: | p: |
|---|---|---|---|---|---|
| PAIR 1: | 43 | 25 | 18 | -0.915 | 0.363 |
| PAIR 2: | 37 | 23 | 14 | -1.315 | 0.190 |
| PAIR 3: | 50 | 24 | 26 | -0.141 | 0.889 |
| PAIR 4: | 52 | 29 | 23 | -0.693 | 0.490 |
| PAIR 5: | 35 | 23 | 12 | -1.690 | 0.091 |

Control subjects:

| | Total no. of grooms: | Number of grooms by resident: | Number of grooms by intruder: | z-score: | p: |
|---|---|---|---|---|---|
| PAIR 6: | 25 | 24 | 1 | -4.400 | <0.0001 |
| PAIR 7: | 49 | 35 | 14 | -2.857 | 0.004 |
| PAIR 8: | 28 | 14 | 14 | 0.000 | 0.500 |
| PAIR 9: | 56 | 30 | 26 | -0.401 | 0.689 |
| PAIR 10: | 67 | 48 | 19 | -3.421 | <0.0006 |

group.

For both parts of the experiment, an ANOVA was carried out on the percentages of the daily totals of allo-grooming in each pair that were performed by the resident partner. The results of these are shown in Table 4.4.7. Figs. 4.4.5(a,b) show, for parts one and two of the experiment respectively, the means and standard deviations for these data.

There was a significant interaction between group and day of treatment in part one of the experiment ($p<0.01$), but no other statistically significant results were obtained from this analysis, nor from the corresponding ANOVA on the data from part two. Examination of fig. 4.4.5(a) reveals a decline in the proportion of daily allo-grooming that was performed by residents in part one of the experiment, with a marked decrease on the first day after food-deprivation had ended. In contrast, subjects in the control group in part one displayed an increase over days in the proportion of resident-performed allo-grooming. The interpretation of these effects is unclear, especially compared to the consistency over days exhibited by both the experimental and control subjects of part two.

The general conclusion from these data is the same as that from the data on levels of pinning: food-deprivation appears to have had litle effect on the relative frequencies with which the resident and intruder of each pair groomed each other. Residents appear to have groomed

TABLE 4.4.7: RESULTS OF ANOVAS ON EFFECTS OF FOOD-DEPRIVATION ON ALLO-GROOMING BY "RESIDENTS" AND "INTRUDERS":

(a) EFFECTS OF FOOD-DEPRIVATION ON THE PERCENTAGE OF THE DAILY FREQUENCY OF ALLO-GROOMING PERFORMED BY THE RESIDENT OF EACH PAIR IN PART ONE:

| Source of variance | | SS | DF | MS | F | p |
|---|---|---|---|---|---|---|
| Deprivation / no deprivation (A) | : | 394.00 | 1 | 394.00 | 0.506 | ns |
| Error AS | : | 3111.28 | 4 | 777.82 | | |
| Day of treatment (B) | : | 2092.84 | 4 | 523.21 | 1.312 | ns |
| Interaction A*B | : | 8562.18 | 4 | 2140.55 | 5.368 | p<0.01 |
| Error B*AS | : | 6380.53 | 16 | 398.78 | | |
| Total | : | 20540.83 | 29 | | | |

(b) EFFECTS OF FOOD-DEPRIVATION ON THE PERCENTAGE OF THE DAILY FREQUENCY OF ALLO-GROOMING PERFORMED BY THE RESIDENT OF EACH PAIR IN PART TWO:

| Source of variance | | SS | DF | MS | F | p |
|---|---|---|---|---|---|---|
| Deprivation / no deprivation (A) | : | 1158.42 | 1 | 1158.42 | 1.140 | ns |
| Error AS | : | 8127.07 | 8 | 1015.88 | | |
| Day of treatment (B) | : | 277.58 | 3 | 92.53 | 0.371 | ns |
| Interaction A*B | : | 383.57 | 3 | 127.86 | 0.513 | ns |
| Error B*AS | : | 5984.34 | 24 | 249.35 | | |
| Total | : | 15930.99 | 39 | | | |

FIG.4.4.5(a): EXPERIMENT THREE (PART ONE): MEAN PERCENTAGE OF TOTAL DAILY ALLO-GROOMING PERFORMED BY 'RESIDENTS' IN EXPERIMENTAL AND CONTROL CONDITIONS:

FIG.4.4.5(b): EXPERIMENT THREE (PART TWO): MEAN PERCENTAGE OF TOTAL DAILY ALLO-GROOMING PERFORMED BY 'RESIDENTS' IN EXPERIMENTAL AND CONTROL CONDITIONS:

their intruders more frequently than intruders groomed residents, although this was not statistically significant in the majority of cases. There appear to be no fundamental differences in these resident/intruder allo-grooming relationships thatare attributable to any effects of the food-deprivation variable.

4.4.3.2.3: The effects of the "resident"/"intruder" variable on social olfaction:

Analyses similar to those for pinning and allo-grooming, above, were also carried out on the numbers of individually-distinguishable sniffs by pair-members. Table 4.4.8 shows the overall totals of sniffs by each individual of each pair, and the results of binomial tests on these data, as before. In all pairs in part one of the experiment, and in 9 out of 10 in part two, the resident sniffed the intruder more frequently than vice versa. For 4 of the 6 pairs in part one, this reached statistical significance (two pairs from each condition), whereas this was the case for only 3 pairs in part two (two control pairs, and one experimental). Thus, although the residents appear to have olfactorily-investigated their intruders more frequently than they themselves were investigated, this bore no relation to which experimental condition the pairs were in.

ANOVA's on the percentages of the daily pair-totals of sniffs which were performed by the resident in each pair (table 4.4.9) showed no significant results for

FIG.4.4.6(a): EXPERIMENT THREE (PART ONE): MEAN PERCENTAGE OF DAILY TOTAL OF SOCIAL SNIFFING PERFORMED BY 'RESIDENTS' IN EXPERIMENTAL AND CONTROL CONDITIONS:

FIG.4.4.6(b): EXPERIMENT THREE (PART TWO): MEAN PERCENTAGE OF DAILY TOTAL OF SOCIAL SNIFFING PERFORMED BY 'RESIDENTS' IN EXPERIMENTAL AND CONTROL CONDITIONS:

TABLE 4.4.8: RELATIVE FREQUENCY OF SOCIAL OLFACTION BY "RESIDENTS" AND "INTRUDERS":

("z-score" refers to the result of the binomial test, using the normal approximation to the binomial for N>25; "p" refers to the probability of obtaining that score, under the null hypothesis that both players groom with equal frequency; all tests are two-tailed)

(A) PART ONE:

Experimental subjects:

| | Total no. of sniffs: | Number of sniffs by resident: | Number of sniffs by intruder: | z-score: | p: |
|---|---|---|---|---|---|
| PAIR 1: | 70 | 42 | 28 | -1.554 | 0.121 |
| PAIR 2: | 88 | 59 | 29 | -3.091 | 0.002 |
| PAIR 3: | 61 | 49 | 12 | -4.609 | <0.00001 |

Control subjects:

| | Total no. of sniffs: | Number of sniffs by resident: | Number of sniffs by intruder: | z-score: | p: |
|---|---|---|---|---|---|
| PAIR 4: | 58 | 41 | 17 | -3.020 | 0.003 |
| PAIR 5: | 40 | 27 | 13 | -2.055 | 0.040 |
| PAIR 6: | 59 | 30 | 29 | 0.000 | 0.500 |

(B) PART TWO:

Experimental subjects:

| | Total no. of sniffs: | Number of sniffs by resident: | Number of sniffs by intruder: | z-score: | p: |
|---|---|---|---|---|---|
| PAIR 1: | 39 | 25 | 14 | -1.601 | 0.110 |
| PAIR 2: | 63 | 42 | 21 | -2.520 | 0.012 |
| PAIR 3: | 33 | 26 | 7 | -3.133 | 0.002 |
| PAIR 4: | 65 | 37 | 28 | 0.992 | 0.322 |
| PAIR 5: | 35 | 21 | 14 | -1.014 | 0.312 |

Control subjects:

| | Total no. of sniffs: | Number of sniffs by resident: | Number of sniffs by intruder: | z-score: | p: |
|---|---|---|---|---|---|
| PAIR 6: | 45 | 35 | 10 | -3.578 | 0.0005 |
| PAIR 7: | 39 | 22 | 17 | -0.641 | 0.522 |
| PAIR 8: | 52 | 21 | 31 | -1.248 | 0.211 |
| PAIR 9: | 58 | 30 | 28 | -0.131 | 0.897 |
| PAIR 10: | 57 | 33 | 24 | -1.060 | 0.289 |

TABLE 4.4.9: RESULTS OF ANOVAS ON EFFECTS OF FOOD-DEPRIVATION ON SOCIAL OLFACTION BY "RESIDENTS" AND "INTRUDERS":

(a) EFFECTS OF FOOD-DEPRIVATION ON THE PERCENTAGE OF THE DAILY FREQUENCY OF SOCIAL OLFACTION PERFORMED BY THE RESIDENT OF EACH PAIR IN PART ONE:

| Source of variance | | SS | DF | MS | F | p |
|---|---|---|---|---|---|---|
| Deprivation / no deprivation (A) | : | 597.19 | 1 | 597.19 | 1.303 | ns |
| Error AS | : | 1833.08 | 4 | 458.27 | | |
| Day of treatment (B) | : | 2316.46 | 4 | 579.12 | 2.810 | ns |
| Interaction A*B | : | 1757.37 | 4 | 439.34 | 2.132 | ns |
| Error B*AS | : | 3297.41 | 16 | 206.09 | | |
| Total: | : | 9801.52 | 29 | | | |

(b) EFFECTS OF FOOD-DEPRIVATION ON THE PERCENTAGE OF THE DAILY FREQUENCY OF SOCIAL OLFACTION PERFORMED BY THE RESIDENT OF EACH PAIR IN PART TWO:

| Source of variance | | SS | DF | MS | F | p |
|---|---|---|---|---|---|---|
| Deprivation / no deprivation (A) | : | 413.71 | 1 | 413.71 | 0.749 | ns |
| Error AS | : | 4419.36 | 8 | 552.42 | | |
| Day of treatment (B) | : | 314.07 | 3 | 104.69 | 0.719 | ns |
| Interaction A*B | : | 374.57 | 3 | 124.86 | 0.857 | ns |
| Error B*AS | : | 3495.87 | 24 | 145.66 | | |
| Total: | : | 9017.58 | 39 | | | |

either part of the experiment, thus further suggesting that the food-deprivation variable had no effect on frequencies of social olfaction. Figs. 4.4.6 (a,b), for parts one and two of the experiment respectively, show clearly that there were no changes on this measure, either between groups or over days of the experiment.

4.4.3.3: Effects of food-deprivation on subjects' weights:

Some data on the weights of the subjects were obtained, although unfortunately not on all subjects on all days. The weights of all individuals in part one of the experiment were taken on the second day of food-deprivation, and on both recovery days. Four pairs of subjects in part two (two experimental pairs, and two control) were weighed on all four days of their procedure. These measurements were made immediately after the end of each observation-session.

Fig. 4.4.7(a) shows the mean weights of experimental and control subjects in part one of the experiment, on each of the three days on which weights were taken. On the second day of food-deprivation, there was a difference of 28.8 grammes between the mean weights of the two groups; after 20 hours of ad lib feeding, this difference decreased somewhat, but still amounted to 20.2 grammes. On R2, the last day on which observations were made, experimental subjects were still 17.3 grammes lighter than their control counterparts - if the controls' weights are

FIG.4.4.7(a): EXPERIMENT THREE (PART ONE): EFFECTS OF FOOD-DEPRIVATION ON SUBJECTS' WEIGHTS:

FIG.4.4.7(b): EXPERIMENT THREE (PART TWO): EFFECTS OF FOOD-DEPRIVATION ON SUBJECTS' WEIGHTS:

taken as a rough approximation of what the experimental subjects' weights should have been at that age, then the latter were still at only approximately 85% of their natural body-weight at the end of the experiment.

Fig. 4.4.7(b) depicts the mean body-weights of the four pairs of subjects in part two of the experiment for which there are weight-data. The mean weights of the exerimental and control subjects were within a gramme of each other on day one of the experiment, but after 20 hours' food-deprivation the mean weight of the experimental group was 15 grammes less than that of the controls. After 20 hours' ad-lib feeding, experimental subjects were 6.7 gms lighter than the controls (ie, at approximately 95% of what their body weight would have been on this day had they not been deprived). This difference persisted to the end of the experiment.

A comparison was made of the weights of the residents and intruders of each pair. In seven of the ten pairs of animals for which there are data, the resident was heavier than the intruder, on all days of the experiment. Independent-measure "t"-tests, comparing weights of experimentals to controls, revealed that these diferences were not statistically significant, however. (In part one of the experiment, the animals' weights were compared on the final day of the experiment: $t= 0.8173$, with 10 df, $p>0.05$; in part two of the experiment, the subjects' weights were compared on the first and last days of the experiment: t's =2.4278 and 1.1264 respectively,

both with 6 df and $p>0.05$).

### 4.4.4: Discussion:

To summarise, the main finding of this experiment is that food-deprivation led to a marked decrease in levels of play, especially under conditions of extreme deprivation as in part one of the experiment. The frequency of allo-grooming was to some extent affected by deprivation, but not consistently so; grooming was reduced in subjects in part two, but not in part one. There were no clear effects of food-deprivation on levels of social olfaction, in either part of the experiment. These results are consistent with an interpretation in terms of play being motivationally distinct from other social behaviours (and hence differentially affected by external factors such as food-deprivation); however, an equally-valid view is that play behaviour is most affected by food-shortage simply because it is more vigorous than grooming or sniffing.

Few differences were found in the relative frequencies with which residents and intruders interacted socially. Although residents tended to groom and sniff their partners more frequently than they themselves were sniffed and groomed, these differences were not statistically significant. In the case of play behaviour, less than half the pairs of subjects (seven out of sixteen) showed significant inequalities in the frequencies with which they pinned each other; and in only

four of these pairs did the resident pin most. In addition, there were no systematic differences in the effects of food-deprivation on the behaviour of residents and intruders: deprivation did not lead to residents peforming a greater percentage of the observed numbers of pins, grooms or sniffs.

These results confirm the results of the studies described in earlier chapters, that play is not related to defence of resources and/or territory; if it were, then one might expect levels of pinning by the resident to increase under conditions of food-shortage, or at least for the proportion of pinnings peformed by the resident to increase. The few differences between pair-members that were observed, are probably due to the fact that intruders were less familiar with the test environment than were residents (since the former spent only an hour per day in it) and so spent relatively more of their time investigating the inanimate environment. Indirectly, the fact that intruders generally did initiate a fair proportion of the observed behaviour of a subject-pair, shows the strength of the drive to interact following isolation.

The need for social interaction is shown clearly by examining the effects of deprivation on play. As Baldwin and Baldwin (1974) have noted in the case of squirrel monkeys, what is most striking about the effects of food-deprivation on levels of play is not that deprivation suppresses play, but that even under conditions of extreme

food shortage, some play is still seen. The same conclusion appears to apply to rats, as shown by the present experiment: the mean weight of food-deprived subjects in part one of this study, on the second day of food-deprivation, was less than 75% of that of their controls - and yet play still occurred. Even more remarkably, after less than 24 hours of ad-lib feeding, the experimental subjects in both parts of the experiment were showing levels of play comparable to (if not higher than) those of their controls- and yet, even by the end of the experiment, neither set of experimental subjects had made good their weight loss.

While the persistence of the drive to play is impressive, the major significance of this study is that these results represent further evidence in support of previous reports that play is suppressed in stressful conditions, including hunger. This experiment reinforces a view of play as being intimately tied to the social and physical environments within which it occurs; when play becomes too energetically "costly", it is dropped from the animals' behavioural repertoire. On the other hand, once ad-lib feeding was re-established, levels of play returned to normal, despite the fact that the animals were still physiogically stressed (as shown by their weights).

This latter finding might be related to the 23 hours' social isolation per day that these animals were enduring, in addition to their food-deprivation. This experiment does of course confound two different variables:

social deprivation and food deprivation. Experiment one showed how social isolation increased play-levels, and it may be that in the present experiment the drive to play produced by the social isolation simply outweighed the depressive effects on play of food deprivation. If opportunities for social play are uncertain, but food-supplies appear stable (even if conditions of food-shortage have occurred in the past), then it may pay a young rat to adopt the strategy of playing whenever he gets the chance, despite the fact that he is still physiologically deprived.

The severity of the food-deprivation experienced by the subjects in this experiment probably explains why a "rebound" effect similar to that reported by Baldwin and Baldwin (1974) was not observed. Their subjects were under very mild conditions of food-shortage compared to those imposed here, so that the balance between the conflicting requirements for social play and food may have been biased more towards the former than the latter than was the case in the present study. Thus there is no contradiction between the two experiments; it is simply that their "rebound" effect has been swamped in this experiment by the use of much more severe food deprivation. There is obviously scope here for more sensitive examination of the relationship between levels of physiological stress and the frequency of play, than in the present experiment.

This experiment suffers from numerous methodological

weaknesses: as just mentioned, the independent variable of interest (food-availability) was manipulated in an extremely gross manner; there are difficulties of interpretation imposed by the consequences of simultaneously manipulating two independent variables (food and social deprivation); and relatively small numbers of subjects were employed, especially in part one of the experiment.

All of these factors mean that considerable caution must be exercised in interpreting the significace of these results. However, this experiment does at least suggest a number of points. The lack of resident-intruder effects, even under conditions of resource-shortage, is evidence against one possible function of play - that play is related to the establishment of dominance and/or territoriality - and once again emphasises the reciprocity of the majority of playful interactions. The differences between the effects of deprivation on play and on other social behaviours to some extent represent further evidence that play is a valid, distinguishable, category of behaviour in its own right. But the main function of this experiment is that, as with the rest of the work in this thesis,it emphasises the relationship between social play and its environment (both internal and external). If play does have significant costs, both in energetic and evolutionary terms, then these would be minimised by decreasing levels of play once it became too "expensive", as in the present experiment. At the same

time, play-deprivation produces a very powerful drive to play, and the surprisingly high levels of play seen during and after food-deprivation in the present study perhaps reflect the net result of the interaction between these two opposing forces.

# CHAPTER FIVE: DISCUSSION:

# 5: DISCUSSION:

## 5.1: Summary of main findings:

This section will briefly restate the main results of the previous three chapters.

### 5.1.1: The main findings of chapter two:

The observational studies described in chapter two looked at social play in relation to other behaviours, on a very broad level of analysis. These studies showed that social behaviours of any kind accounted for a comparatively small proportion of the total activity budget of young rats aged between 21-60 days. Social play represented only 2.5% of all time-samples made during this period. Play was the major form of social interaction, however, accounting for 30% of all social behaviour observed between 21-60 days.

Most social behaviour was amicable; competitive and agonistic behaviours accounted for less than 20% of all social behaviour, and even then consisted mainly of instances of cmpetition for nipple access. "Serious" fighting was very rare.

Over the course of the period studied, age-related trends were discerned in social behaviours. Play and exploration (the latter operationally defined as olfactory investigation of the inanimate environment) showed similar ontogenetic patterns, in the form of an inverted "U" -

shaped distribution with a peak at 31-35 days. Agonistic activities (as a group) declined with age, mainly due to the decline with weaning in the frequency with which pups competed for nipple access. Sexual behaviours were observed infrequently at all ages, but peaked at some time after 45 days of age.

Age-trends were also identified within certain behaviour-categories. With increasing age, pups came to show a preference for play with partners of their own sex, rather than the opposite sex. Towards the end of the period of observations, females ceased to play, either with each other or with males. Another age-related trend associated with play was the marked rise in "on top" behaviour at weaning. Males pinned females more than females pinned males, and this tendency increased with age. The frequency of within-sex allo-grooming also rose with age.

An examination of individual differences in play and other social behaviours revealed that all pups of a given litter played to similar extents, pinned and were themselves pinned. There was no increase in "dominance" by particular individuals with age. Neither were there any relationships between an individual's level of playfulness and his level of other social behaviours, either amicable or agonistic.

Finally, the mother was found to be a potentially significant source of social interaction, including play.

5.1.2: The main findings of chapter three:

Chapter three investigated two main points. Firstly the temporal features of the play itself were examined; and secondly the relationship of play to other behaviours was studied in close detail.

The temporal analysis revealed that if play were defined as commnencing with a pounce and ending with the cessation of contact between the players, then most play bouts were extremely short - two-thirds of them were less than 20 seconds long. Probability of termination is apparently randomly-determined. There were no age- or sex-differences in the duration of play, except that during the first two age-periods, play between males lasted somewhat longer than play involving females.

An investigation was made of the percentage of the bout spent in the "on top" position by each of the interactants. Two-thirds of bouts involved the initiator remaining on top of the recipient throughout the interaction. There were no age- or sex-differences in this pattern, that could not be attributed to sampling error.

The observations on the number of role reversals occurring within a bout showed a similar picture. Two-thirds of play bouts involved no role reversals, and it was very rare for more than one reversal to occur. There were few age- or sex-differences on this measure, except that more role-reversals occurred in male-male and female-male play than in female-female play or male-female play.

Finally, there was a low correlation between the duration of a play bout, and either the percentage of on-top behaviour shown, or the number of role reversals occurring within it.

The data on the context within which play occurs are flawed by the lack of data on the context of non-play behaviours against which to set them in perspective. However, these data do show that play occurs within a milieu of olfactory exploration, other play, and activity. Play was not associated with sedentary activities - eating, drinking, grooming and sleeping. Nor was play preceded or followed by agonistic and competitive behaviours; only 2% of all play-bouts were followed by behaviours which could even remotely be termed agonistic. Initiators and recipients of play showed roughly similar patterns of antecedents and consequences.

An examination of the way in which play-bouts actually appeared to end, suggested that the most common ending was for one animal simply to move away from the other. 43% of all bouts ended in this manner, 23% being terminated by the initiator and 20% by the recipient of the play. This behaviour - often truncated to little more than a turning-away of the head and upper body - amounted to a play signal denoting that the animal performing it was terminating the encounter. The seond most common bout-ending was for one of the animals to begin to investigate the environment, olfactorily. 26% of all play ended in this way (17% by the initiator and 8% by the

recipient). The third major ending of play-bouts was by one of the interactants (mainly the initiator) being distracted by a third animal. This latter category accounted for 18% of all bout endings. Overall, 60% of bouts were ended by the animal who had initiated them. Except for an age-related increase in the frequency with which play was ended by the initiator sniffing the recipient, there were no consistent age-differences on this measure; nor were there any sex-differences in how play ended.

An analysis of where play took place within the environment, revealed that players showed a strong thigmotaxis during interactions; 71% of all play occurred within 10 cm of a cage-wall. Play occurred where the animals were most active, and not particularly frequently in places with potentially-high resource value such as near the food-hopper or water-spouts. 46% of play-bouts involved the initiator approaching the recipient; 30% of play occurred between animals who were already close to each other; and 18% of play involved the recipient being pounced upon as he approached the initiator. With increasing age, there was an increase in the relative frequency of the initiator approaching the recipient, so that play appeared increasingly to be less of a "spontaneously"-occurring event. Other than this, there were no age or sex differences in who approached whom.

Finally, an analysis was performed of whether or not players were in close proximity to each other before and

after play. 56% of play involved players being close to each other beforehand, and 44% involved no mutual proximity. These differences attained statistical significance, but only because of the large number of observations involved. Similarly, 58% of play bouts were followed by the interactants remaining near to each other, and 42% of bouts were not. Overall, 38% of play-bouts involved the players being in close proximity to each other both before and after the play.

5.1.3: The main findings of chapter four:

The three experiments described in chapter four provided the following information.

Experiment one showed that short-term deprivation of whole-body physical contact leads to a "rebound" effect when opportunities for such contact are reinstated. This effect consists of a dramatic but relatively short-lived increase in the quantity of play observed. Partial physical contact during the period of deprivation, through a wire mesh, produced effects on subsequent levels of play which were largely indistinguishable from those produced by total physical isolation. There did not appear to be a cumulative effect of deprivation over days; one hour of social contact per day appeared to be sufficent to "make good" whatever deficit was induced by deprivation.

Mere disturbance of control animals in experiment one appeared to increase their levels of play (though not significantly so). This phenomenon was investigated

further in experiment two, in which levels of play were measured following the introduction of a "novel" object into the cage. Within the confines of the experimental procedure employed, however, this manipulation actually appeared to suppress levels of play, rather than enhance them. Food-deprivation (in experiment three) also suppressed play, while leaving the frequencies of other social interactions relatively unchanged. Some play was still performed, however, even under conditions of extreme food-deprivation, which hints at the strength of the drive to play in play-deprived animals such as these.

Experiments two and three addressed the question of whether "dominance" (defined as a marked asymmetry in levels of pinning as opposed to being pinned) develops between individuals during the course of play. The levels of pinning performed by each member of a pair of animals were measured. In experiment two, pair members were continuously housed together, whereas in experiment three, an "intruder" was placed into a "resident's" cage.

Experiment two revealed no evidence for the development of "dominance" during play; and experiment three confirmed that this was also the case when the value of the resources at stake was increased by means of food-deprivation. Together these two studies confirmed the conclusions drawn from the observational studies, that there is no evidence for the development of stable "dominance" relations between members of a pair over successive encounters. Experiment three suggests that play

is not in any way related to territoriality or defence of resources in this species.

## 5.2: Implications of these results:

This section will deal with some of the implications of the results just summarised.

### 5.2.1: The extent to which play has significant "costs":

Fagen (1981) in particular, has emphasised the "costs" of play to players, in terms of the energy expenditure incurred in vigorous physical activity, and the increased risks of death and injury produced by this behaviour. Martin (1982, 1985) has estimated that the energy costs of play (defined as the net daily energy expenditure in excess of resting metabolism that is due to play) may be relatively trivial under conditions of food abundance. The studies summarised in the previous section suggest that the survivorship costs of play may also have been greatly overestimated, since many features of play actually appear to minimise its potential costs.

Firstly, experiment three shows that food-deprivation markedly suppresses play, but not other behaviours; this suggests that rats will only play in conditions which allow them to compensate readily for any energy-deficits incurred by playing, and will not play when the energy costs of play become relatively too "expensive". In short, these results imply, as Martin (1982) suggests, that play

will only occur when it can be "afforded", energetically, by the players. This result is in line with those reported for other species under conditions of food-deprivation, whether experimentally-induced (eg. Muller-Schwarze et al. 1982) or naturally-occurring (eg. Baldwin and Baldwin 1974).

Secondly, some of the results of the observational studies, and the results of experiment two, suggest that the potential costs of play in terms of the increased risk of exposure to danger may in practice be minimised. Although, subjectively, play often appears to be performed with a spirit of reckless abandon, the behaviour seems to contain within itself certain safeguards which perhaps reduce the potential costs of playing. Rats show a strong thigmotaxis during play; environmental changes, as in experiment two, may initially suppress play; and informal observations suggest that play is readily disrupted by loud or sudden noises, or sudden movements on the part of the observer. Taken together, these phenomena presumably reduce the conspicuity of players to some extent and mean that play will cease if a potential source of danger (such as a predator) appears.

To sum up, these studies reinforce Martin's (1984) claims that the costs of play may have been over-estimated, although of course the actual costs of play for animals in the wild need to be assessed more accurately before this statement can be fully accepted. If these conclusions do apply equally validly to animals in

their natural habitats, then it may be that "play is an activity which has only marginal costs and marginal benefits" (Martin 1984); but alternative possibilities do remain open - for example that play has low costs but major benefits, or that play is an activity which can provide major benefits but which can be done without if necessary (Baldwin and Baldwin 1974).

It is erroneous to claim that "play has low costs, therefore play is trivial", since (a) how great the costs of playing actually are, and (b) how much significance play has evolutionarily, are logically quite independent issues.

5.2.2: The distinctiveness of the motivation to play:

This topic has been returned to on a number of occasions in this thesis, so little space will be devoted to it here. Experiments one and three show that levels of play may readily be affected by manipulations which have effects fairly specific to play itself - for example, in that social deprivation leads to a subsequent increase in play, which cannot apparently be ameliorated by alternative non-playful forms of social contact (experiment one), and that food deprivation reduces levels of play to a much greater extent than it affects other social behaviours (experiment three). The observational studies in chapter two showed that play had a rather distinctive ontogenetic patterning within the age-period covered. The studies of chapter three show that the

context within which play occurs is one of exploration and activity.

Taken together, these data suggest that social play is a behaviour with a rather different motivational basis to that underlying both agonistic activities and other amicable behaviours; by highlighting the distinctiveness of play's motivation, these results emphasise the distinction between play and the agonistic behaviours it is commonly supposed to resemble.

5.2.3: Play, reciprocity and "dominance":

One of the issues which these studies set out to investigate, was to what extent there was "reciprocity" in play and how this varied with age and sex of participants. Whether or not "reciprocity" is a prominent feature of play in the rat, depends on one's definition of reciprocity. In terms of the percentage of a particular bout for which each interactant was in the "on-top" position, or the number of role-reversals occurring within a given bout, then rat play shows a marked lack of reciprocity. Most bouts were heavily "dominated" by the animal who initiated the bout.

In terms of how many bouts were spent in the "on-top" position by any particular individual within a litter, then play appears to be remarkably reciprocal, with most littermates pinning and being pinned with equal frequency. This latter kind of reciprocity was also a feature of the play of pairs of animals in experiments two and three -

even if, as in the latter study, one member of each pair was an "intruder" into a cage which was unfamiliar to him.

There were few age- or sex-related variations in reciprocity, whichever of these definitions were used. The data do show some evidence of a trend for play between males and females to be somewhat less reciprocal than play between males or between females - a phenomenon possibly related to the tendency for females to drop play from their behavioural repertoires sooner than males. This trend, however, was present at all ages; there was certainly no marked tendency for play to become less reciprocal (in either of the above senses) with increasing age.

As mentioned in chapters two and three, these findings contradict earlier reports of the development of "dominance" in rat play (Meaney and Stewart 1981; Panksepp and Beatty 1980; Panksepp 1981). The weakness of the basis for these researchers' claims has already been discussed (see chapter two). The results of the present studies support the conclusions of Chivers (1982), who suggests that dominance relations are not a significant feature of adult rat behaviour. Chivers (1982) found no evidence for organisation of male rats into functional dominance hierarchies. Agonistic behaviour was found to be more important in the exclusion of intruders from a group, than in determining within-group relationships.

In short, not only is there no sound evidence that social play leads to the development of dominance

relationships between players (or even reflects dominance relationships established by other means), but also there is no evidence that such relationships are important in adult rat social organisation.

5.2.4: The benefits provided by play:

The studies reported in this thesis are primarily correlational in nature, and so they can only be used to examine the function of play in an indirect way, insofar as they might be more compatible with certain interpretations of play rather than others. A few of the hypothesised functions of play will be evaluated in this section, in the light of the findings of this thesis.

5.2.4.1: Play as practice for specific adult behaviours:

It has been suggested that social play serves as direct practice for two sets of adult behaviours which are important for individual survival but which could never be practised in their "serious" contexts. Playful wrestling is claimed to serve as practice for adult intra-specific aggression, and playful chasing is held to represent practice of emergency locomotor behaviour such as flight from predators (Aldis 1975; Symons 1978; Smith 1982).

5.2.4.1.1: Playful wrestling as fighting practice:

The dissimilarities between play and aggression - during the same period in ontogeny - have already been

* An alternative possibility, in view of Chivers (1982) findings that agonistic behaviour in adults was more important in the exclusion of intruders from a group rather than in within-group relations, is that the former type of agonistic behaviour may differ from within-litter aggression in ways that make play more suitable practice for territorial defence than for intra-group fighting.

discussed. The lack of any correlation between each individual's levels of play and agonistic behaviours suggests, albeit not very conclusively, that there is little relationship between the two behaviours. Perhaps stronger evidence against the hypothesis that play serves as practice for adult aggression is the fact that the two behaviours do occur at the same time in ontogeny. As far as a human observer can tell, young rats appear to be perfectly capable of "serious" agonistic behaviours at the same time as they are stil showing high levels of play. This does not however altogether rule out the possibility that young rats might nevertheless refine their agonistic behaviours in the light of playful experience.*

Another problem for the hypothesis that play serves as direct practice of adult aggressive behaviours, is the fact that if the principal behaviour of rough and tumble wrestling can be said to resemble any adult behaviour, then it resembles not the behaviour-patterns employed in winning a fight - boxing and lateral side-attack - but the "consummatory" behaviour of rat aggression, the "paws-on" behaviour which is supposed to represent dominance and occurs once the opponent has been defeated. At first sight, it seems rather implausible that play should represent practice of this behaviour, rather than of the former patterns whose skilled use might appear more crucial for winning fights. There is, however, one way in which this strange state of affairs could be satisfactorily explained in terms of a pratice theory.

During the course of the observational studies, the impression was gained that one thing young rats might perhaps learn through play, was how to use their body-weight effectively against an adversary. Pinning appeared to change subtly with age. In the case of pins at around 21-25 days or so, an animal who was pinning appeared to do little more than simply lay over his opponent, and the animal underneath merely struggled in a generalised manner. By 40 days or so, the animal underneath appeared to be using techniques of leverage in order to right himself, and the animal on top often seemed to be responding to the movements of the animal underneath so as to counter them effectively by means of subtle movements of his own body, maximising the use of his own weight as a check on his partner's struggles.

Unfortunately, there are no hard data to support these impressions, but the changes are in principle quantifiable and so open to experimental verification. An alternative interpretation that has to be considered, is the possibility that these changes merely reflect ontogenetic changes in the players' morphology. With increasing age, young rats become proportionately longer and thinner, which might mean that the behavioural changes observed were not so much the product of learning within play, so much as due to the fact that the pinning strategies employed later in life are simply not effective for younger animals. The problems of distinguishing learning and maturational phenomena in play are of course

common to all hypotheses which postulate "practice" benefits from play. If these impressions - and the interpretation of them - are correct, however, then this might represent a benefit that was obtained largely from playful experience, since there appears to be no other context within which to learn such skills, during this period of the rat's ontogeny.

As Symons (1978) has pointed out, there is no logical necessity for play to resemble the behaviour for which it serves as practice. In the few (unquantified) observations of adult aggression observed by the present author, what seems to be an important factor is the effective use of body-weight against the opponent - both in the case of boxing (where the objective appears to be to push against the opponent as much as possible, to unbalance him, yet without becoming unbalanced oneself), and particularly in the lateral attack - which effectively represents a throwing of as much of the body as possible against theopponent in an intimidatory manner. Play may represent a practice of the principle behind adult aggression (ie, effective weight-utilisation) without serving as practice of the actual behaviour patterns of adult aggression themselves.

5.2.4.1.2: Play-chasing as practice for locomotory skills:

The major focus of this thesis was on the wrestling components of play, and chasing was studied only to the extent that it often formed part of rough and tumble

interactions. Humphreys (1982), who investigated play-chasing more thoroughly, suggested that it might serve as practice of anti-predator evasive behaviours, in a similar fashion to the "jinking" behaviour of the African ground squirrel (Ewer 1966).

Play-chasing certainly has the potential for providing the interactants with information about how best to avoid a pursuer, and how best to "head off" a pursued animal. This latter information might prove useful in the context of sexual behaviour, where skilled anticipation of an oestrous female's darting and running behaviour might mean the difference between obtaining an opportunity for an intromission and just being one of the group of males chasing the female. Whether or not such information is actually acquired through play-chasing (either wholly or in part) is of course open to question.

5.2.4.2: Play as exercise:

As mentioned in chapter one, Fagen (1974, 1981) has been the chief exponent of this hypothesis. He has made a number of predictions about the form that play should take if it is to supply certain types of phsyical training. One problem with testing these predictions is that different types of exercise may provide different types of training. Thus if, say, the observed duration of play does not approximate to that which would be predicted by the hypothesis that playful exericise provides endurance training, then it will probably fit an alternative

exercise hypothesis, for example matching the required parameters for rapid exercise. In this way, the hypothesis that play serves as physical training can be rendered almost impervious to disproof, rather than being as empirically testable as Fagen (1981) suggests.

The present studies revealed that, although play-bouts were typically brief events (mostly under 20 seconds in length), termination of play was essentially random (see chapter three). This latter finding corroborates the results of McDonald (1977) for the duration of play bouts in the Columbian ground squirrel; and also confirms the results of Humphreys (1982), who measured the duration of play bouts in laboratory hooded rats but used different criteria to determine when play had ended (a ten-second break, rather than the three seconds used here). These results do not offer much support for an exercise hypothesis, which would predict that for optimal benefits to be obtained, a given type of exercise should be performed for a certain period of time (Fagen 1981).

However, play might still provide useful exercise, regardless of whether or not this is its primary function. In the present studies, rough and tumble, and the chasing that accompanied it, were virtually the only vigorous activities observed before puberty. In fact, apart from play, the only vigorous activities seen in these animals were chasing the mother in order to attempt to suckle, food-stealing, and the chasing and being chased which

accompanied sexual behaviour from around 45 days onwards. Only the last form of behaviour provided any prolonged exertion. Whether or not this is true for young rats in the wild is of course an entirely different matter.

The play-chasing component of social play may thus provide a useful source of exercise for chasing sexually-receptive females, during oestrus. Small differences in running speed may also make all the difference between being caught by a pursuing predator and escaping unharmed. (Note that these postulated benefits are conceptually distinct from those described for chasing play in section 5.2.4.1.2; here, what is suggested as being important is the non-specific enhancement of physical performance, whereas in the earlier section it was the behaviour-patterns themselves which were suggested as being important. In practice, distinguishing between these two kinds of interpretation might be virtually impossible).

Rough and tumble play provides a more static form of exercise (Humphreys, 1982). During pinning, both animals obtain static exercise, but interestingly, the most benefit from this kind of behaviour may accrue not to the animal on top but to the animal underneath, who is effectively weight-lifting the animal pinning him down. Humphreys (1982) has suggested that this type of physical training might be useful in developing muscles used in situations such as digging, dragging large food items and retrieving young.

5.2.4.3: Social benefits of play:

There are a number of social benefits which could be obtained from play. Because of the artificiality of the social groupings of subjects in the studies described in this thesis, firm conclusions about normal socialisation processes in the rat cannot be drawn from these data. However, Symons (1974, 1978) has produced cogent arguments against the hypothesis that primates either learn or refine agonistic communicative skills in play, and Meier and Devanney (1974) have similarly refuted suggestions that play serves as practice of social communicative skills, since young primates are already functioning members of their social groups. There seems no reason why these arguments should not apply with equal force to young rats. The impression obtained from these studies is that young rats are already socially-competent individuals; in any case, there would appear to be few opportunities for learning social skills within the context of social play.

A more plausible hypothesis is that play might provide opportunities for rats to learn each other's physical characteristics. Playful wrestling would appear to be an ideal means of obtaining detailed information about one's playmates. This information consists of the visual characteristics of the play-partner, from all angles and orientations; and detailed olfactory information from the anogenital and

ventral olfactory investigation that often accompanies play. The studies described in chapters two and three of this thesis certainly suggest that play occurs in a milieu of olfactory investigation of the animate and inanimate environments (the latter almost certainly also containing many socially-significant odour cues). This information could be used as a basis for discriminating kin from non-kin, and familiar from unfamiliar conspecifics (Hepper 1983), information which might be useful in determining adult mating preferences (ie, by avoiding excessive inbreeding) and in territorial defence (Chivers 1982).

5.2.4.4.: Cognitive benefits of play:

As mentioned in chapter one, the only benefits of play which have been experimentally demonstrated are cognitive ones: increased behavioural flexibility and enhanced spatial learning abilities on the part of animals which have had social contact including play, compared to subjects experiencing social contact without play (eg, Einon, Morgan and Kibbler 1978).

While the present studies (in particular, experiment one) corroborate Einon et al's demonstrations that young rats have a powerful drive for specifically-playful contact (Humphreys and Einon 1981), it is difficult to see why playful wrestling and chasing should provide cognitive benefits. In chapter one, the possibility was mentioned that these benefits might be side-effects, play acting in

a therapeutic way for abnormally-reared animals. However, as Symons (1978) points out, we know very little about the processes by which animals actually obtain skilled activities; the same point applies to the development of cognitive benefits. Einon (personal communication) has suggested that the anticipatory skills needed and presumably developed through play (for example "heading off" partners which are being chased, and anticipating the other animal's incipient movements during wrestling) may enhance spatial abilities, etc. The present thesis can provide no insight on this point, except to confirm that players do appear to respond to very subtle behavioural cues provided by their partners.

5.2.4.5: Conclusions - the possibility of immediate benefits:

As Chalmers (1984) has pointed out, in our present state of knowledge, facts can be found to support any of the hypothesised functions of play; the only limitation is the proponent's skill in advocacy. Humphreys (1982) suggests that a number of functions of play might have been selected for, so that the observed form of play actually represents a compromise, the net result of a number of different, possibly-conflicting requirements. Related to this is the point made in chapter one of this thesis, that the "design features" approach to play fails to allow for the possibility that not all of the observed appearance of play might reflect design for a particular

function; that instead, much of the observed behaviour might be taken up with fulfilling a metacommunicative function.

The studies described in this thesis do not strongly support or contradict any of the hypotheses about play's function that have been described above. What they do reveal, however, is (a) that rat play displays a number of features which may serve to minimise the relative costs of playing (eg, strong thigmotaxis during play, and sensitivity to disturbance and food-deprivation) ; and (b) the possibility that rat play might have immediate, rather than deferred, benefits to the animal.

The latter point has been raised in connnection with social play in the domestic cat (Martin and Caro 1985), and there is some suggestion that it may also apply to the laboratory rat. One immediate benefit of play - physical exercise - has been mentioned. There is another potential immediate benefit, more specific to the nature of the play-wrestling itself: much of the play interaction is taken up with allo-grooming, performed mainly by the animal on-top. The peak of play occurs around or just after the time at which the pups are weaned (30-35 days), a time when mothers were observed to actively avoid their litters as much as possible because of the pups' persistent attempts to continue to suckle. Given that the mother performed the bulk of infant grooming up to the time of weaning (see chapter two), her avoidance of pups would lead to them experiencing less allo-grooming than before. A significant, immediate

benefit of rough and tumble play in the rat is that it provides a source of allo-grooming during the period when the mother is avoiding them.

## 5.3: Overall conclusions and suggestions for further research:

### 5.3.1: External validity of the present studies:

The methodological inadequacies of the studies described in this thesis have already been discussed, at the ends of each of the relevant chapters. Those criticisms are principally ones of internal reliability and validity (the extent to which these studies actually show what they purport to show), but a larger issue is the degree of external validity of the studies described in this thesis: to what extent conclusions drawn from observations on laboratory-bred domesticated rats can be extrapolated meaningfully to their wild counterparts. The intention of this thesis was to obtain information about play as a developmental phenomenon in semi-naturalistic conditions, but it is clear that both the animals and rearing conditions used might well bear little resemblance to those observed in the wild. Each of these points will be discussed in turn.

Despite claims that the laboratory rat is "degenerate" compared to wild rats, both physiologically (Richter 1959) and behaviourally (Barnett 1975) there is no evidence to support the notion that laboratory rats are

"degenerate" intellectually (Boice 1973). Behaviour patterns such as those of aggression appear not to have been lost in the laboratory rat, but merely either to have higher thresholds for elicitation, or typically to lack opportunities for their expression in a normal laboratory environment (Boice 1973, Silverman 1973, Price 1978).

The social behaviour of the laboratory rat (including play) may thus differ only quantitatively from that of its wild counterpart, rather than qualitatively. A more serious threat to the external validity of these studies lies in the nature of the rearing conditions employed. The cage used for the studies described in chapters two and three was large, but must still represent an extremely impoverished environment compared to natural conditions.

The social groupings were also unnatural. In the studies reported in chapter three, the animals were weaned at 21 days and confined without access to any other conspecifics. Subjects in the studies of chapter two were more normally raised in that the mother was present. Calhoun (1962) suggests that the single mother-litter unit may be comparable to the state of affairs in the wild, at least for the first 60 days of the pups' lives. This may be so, but presumably some social contact is obtained with other animals during this time, at least in the case of the mother. The single mother-litter paradigm was used primarily for the sake of simplicity, but it may well have introduced distortions into the group's behaviour, especially around weaning when the mother could not get

away from the pups.

5.3.2: Suggestions for further research:

Fron the point of view of investigating play, the laboratory rat was chosen because of its many advantages: what it lacks in "naturalism", it makes up for in convenience in terms of reduced emotionality, decreased neophobia and increased docility. However, it would be interesting to know how many of the features of play described in this thesis would relate to the behaviour of wild rats, in a more natural habitat. The possible relationship of play to novelty, for example, would be affected by the wild rat's profound neophobia (if it is not an artifact of environmental impoverishment). It would be interesting to know how the thigomtactic behaviour of young playing rats manifested itself in the wild, so that under natural conditions play occurred near burrow entrances, for example. The relationships of young rats to older members of their social group would be informative. The ideal would be to look at rat play (and indeed all early social behaviour) in the wild; however, a more feasible alternative might be at least to construct an artifical burrow system, given the profound methodological difficulties involved in studying rodent social behaviour in the wild.

As well as observing rats in more natural habitats, future studies should observe them for longer, using more sophisticated behavioural indices. The most insight into

play in recent times, has come from those observational studies which have been developmental in orientation and which have used multiple measures of "play" behaviour - for example, the studies of Bateson (Barrett and Bateson 1978, Bateson and Young 1979) and Chalmers (eg, Chalmers and Locke-Haydon 1984). Following Chalmers' lead, the studies described in chapter two of this thesis should be repeated with more detailed measures of play than whether or not it had occurred, and continued into adulthood. Preferably event-sampling rather than time-sampling should be used, since contextual and temporal data could then be obtained at the same time.

5.3.3: Conclusions:

In conclusion, the studies described in this thesis confirm some of the earlier findings on play in the rat (for example its apparently highly-typical ontogenetic profile), while throwing doubt on others (in particular the idea that "play leads to dominance").

These studies make an original contribution to our understanding of play in the following ways. The studies in chapters two and three examine play in relation to the other behaviours being performed by the developing young rat, whereas previous researchers on play in this species (and in most others) have tended to look at play in isolation from other behaviour. Chapter three provides new data on aspects of play which have hitherto received little attention: its immediate context, and its temporal

factors.

The experiments in chapter four further delineate the crucial factors in previous experiments on play deprivation (experiment one), and demonstrate the interrelationship between play and environmental conditions (experiments two and three). The existence of this latter relationship has tended to be overlooked in research on play, and yet is vitally important: if the experiments on immediate causation have any value, it is that they show that social play may be markedly affected by the environment which supports it, both in a quantitative and qualitative sense. This has serious implications for the validity of comparisons between different playing species, or even between different studies made on the same species. However, on a more optimistic note, these experiments also suggest that some of the features described for play in other species (for example the response to social and food deprivation) apply equally well to rat play, and this may prove to be a useful means of establishing generalities about play that can validly transcend species boundaries.

The studies described in this thesis have probably raised more questions than they have answered. The function of rat play remains as much of an enigma as before. This is hardly surprising: what is really interesting about play is that it encapsulates all of the problems of contemporary behavioural biology - definition, causation, function, and above all, development.

E. O. Wilson (1975) suggests that one would need to spend one thousand hours in observation in order to obtain a sound idea of the nature of individual relationships, behavioural ontogeny and socialisation in a species. He was talking about primates, but after observing the behaviour of the subjects of this thesis, the present author believes Wilson's statement is just as true for "simpler" species. Wilson cites Fraser Darling (1938): "How surely it has been borne upon me that the glimpses of minutes, hours, days or even weeks... are inadequate for an interpretation or solution of the deeper problems of evolution, natural selection and survival...!" One could add to this list - play.

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## APPENDIX 1: RELIABILITY, VALIDITY AND SENSITIVITY IN BEHAVIOURAL OBSERVATION:

### 1: Reliability, validity and sensitivity:

There are at least three separate problems in making measurements of behaviour: the issues of reliability, validity and sensitivity. "Reliability" refers to the consistency with which a measurement can be made - ie, the extent to which the measurement would remain the same if it were repeated by different observers or by the same observer at different times. "Validity" refers to the extent to which a measurement does indeed measure what it purports to measure. "Sensitivity" refers to the degree of precision with which measurements are able to track change in the variable being measured.

The reliability and validity of a measure are theoretically distinct issues. A measure can be highly reliable without it being a valid measure of the phenomenon under study; this is especially likely in the case of social play, where we simply do not know what features (if any) of the behaviour have significance developmentally.

Sensitivity, however, is related to reliability. Concern for reliability imposes an upper limit on how sensitive measurements can be, and conversely, the need for sensitivity in measurement must be taken into

account when deciding on what will be taken as an acceptable level of reliability. Highly reliable but very insensitive measurements are as uninformative as highly sensitive but unreliable ones; the optimum measure lies somewhere between the two extremes.

2. The usefulness of tests of observer agreement:

In the light of the discussion above, tests of intra- and inter-observer agreement on measuring behaviour can be seen to have the following uses and limitations.

(a) Such tests can directly measure the reliability (ie, replicability) of measurements.

(b) They have little practical relevance to issues of validity. Definition by common consensus is a logically-unsound practice; at its worst, inter-observer agreement merely shows that different individuals share the same prejudices, and has no bearing on the accuracy or otherwise of those prejudices.

(c) They can provide information which can be used indirectly to assess how sensitive measurements are. If the degree of variation in the measured behaviour is greater than the measuring device's unit of measurement, and the measures can be shown to be reliable (by intra- or inter-observer consistency) then the measures may be assumed to be sufficiently sensitive on the dimensions concerned.

3. Intra- and inter-observer agreement:

Inter-observer agreement in behavioural measurement can be of two kinds. One can assess the extent to which different observers agree on the nature of the behaviour categories themselves; or one can examine the degree to which observers agree on using behaviour categories which have been defined previously. Agreement in the first case shows that different observers share the same opinions on what constitutes a behaviour category. Agreement in the second case demonstrates that a given set of definitions can be used in the same way by different observers. Only agreement in the latter sense will be investigated below, since Humphreys (1982), and Matthews and Matthews (1982) have shown that inexperienced observers genrally show good consensus on what does and does not constitute "play", and informal discussions with other workers on play suggest that they share the present writer's opinions on what constitutes social play in the rat.

Intra-observer reliability is an especially important problem for longitudinal studies. In any longitudinal study of animal behaviour, a potentially serious source of bias is that genuine changes in behaviour (those occurring as a function of the animals' development) may be confounded with changes in the observer's criteria for classifying behviour into one category or another. With increasing familiarity, or simply with the passage of time, observers may change

their classifications of behaviours in systematic ways.

To some extent, the occurrence of such biases can be forestalled by the use of unambiguously defined, simple measurements that are easy to score. This minimises the possibility of an observer unconsciously altering his definition of behavioural categories over time. However, an added safeguard is to check on whether or not biases have developed despite these precautions. This can be done in at least two ways:

(a) By comparison against other observers at various intervals within the course of the study - preferably against observers who remain at the initial level of familiarity, so that any changes as a function of increased familiarity, etc, may be detected.

(b) By comparison within the same observer, by recording samples of behaviour early in the study; scoring them later in the study (so that the early behaviour is effectively scored by the older, more experienced observer); and then comparing these later scorings to the original early scores.

When the studies described in this thesis were carried out, steps were taken to forestall bias. (For example, as mentioned in section 3.2, bias in chapter three was minimised by analysing tapes in a random order with respect to the order in which they were filmed, so that age-changes in the animals' behaviour did not correspond in any systematic way with changes over time in the observer's behaviour. This was not possible in

chapter two, where behaviour was recorded "live" rather than from pre-recorded tapes, but the behaviour categories used in chapter two were simple to use, and the time-sampling conventions used were chosen with a view to minimising observer fatigue and maximising observer reliability). However, at the time that these studies were performed, no systematic checks were made to determine whether any biases did in fact exist, or to assess the reliability of the behavioural measures that were made. The following analyses have thus been performed subsequently, as an additional check on the reliability of the studies in this thesis.

4. Observer reliability measures for data in this thesis:

Tests were made of inter- and intra-observer reliability for a number of the measures used in this thesis.

Following Caro et al (1979) and Humphreys (1982), the coefficient of concordance was used to determine the level of agreement between observers, or within the same observer at different times:

$$C = A/(A/(D/2))$$

where C = the coefficient of concordance, ranging from 1.00 (total agreement) to 0.00 (total disagreement); A = the frequency of agreement; and D = the frequency of

disagreement (A+D representing the total number of decisions made).

This measure was used to examine the extent of inter- and intra-observer reliabilty on the time-smpling method used in chapter two, and on some of the measures of play itself which were made in chapter three - namely the duration of play, the number of role-reversals occurring within a bout, and the percentage of time each animal was in top during the play.

4.1: Procedure:

Measurements were made by the experimenter, and by two other observers - SC, who is experienced in observing adult rodent social behaviour but relatively inexperienced in watching rat play; and JB, who is experienced in looking at play in mustelids and carnivores, but is relatively unfamiliar with rodent behaviour.

4.1.1: The time-sampling studies:

A ten-minute section of tape was chosen randomly from a video-tape of one of the litters observed in chapter three. Each observer viewed this section of tape twice. In the case of the experimenter and SC, these two viewings were separated by at least a day; JB's two viewings werew made on the same day, but at an interval of some hours. The observer was familiarised with the list of behaviour categories used for the studies in chapter two, and asked to classify a target animal's

behaviour into one of those categories every ten seconds, at the instant a tone sounded. This gave 60 instantaneous samples of the animal's behaviour, by each observer.

Coefficients of concordance were calculated for each pairing of observers (to give an estimate of inter-observer agreement), and between each observer's first and second viewings of the tape (thus providing an estimate of intra-observer agreement for each of the three observers). In the case of inter-observer concordances, different observers' first viewings of the tape were used. "A" was taken as the total number of spot-samples in which the two observers (or two scorings by the same observer) scored the animal's behaviour into the same behavioural category (eg, when both observers agreed in scoring the animal as "allo-grooming", or "playing", etc). Similarly, "D" was the total number of samples in which the two observers scored the observed behaviour into different categories.

4.1.2: The duration measures:

Nineteen play-bouts were selected at random from a video tape of the animals used in chapter three. Each observer watched each play-bout four times: once to familiarise themselves with what was going on, and thereafter to measure the overall duration of the play-bout, the amount of time that the initiator was on top, the amount of time that the recipient was on top, and finally to record the number of role reversals

occurring within the bout. The "on-top" measures were subsequently converted to percentages of that observer's estimate of the overall bout duration, and the coefficient of concordance was calculated on these.

In calculating the coefficient of concordance for duration measures, as opposed to calculating it for discrete samples as in section 4.1.1, it is necessary to define, a priori, exactly what is to be considered as an "agreement" between observers. In the course of performing the studies described in chapter three, it was found that repeated independent measurements of the duration of a play bout yielded durations that were consistent to within half a second of each other, and often much less. Consequently, in assessing inter-observer agreement, two sets of coefficients were calculated: in the first, observers were scored as "agreeing" on their measurements of a bout's duration, if they were within a second of each other; and in the second, a criterion of half a second was used.

Because of the time-consuming nature of measuring temporal features of play bouts, intra-observer consistency was measured only for the author, and then only for seven bouts out of the initial nineteen.

## 4.2: Results:

### 4.2.1: Results for the time-sampling studies:

Intra-observer consistency (ie, consistency between the two separate viewings of the video-tape) was as

follows: C = .78 for the author, GH; .64 for JB; and .67 for SC. Inter-observer agreement was .88 between GH and SC; .82 between GH and JB; and .74 between SC and JB.

4.2.2: Results for the duration measures:

4.2.2.1: Overall duration of play-bouts:

The coefficients of concordance for overall bout duration, taking scores as being in agreement if they were within one second of each other, were as follows: .85 for GH versus JB; .88 for GH versus SC; .81 for SC versus JB; and 1.00 for GH (first viewing) versus GH (second viewing). When the criterion for agreement was taken as 0.5 seconds, the coefficients dropped to .69 (GH/JB), .64 (GH/SC), .69 (SC/JB) and .83 (GH/GH).

4.2.2.2: Percentage of "on-top" by the initiator:

Taking scores as being in agreement when they were within 10% of each other, the coefficients of concordance for this measure were: .67 for GH versus JB, and for SC versus JB; .82 for GH versus SC; and .83 for GH (first attempt) versus GH (second attempt). When the criterion for agreement was raised to scores having to be within 5% of each other, the coefficients were as follows: .67 for GH versus JB, and for GH versus SC; .57 for SC versus JB; and .83 for GH (first attempt) versus GH (second attempt).

4.2.2.3: Percentage of "on-top" by the recipient:

Scores were considered to be in agreement if they were within 5% of each other. The coefficients were as follows: 1.00 (GH/SC and GH/GH); .95 (GH/JB and SC/JB).

4.2.2.4: Number of role reversals in play:

The coefficients of concordance on this measure were .95 (GH/SC and GH/JB); .89 (SC/JB); and 1.00 (GH/GH).

4.3: Conclusions:

Overall, these measures show a high degree of consistency, both within and between observers.

4.3.1: The time-sampling studies:

Although a concordance level of about 70% is quite an acceptable figure, it should be pointed out that the levels of agreement for the time-sampling data shown in section 4.2.1 are probably under-estimates. There are two factors in this. Firstly, the quality of the video-recording was quite poor, so that it was difficult in places to determine exactly what the target animal was doing (with the result that the observers tended to be uncertain about whether the animal was allo-grooming or sniffing another animal, for instance). This, of course, was not a problem when the studies described in chapter two were carried out, since observations were made directly rather than from tape.

Secondly, it proved difficult to obtain perfect synchronisation between the video- tape and the 10-second tones, so that the latter occurred precisely at the same places on the tape each time it was played. Given the rapidity with which the target animal switched between different behaviours in the course of the

ten-minute session, this meant that effectively slightly different samples of behaviour were taken on each viewing. A better technique would, of course, be to dub the tones directly on to the video-tape's soundtrack. Nevertheless, the test successfully demonstrates that the time-sampling method employed for the studies in chapter two was reliable.

4.3.2: The duration measures:

The second set of tests also showed generally highly reliable results. Using the criteria outlined in chapter three, different observers were able to agree quite closely on play-but durations, to within a second or less. Given that the average play-bout length was found to be 11 seconds, this suggests that the measurements used in chapter three were more than adequately sensitive for the task in hand.

It will be noted from the figures given in 4.2.2, that inter-observer agreement on the percentage of "on top" behaviour by the initiator of play was not so close as agreement on the amount of "on top" behaviour shown by the recipient. This paradox is explained by the fact that in many of the nineteen play-bouts observed, the recipient showed no on-top behaviour at all. Obviously, it is easier to agree that no behaviour has occurred, than it is to measure a behaviour's duration. However, for those bouts where the recipient did show "on-top" behaviour, the observers' estimates were typically within 2% of each other or less.

The high level of observer agreement on role-reversals in play also reflects the fact that many of the observed play-bouts showed no role-reversals whatsoever.

To sum up, observer consistency on these measures of play is generally high, but these data clearly reflect the fact that some decisions (bout duration and number of role reversals) were easier than others.

5. Overall conclusion:

These tests show that inter- and intra-observer consistency were generally acceptable, and in some cases, at remarkably high levels. The measures selected for testing thus appear to be highly reliable. However, it should be pointed out that because these tests were performed at some considerable time after the original data were collected, the possibility remains that systematic biases might have occurred in the original studies (especially in the case of chapter two). While this seems unlikely in practice, future work of this kind should ideally incorporate observer consistency checks from the outset.