

**Cooperation, Paternal Care and the
Evolution of Hominid Social Groups**

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ABSTRACT

Humans are social animals. Human societies emerge from vast networks of cooperative interactions between many different individuals. In this respect, humans are similar to most other primates. However, human societies are unusual among primates in the number of different types of cooperative relationships that are involved. In humans, males and females form strong pair bonds within large multi-male, multi-female societies in which many other cooperative relationships are also important. How and when did human social systems arise? Do males and females use different types of cooperative strategies? Under what conditions does paternal care evolve? Do males and females have different constraints, and how do these affect the types of social strategies they employ? How do factors such as environment quality and seasonality modify these strategies? This thesis seeks answers to these questions using computer simulations based on the iterated Prisoner's Dilemma. The hypotheses generated by these models are tested using data from living primates. They are then used to investigate the kinds of societies that our hominid ancestors may have lived in.

The theoretical and empirical evidence presented in this thesis suggests that sex differences in the energetic cost of reproduction determine the cooperative strategies, and ultimately the types of social groups, that evolve. It is proposed that during hominid evolution female energetic costs increased greatly, in comparison to male energetic costs, due to changes in body size dimorphism, diet and brain size. A two-stage model of hominid social structure is developed. The first stage, at the transition from the australopithecines to *Homo erectus*, would have involved an increase in female cooperation, especially food sharing. The second stage, occurring between 500,000 and 100,000 years ago, would have involved male care giving, the formation of pair bonds and the sexual division of labour within the context of a wider cooperative network.

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PREFACE

“The absurdly ambitious ultimate aim of a gamester [game theorist] is imperialistic: to provide a universally applicable theory of conflict and cooperation, both in animal and human societies.”

(Binmore *et al.* p.2).

I am not a gamester. I am an anthropologist. Yet, it seems to me that my aims in this thesis are coincident with those of game theorists. This research models the processes of cooperation and competition in animals, especially primates, and in doing so attempts to understand how societies emerge. The ultimate aim is to build models of how human society has evolved, and to explore what the social groups of our hominid ancestors might have been like. In order to do this I borrow one of the methods used by game theorists to view cooperation and conflict: a game called the Prisoner’s Dilemma. I am now aware that there are many other games, or ways of viewing the world, that I could have chosen. Furthermore, in doing this research I have not been transformed from an anthropologist into a game theorist. My hope is that by combining the approaches of anthropology and game theory I have created a piece of work that people from both fields will find thought-provoking. None the less, this research lacks the formalism of game theory and I apologise to game theorists who may find my approach rather unusual.

While writing a thesis about cooperation, I became very aware of the number of people who have helped and supported me. Indeed, this thesis could not have been written without considerable help and support from colleagues, friends and family. The following is a list of people who have given me data, discussed this research and other research questions with me, read through parts of my work, or who have provided friendship and support: Louise Barrett, Adam Biran, Mukesh Chalise, Maxine Chappell, Margaret Clegg, Mark Collard, Guy Cowlshaw, Robin Dunbar, Claire Imber, Kristen Hawkes, Katherine Homewood, Kate Jones, Tania King, Andreas Koenig, Nicola Koyama, Mark Lewis, Ann MacLarnon, Heidi Marriott, Theya Molleson, Amy Parish, Camilla Power, Ruth Mace, Steven Mithen, Phil Neil, Dan Nettle, Jim O’Connell, Sara Randall, Caroline Ross, Dan Sellen, Buck Schieffren, Volker Sommer, Simon Strickland, Tom Westerdale, Daisy Williamson, and Bernard Wood. Thank you all.

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CHAPTER 1

Modelling the Evolution of Human Social Organisation: Questions, Assumptions and Implications

1.1: Introduction

Humans, like the majority of other primate species, live in social groups. These groups are often large and involve complex cooperative relationships between individuals of every age and sex: mothers and offspring; husbands and wives; fathers and offspring; siblings; unrelated friends of both sexes; grandmothers and grandchildren; even total strangers. It may be that language and ritual evolved to help us develop and maintain our relationships with individuals whose goals and desires are very different from our own (Dunbar 1993; Knight *et al.* 1995). Humans are unique amongst primates in the range and extent of their social relationships, although the behavioural and cognitive origins of human cooperation are clear throughout the primate order.

There is wide cross-cultural variation in the size and structure of human social groups. This means that it is difficult to define human social organisation as simply “monogamous” or “polygamous”. None the less there are several important characteristics which most human societies have in common. Humans usually live in fairly large groups which contain many adults of both sexes. Within these groups pair-bonds are usually formed between males and females which involve rules about mating access and a commitment by the male to assist the female in offspring care. Finally, human groups usually involve complex networks of cooperation that extend beyond immediate family. In short, human social structure typically involves strong bonds between reproductive partners within a wider network of social relationships. There are two ways in which this type of social structure is unusual. Firstly, male involvement in offspring care is very rare amongst primates, occurring in just 15% of primate species (Rutberg 1983). Secondly, human society involves extensive cooperative networks, involving non-relatives as well as relatives, that cross all boundaries of age and sex to an extent not seen in any other primate group. Together these two factors make human social organisation unique. Herein lies the challenge

of this thesis. On the one hand, human social structure must be understood in terms of the processes that underlie the structure of all primate societies. That is, we must ask ourselves under what *general* conditions we would expect a) intense cooperation between a male and female in offspring care, and b) widespread cooperation between individuals of different age, sex and relatedness. However, we must also determine what kinds of *exceptional* conditions could shape a social system which involves both of these processes.

The following sections will focus on male care giving and the evolution of cooperation. Since both of these topics are discussed at length throughout this thesis this introduction will not be comprehensive. Instead, it will look at how these processes have been incorporated into theories about the evolution of hominid social groups.

1.1.1. The evolution of male care giving

In 1972 Robert Trivers wrote a highly influential and frequently quoted paper entitled “Parental investment and sexual selection”. In it he argued that breeding systems are a function of one main variable: the relative parental investment made by each sex. Trivers defined parental investment as (1972 p.139):

“any investment by the parent in an individual offspring that increases the offspring’s chance of surviving (and hence reproductive success) at the cost of the parent’s ability to invest in other offspring.”

Trivers showed that the sex that has invested most in an offspring at any given time is the most likely to continue that investment. Since mammalian females are responsible for gestation and lactation, parental investment is high in comparison to the male. As a result, females are more likely than males to continue to invest in any given offspring. Because the mating success of males is limited by their ability to fertilise females, they are likely to compete amongst themselves for mating opportunities rather than investing in individual offspring. For these reasons it is not surprising that care giving is a highly unusual male mating strategy in mammals. Maynard Smith (1977) suggests that there are three circumstances in which males may contribute to offspring care. Firstly, male investment may be necessary if a female has already invested so much in reproduction that she is unable to provide the rest of the investment required to raise the offspring to maturity. Secondly, if two

parents can raise twice as many offspring as a single parent then it may be to the male's advantage to forego other mating opportunities. Finally, males may choose not to desert the mother and her offspring if the chances of re-mating are small.

The work of Trivers and Maynard Smith provides the framework from which many theories of male care-giving are derived. Kleiman (1977) argues that paternal care occurs whenever a female is unable to rear her offspring successfully without male help, for instance with carrying infants or territory defence. Dunbar (1988) suggests that high energetic costs associated with lactation are likely to determine whether or not males participate in infant care. Among primates, paternal care is most common in the cebids (e.g. owl and titi monkeys) and callitrichids (tamarins and marmosets). Explanations for paternal care in the callitrichids generally focus on the high costs incurred by females who usually give birth to twins and often produce two litters per year (Goldizen 1990; Leutenegger 1980; Ross 1991; Tardif 1994; Tardif *et al.* 1993). Ross (1991), for example, argues that in callitrichids, females can only sustain high birth rates, litter weights and high litter growth rates if males assist in infant transport. Rylands points out that these are not complete explanations (1996 p.6): "the argument that males show parental care because females have large twins does not answer the question of why females have large twins." Furthermore, these explanations are not applicable to non-twinning species such as the cebids and the siamang.

Paternity certainty is often assumed to be an important condition for the evolution of male care (see for example Alexander and Noonan 1979; Bales 1980; Busse 1984; Kurland 1977). Yet, even in tamarins and marmosets paternity certainty is not a straightforward issue. There is considerable intra- and inter-specific variation in the composition of tamarin and marmoset groups, but typically they will contain between 5 and 18 individuals including more than one adult of each sex (Garber 1997). Even though only a single female reproduces at any one time, males do not appear to compete for reproductive access and all adult males mate with the breeding female. The implication of this is that there is no way that a male can ascertain whether he has fathered a particular offspring. None the less all adults, including the males, assist in offspring care. Garber (1997) describes tamarin groups as immensely cooperative. His studies of *Saguinus mystax* indicate that cooperative interactions, such as food sharing, group defence and infant transport, are over 50 times more likely than aggressive ones.

How can paternal care evolve without paternity certainty? This is an issue not only for the callitrichids, but for most species in which male care occurs. Particularly intriguing are those cases in which male care giving occurs in the context of a multi-male group (e.g. black-capped capuchin, olive baboon, yellow baboon, chacma baboon, barbary macaque, stumptail macaque and Japanese macaque (Smuts and Gubernick 1992)). In olive baboons, males form special friendships with particular females and their offspring. These friendships involve substantial benefits for the infants in terms of protection from predators and other male baboons and access to the best feeding sites (Smuts 1985). Males are unlikely to be related to the infants that they care for, however, females are likely to reward their special friend with future mating opportunities. Thus, Smuts and Gubernick (1992) describe this type of male care as mating effort rather than paternal investment. Further data on rhesus macaques (Berenstain *et al.* 1981), Japanese macaques (Gouzoules 1984; Takahata 1982) and yellow baboons (Altmann 1980; Stein 1984) supports their conclusion that (Smuts and Gubernick 1992 p.16, their italics):

“male care of infants represents mating effort rather than parental investment whenever selection favours male care because of the benefits males receive *in exchange for* this care rather than because of enhanced survivorship of their own infants.”

Affiliated infants will often cooperate with the male, particularly during aggressive interactions with other males when the infants may be used as “agonistic buffers” (Collins 1986; Packer 1980; Stein 1984; Strum 1984). Furthermore, in species such as chimpanzees (de Waal 1982), rhesus macaques (Chapais 1983) and vervets (Raliagh and McGuire 1989) support from a female ally can be important in determining a male’s rank. Thus, male macaques seek to establish affiliative relationships with the infants of high ranking females (Gouzoules 1975; Manson 1994). In short, male care giving is not necessarily directly related to parental investment. Rather, male care giving may often be characterised as one aspect of a reciprocally cooperative relationship between a male, female and her offspring where all parties stand to gain substantial benefits.

Humans are unusual amongst catarrhines (Old World monkeys and apes) in that there is extensive male investment in offspring, particularly in the form of provisioning. However, in keeping with the preceding discussion, there is much

debate as to whether this is really parental investment, or a male mating strategy. Hawkes (1990, 1991, 1993, see also Hawkes *et al.* 1991) argues that large animal hunting by males is a method of intra-sexual competition, whereby successful hunters hope to gain status and attract mates. Hawkes and her co-workers show that among the Hadza, hunting large game benefits the group as a whole by providing more calories per head than other hunting or foraging strategies. But, at an individual level, it is a risky strategy, as the likelihood of catching an animal on any given day is very low. Hunting small game would be a more reliable strategy; moreover since small animals are not shared with the whole group (as large animals are) the entire products of the hunt would go to the hunter's family. Hawkes argues that since men target those resources that are most widely shared, the purpose of hunting is to "show off" to potential mates. Unlike Smuts and Gubernick (1992), Hawkes does not view male hunting as part of cooperative relationship since the sharing of game is not reciprocated in kind. However, as Hawkes herself states (1993 p.341):

"if those who provide public goods are listened to and watched more closely than others and favoured as neighbours and associates, they have a larger, readier pool of potential allies and mates."

In other words, males are providing meat *in exchange for* allies and reproductive access to females.

In contrast to Hawkes and colleagues, male provisioning of offspring in human groups is usually viewed as male investment. Indeed, the evolution of paternal care is often portrayed as the key element in the evolution of human society. For example, Lovejoy (1981) suggests that bipedalism, by freeing the hands, was an adaptation to aid male provisioning and that sexual dimorphism in body size and locomotor style in *Australopithecus afarensis* is the first evidence of a sexual division of labour. Male provisioning and monogamous social groups are generally viewed as evolving in parallel with biological and behavioural changes in females that manipulate the chances of paternity certainty. For instance, continuous female sexual receptivity and concealed ovulation are expected to reinforce the pair bond by encouraging mate guarding (Turke 1984).

Unfortunately, social systems leave little trace in the fossil and archaeological record, making it very difficult to judge exactly when male provisioning may have evolved. Hence theories differ enormously in terms of the timing of this change in

social organisation, but most assume that male provisioning was a response to an increase in costs to the female of raising altricial, large brained offspring. Over the course of human evolution there has been a three-fold increase in the size of the brain, a change which has important energetic implications (Aiello and Wheeler 1995; Aiello 1997). The brain is one of the most energetically expensive organs in the body since brain tissue has over 22 times the mass specific metabolic rate of skeletal muscle. Other energetically expensive organs are the gastrointestinal tract, heart, liver and kidney which, together with the brain, are responsible for nearly 70% of the human body's energy requirements (Aiello and Wheeler 1995; Aiello 1997). However, while humans have larger brains than would be expected for an average primate of our body mass, the mass of the gastrointestinal tract is only 60% of the size expected. It appears that in humans the high metabolic costs of having a large brain are balanced by a reduction in the energetic costs of the gastrointestinal tract. Aiello and Wheeler (1995) argue that a change in gut size must have been accompanied by a change in diet to a less bulky, more digestible food source. Animal based products (e.g. meat or bone marrow) would satisfy this criterion.

The adaptive complex of an increase in brain size and a reduction in gut size, mediated by a change to an animal-based diet, implies a profound change in the energetic costs incurred by females. Firstly, an increase in brain size directly increases the energetic load on the mother, since the main period of brain growth occurs in utero and during the post-natal period prior to weaning (Martin 1981, 1983, 1996). Foley and Lee (1991) estimate that up to the age of 18 months human infants are around 9% more energetically costly than chimpanzee infants. Secondly, a change to a diet with a high meat component requires that females provision their offspring until they have gained the necessary skills to acquire meat for themselves (Aiello 1998). The dual loads of extensive food-sharing between mother and offspring, and the training necessary for the offspring to find its own resources would significantly increase the period of maternal investment beyond the weaning period.

There have been two main periods of brain expansion when male care giving may have evolved (see figure 1.1). The first of these coincides with the appearance of *Homo erectus*¹ 2 million years ago. *Homo erectus* had an average cranial capacity of 1000cc, considerably larger than that of its australopithecine predecessors,

¹ *Homo erectus* is assumed here to include both the African and Asian *Homo erectus* grade hominids.

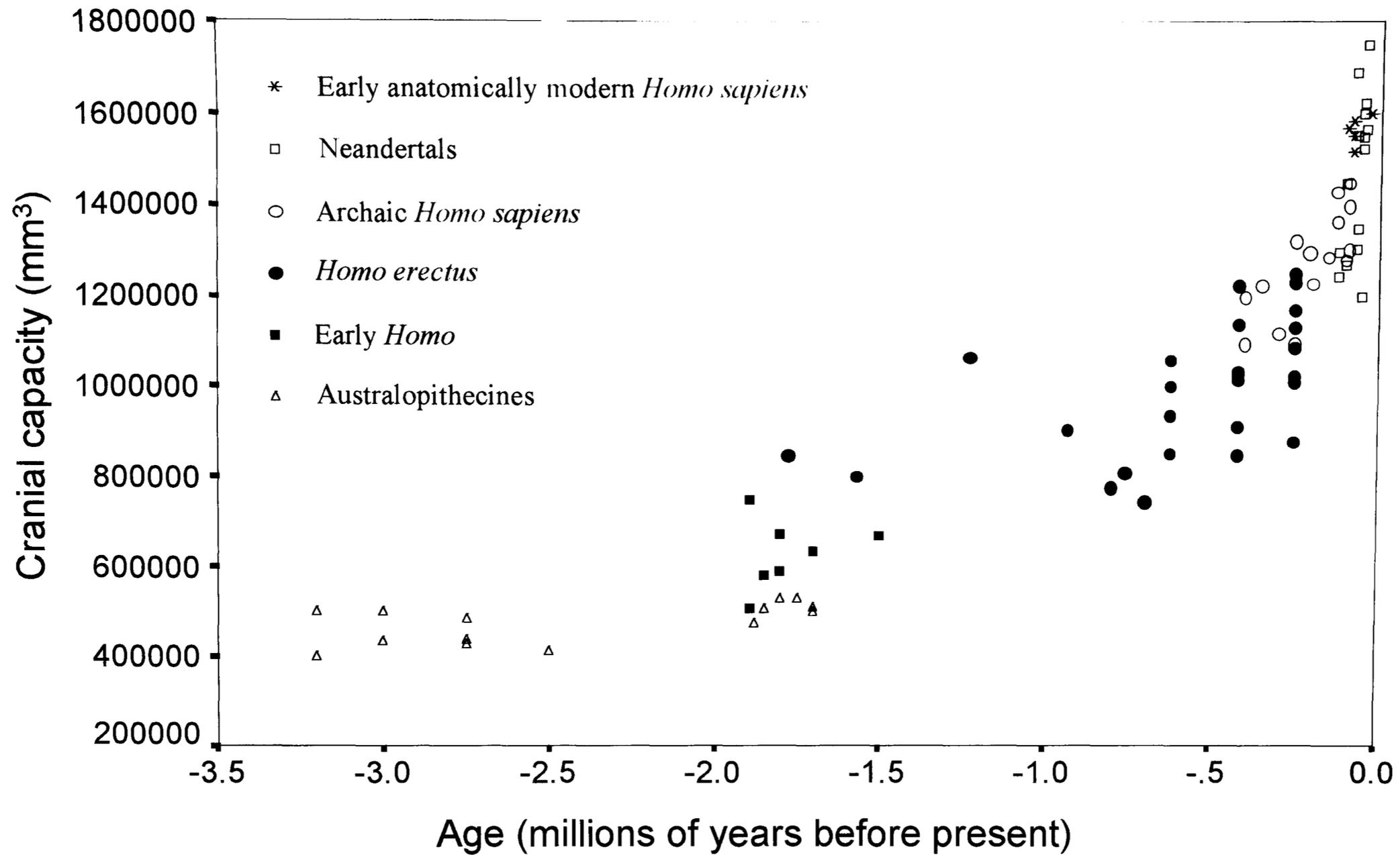


Fig. 1.1: The evolution of hominid brain size

Estimated cranial capacities versus time for the hominids. Data from Aiello and Dunbar (1993).

although this is somewhat compensated for by a corresponding increase in body size. The transition from the australopithecines to *Homo erectus* marks perhaps the greatest suite of anatomical and behavioural changes seen in hominid history. In sharp contrast to the smaller overall size, ape-like body proportions and arboreal-bipedal mix of postcranial adaptations seen in the australopithecines, *Homo erectus* was tall, slim and a fully committed biped. The *Homo erectus* mandible, robust by modern human standards, was slight in comparison to that of both gracile and robust australopithecines indicating a change in diet. *Homo erectus* had the abilities to produce quite sophisticated tools, typified by the hand axe whose carefully crafted, symmetrical form indicates fairly advanced tool making abilities. Finally, *Homo erectus* was the first hominid to leave Africa, colonising a substantial portion of Asia. Given these considerable physiological and behavioural adaptations, it is likely that substantial changes in social organisation also occurred during the *Australopithecus-Homo* transition.

Isaac (1978) used the archaeological record to establish that early *Homo* transported meat (that had either been hunted or scavenged) to a central site or home base. He points out that food transport in modern groups is associated with a sexual division of labour and food sharing and goes on to suggest that (1978 p.106):

“in early protohuman populations the males and females divided subsistence labour between them so that each sex was preferentially tapping a different kind of food resource and then sharing within a social group some of what had been obtained. In such circumstances a mating system that involved at least one male in “family” food procurement on behalf of each child-rearing female in the group would have a clear selective advantage over, for example, the chimpanzees pattern of opportunistic relations between the sexes.”

Detailed taphonomic analysis of the timing of the distribution of bones and artefacts suggests that the sites which inspired Isaac’s model were not home-bases at all (Binfold 1981). None the less, Deacon (1997) also suggests that food sharing, sexual division of labour and male provisioning of a female and her offspring arose in early *Homo*. He proposes that in an unpredictable environment, meat provides an important and consistent food source. However, females burdened with offspring cannot access meat other than through males. This means that pair bonding is required to ensure adequate provisioning of females and their offspring. Deacon

further suggests that this behaviour evolved in tandem with changes in symbolic thought and tool use.

The second possible period during which male care-giving may have evolved began around 500,000 years ago. During this time there was a period of exponential brain expansion (figure 1.1.). This was the era of archaic *Homo sapiens*, who continued the process of migration begun by *Homo erectus* by expanding into Europe. During this time there is a diversification in the archaeological record, and finds at Schöningen and Boxgrove provide the first irrefutable evidence of hunting around 500,000 to 400,000 years ago (Thieme 1997). Knight, Power and Watts argue that it was during this time that male provisioning became important (Knight 1991; Knight *et al.* 1995; Power and Watts 1996). They propose that females formed kin based coalitions whose purpose was to manipulate males into providing meat by using deceptive sexual signals. It is likely that individual females were able to extract meat from males in exchange for sexual access, but a female who is pregnant or lactating will be unable to use such a strategy. This means that it is in the interests of females to mislead males about their fertility state through processes such as concealed ovulation, continuous sexual receptivity and ovulatory synchrony (Turke 1984; Power and Watts 1996). Ovulatory synchrony, in particular, prevents mate-guarding and encourages attention from a large number of males. There is, however, one sure sign of reproductive status, menstruation, the absence of which indicates that a female is not currently fertile. How, then, can females attract continual male investment? Knight, Power and Watts hypothesise that to confuse males, coalitions of females used blood from other females, and at a later stage red ochre, to simulate synchronised menstruation and thus ensure continued male support. Thus, brain expansion in archaic *Homo sapiens* provoked a fundamental change in human behaviour and possibly kick-started the evolution of ritual behaviour.

The archaeological record confounds any simple correlation between brain expansion and behavioural change. Neandertals are the most well known of the archaic *Homo sapiens* species and provide a very interesting contrast with anatomically modern *Homo sapiens* groups. Neandertal sites are generally small and undifferentiated with little evidence of symbolic artefacts or of food transport (Steele and Shennan 1996). Soffer (1994) argues that both sexes were skeletally robust and that Neandertals lived in small, regionalized groups without a sexual division of labour or social differentiation. Archaeological remains associated with anatomically

modern *Homo sapiens* are much more variable from site to site, food transport is indicated and there is clear evidence of symbolism. Soffer suggests that it is only at this point that human social organisation emerged. It is true that archaeological contrasts between Neandertals and anatomical modern *Homo sapiens* produces an interesting conundrum (Mithen 1996). However, the appearance of anatomically modern humans around 100,000 years ago is out of phase with the symbolic explosion in the archaeological record, known as the Upper Palaeolithic transition, around 50,000 years ago. This is a sharp reminder that the relationships between anatomy, social organisation and cognition are still poorly understood.

1.1.2 The evolution of cooperation

Most primates live in social groups, although the size and composition of these groups vary widely. The advantages of group living may be predator defence and/or group defence of resources and there may be further advantages in terms of opportunities for non-maternal offspring care (Dunbar 1988). Conversely, group living carries with it substantial disadvantages. Individuals within groups are in direct competition with each other for resources and mates. Also, for a group to remain cohesive, individual group members must synchronise activities such as feeding, moving and sleeping with those of the rest of the group. Since individuals of different age, sex and reproductive status have different needs, this may require considerable compromise.

To counteract within-group competition, cooperation plays a vital role in primate groups. Individuals cooperate in numerous ways, the most common of which are supporting each other in agonistic conflicts, group defence, feeding together, sleeping together and grooming. An individual's position in the dominance hierarchy is determined by the quality and quantity of his or her allies. To a large extent, the ability to maintain cooperative relationships is a more important determinant of reproductive success in primate groups than physical characteristics such as body size. The importance of maintaining good relations with other group members is such that some primate species have special reconciliation mechanisms. De Waal and Roosmalen (1979) found that after aggressive interactions opponents would engage in a great deal of contact, especially kissing and gentle contact. Stump-tail macaques

have a special “hold-bottom ritual” in which the subject of aggression presents his or her rear to the aggressor to be grasped at the hips (de Waal and Ren 1988). De Waal and Aureli (1996 p.90) believe that “both macaques and chimpanzees follow what seems a general rule among primates; that is, reconciliation aims to restore valuable relationships.”

Cooperation is particularly important during agonistic conflicts, where the number of allies an individual can call upon determines his or her competitiveness (van Hooff and van Schaik 1992). Coalitions provide protection to the individual and there can be intense competition for alliance partners. Many primates, especially Old World monkeys, use grooming to establish and maintain social bonds (Seyfarth 1976, 1977, 1983). In some instances, individuals will sacrifice time spent on other activities in favour of servicing their alliances through grooming. Dunbar and Dunbar (1988) found that lactating gelada females, whose time budgets are seriously constrained due to high feeding requirements, sacrificed resting time rather than reduce their time spent in social activities. Certain individuals within a group, especially those well placed within the dominance hierarchy, are particularly attractive alliance partners, and thus there may be considerable competition to groom them (Fairbanks 1980; Seyfarth 1977, 1980; Stambach 1978). Additional benefits of alliances with high ranking animals include access to resources, predator defence and information sharing (Fairbanks 1980). In vervet monkeys, competition for allies is so intense that adult females attempt to prevent other females from grooming high ranking animals (Cheney and Seyfarth 1990; Seyfarth 1980). Alliances with subordinate animals can also be valuable when the balance of power is delicate (Harcourt 1992) and macaque females actively try to prevent the development of coalitions between subordinates (de Waal and Luttrell 1986; Silk 1982).

Cooperation and competition are two sides of the same coin. Competition for food, mates, allies, sleeping sites, position in the hierarchy and so on create the need for cooperation. This cooperation, in turn, becomes the principal means by which primates compete with each other. Thus, in groups where competition is great, as is the case for many of the Old World monkeys, there is a great dependence on coalitionary support and thus strong cooperative bonds (van Hooff and van Schaik 1992). Conversely, when conflicts are rare there is little need for cooperative alliances and groups are more likely to be egalitarian, as is the case for many colobine monkeys. Patterns of female migration reflect the degree of importance

attached to coalitions, for instance female macaques, vervets and baboons are highly unlikely to emigrate from their natal group, adding a further degree of stability to the social hierarchy. These considerations suggest that an appropriate description of the structure of a primate group would be in terms of the cooperative and competitive bonds from which it arises. This reasoning follows Hinde (1976, 1983) in viewing a social system as the emergent outcome of a consistent set of social relationships which are the product of individual interactions. Of course, many different factors will affect the behaviour of group members, and will affect them in different ways depending on their sex, age, kinship and social status. The aim, therefore, is to look for consistent patterns within these relationships.

Perhaps the most telling predictor of cooperative behaviour is gender. In the previous section, sex differences in parental investment were discussed. Because mammalian females are biologically committed to high investment in offspring, their principal means of maximising their reproductive success is to ensure a good quality diet and protection from predators and other group members. Cooperative bonds or hostile interactions between females should reflect these needs. Because females are often smaller than males, in some species female coalitions are an important buffer against male aggression, for example in bonobos (Parish 1994), capuchins (Perry 1997) and vervet monkeys (Cheney 1983). Males, on the other hand, can best maximise their reproductive success by mating with as many females as possible. This means that cooperation is much less likely between males since reproductive access to a female is less easily shared than, say, food. There are exceptions to the rule, for instance male alliances have been reported in baboons (Packer 1977), bonnet macaques (Silk 1994) and chimpanzees (de Waal 1984). Even in these cases sex differences in the nature of cooperation are clear. De Waal (1984) found that while chimpanzee females formed long term alliances with female friends involving mutual support, male coalitions were more opportunistic and were used to improve status.

Foley and Lee (1989, 1996) mapped out the distribution of same sex alliances for a wide variety of primate species in order to ascertain the most likely pattern of alliances in the hominids. They found that the backbone of Old World monkey societies tends to be kin-based female alliances, whilst in the apes there is a switch to male-based associations. Our closest ancestor, the chimpanzee, lives in social groups

that centre on alliances between male kin and Foley and Lee predict that the early hominids would have had a similar social system (Foley and Lee 1989 p.904):

“The most probable social organisation for the early australopithecines consists of mixed sex groups, with males linked by a network of kinship. Females, forced to forage over larger areas to find dispersed and seasonally limited food and to aggregate in the face of some predation, would be expected to form more stable associations with either specific males within the alliance or with the entire alliance of males.”

Foley and Lee depict male-female bonds as becoming gradually stronger over the course of hominid evolution as a response to increasing costs to the female associated with brain expansion. Here their argument parallels the discussion in the previous section of the possible links between brain size and male provisioning. They pinpoint two key time periods during which there was considerable brain expansion and thus possible changes in social organisation (see figure 1.1). The first period of significant brain expansion is with the appearance of *Homo erectus* around 2.0 million years ago. It is at this time that “initial increases in male-female bonding may have occurred” (Foley and Lee 1996 p.63). The second, and most dramatic period of brain expansion began around 500,000 years ago. Foley and Lee argue that at this point females would be under considerable stress due to the energetic costs of nurturing large brained, altricial infants, with slow growth rates and prolonged periods of dependence. As a response to this male-female bonds would intensify and become more stable.

Wrangham (1987) also takes a phylogenetic approach to modelling hominid social structure. In agreement with Foley and Lee, Wrangham emphasises the importance of male-male alliances, particularly in human and chimpanzee groups. Hence, he concurs that early hominid group structure was based upon closed social networks of related males. Foley, Lee and Wrangham place little importance on the development of female based associations. Wrangham justifies this using evidence that female alliances are “rare” in gorillas, chimpanzees and humans, particularly because female migration means that adult females are usually unrelated to other group members.

The problem with using phylogenetic methods to determine social structure is that no consideration is given to ecological context. The social structure of chimpanzees appears to arise from the dispersed nature of food resources that

prevents females from forming cohesive groups (Dunbar 1988; van Hooff and van Schaik 1992). Close male bonds allow males to defend large numbers of highly dispersed females as a team. Evidence from a group at Bossou, West Africa, suggests that when the habitat permits chimpanzees to live in more compact groups, female bonds are stronger than male bonds and males may emigrate (Sugiyama 1981). This implies that ecology, rather than phylogeny, shapes the nature of chimpanzee social groups. Williamson (1997) has shown that the australopithecines would not have been able to survive if they were living in the same habitats as present day chimpanzees. Furthermore, changes in aridity and seasonality during the PlioPleistocene indicate that much of human evolution has occurred in rather different ecological settings to the African apes. The ecological context of human evolution was almost certainly very different to that of the African apes. This means that phylogenetic models alone are not appropriate for modelling hominid social structure.

Wrangham, Foley and Lee, who emphasise the importance of male bonds, may have underestimated the importance of female alliances in both apes and humans. Unrelated female bonobos form strong alliances (Parish 1994), and female coalitions are not uncommon in chimpanzees (de Waal 1982, 1984). Human females certainly form strong cooperative bonds, however, Wrangham describes these as “friendships” rather than “competitive alliances” and thus discounts their importance. To disregard female-female relationships in this way oversimplifies the evolution of human society. It is exactly these types of relationships, between unrelated females, that demand an explanation beyond that offered by kin selection. Moreover, these relationships are of special interest because of the cognitive demands they place on the individual.

Living in a social world requires sophisticated social intelligence: the larger and more complex that world is, the greater the intelligence required (Dunbar 1992, 1993). Living in a social groups requires the ability to monitor and predict social relationships and to be able to manipulate those relationships (Byrne and Whiten 1988; Whiten and Byrne 1997a). Dunbar argues that as the social world becomes more complex, each individual needs more complex mental mechanisms for managing their social relationships. The neocortex appears to play a major role in this. Dunbar (1992) has shown that the size of the neocortex, relative to the size of the rest of the brain, is closely correlated with group size. In effect, the size of the

neocortex limits the number of relationships that an individual can monitor, and thus ultimately limits group size. Aiello and Dunbar (1993) extend the social intelligence model to the evolution of hominid social groups. They argue that the large brain sizes of *Homo erectus* and *Homo sapiens* are indicative of large group sizes, possibly due to factors such as predation pressure or intra-group conflict. They further suggest that such large groups would require a more efficient mechanism for social bonding than grooming, the time consuming method employed by Old World monkeys and apes. Vocalisation and, eventually, language would fulfil such a role.

Strum *et al.* (1997) and Gigerenzer (1997) point out that the definition of what makes a social world 'complex' is rather fuzzy: "the existence of social complexity does not guarantee the existence of behavioural or cognitive complexity in individuals" (Strum *et al.* 1997 p.61). The quantity of relationships an individual must monitor tells us nothing of their quality and thus the social complexity involved. This is an important distinction if, as seems likely, different types of relationship impose different cognitive demands. For instance, the rule "always cooperate with my daughters" is simple and robust, due to the clear fitness benefits of helping your own kin. However, decisions about when to cooperate are likely to be more complex when non-relatives are involved, as individuals must take into account past interactions, rank effects, and the likelihood of other individuals becoming involved. Vervet females appear to apply different rules depending on relatedness: Seyfarth and Cheney (1984) found that vervet females would respond to pleas of support from non-relatives on the basis of previous cooperative encounters (in this case whether that animal had recently groomed them) but supported relatives unconditionally.

Byrne (1997) also suggests that the relationship between neocortex size, intelligence and social relationships is more subtle than Dunbar's model suggests. He concurs that the social intelligence hypothesis is a good explanation for cognitive differences between strepsirhines (lemurs and lorises) and haplorhines (monkeys and apes). However, distinct differences in social intelligence between monkeys and apes do not coincide with differences in either neocortex ratio or social complexity. In fact, in terms of the number and types of relationships found there is very little difference between monkey and ape social groups. But, "differences emerge, not in what great apes do – which in practice is often much the same as what monkeys do – but in how they do it" (Byrne 1997 p.295). It appears that the apes have something

which monkeys do not: a theory of mind or, in other words, the ability to see the world from another animal's point of view (Premack and Woodruff 1978). Theory of mind is a powerful mental tool which can be used either to trick conspecifics (Byrne and Whiten 1992) or to determine the best individuals with whom to forge cooperative relationships (Strum *et al.* 1997). Experiments in the laboratory and observations in the wild, of deception and social manipulation, suggest that chimpanzees could have a theory of mind, but that monkeys are unable to attribute mental states to others (Cheney and Seyfarth 1990). How can we explain these differences in social intelligence, in the absence of differences in social complexity? Byrne (1997) points out that there are distinct differences between monkeys and apes beyond the social arena (Byrne 1997 p.306 his italics):

“very large body size, locomotion by brachiation, the representational use of tools, construction of sleeping beds, and the ability to build hierarchical programs of actions, are all unique to great apes: separately or in some combination they are then *in principle* suitable candidate hypotheses to explain a special adaptation of the great apes.”

Byrne's point is that one or more of these factors have changed the way that apes think so that apes are able to mentally represent the world and its problems. Once an animal has this ability in one sphere, say technical intelligence, it can be extended to other spheres such as social intelligence (and hence the creation of theory of mind). This point of view sits uncomfortably with a modular view of the brain, in which each mental faculty is seen as distinct and purpose-built. Tooby and Cosmides (1992), in their “Swiss army knife” view of the brain, argue that having distinct mental mechanisms, purpose built for particular activities, is a more efficient way of solving problems than having a single ‘general purpose’ brain. However, Karmiloff-Smith (1992, 1993) takes a rather different perspective on the modularity of the brain. She does not argue against a modular structure to the adult brain, rather she focuses on the process of modularization during development. Karmiloff-Smith proposes that while the human brain is structured in a modular way which involves localised mental processes, there is a general process at work which organises, and more to the point re-organises, the way these local modules are connected. This process, which she terms representational redescription, allows the mind to sort out the information it receives into theories about the way the world

works. In this way, large amounts of small scale, context specific, information can be re-formatted into organising principles which are available to other mental modules.

If Karmiloff-Smith is correct, then Byrne's hypothesis is indeed feasible. Most telling may be the long periods of infant dependency in the great apes which would provide enough time for the process of mental re-representation to occur. Longer periods of growth and development could allow more sophisticated mental representation in all domains of knowledge. We should then expect that dramatic changes in body size, brain size and the timing of growth and development during hominid evolution would have affected all realms of behaviour, including those pertinent to the social and technical worlds. And here we return to the issue of energetic costs, since females are unlikely to be able to support extended periods of offspring dependency without considerable help from other group members. The evolution of extensive networks of cooperation in humans may have allowed significant changes in life histories with profound knock-on effects for the evolution of cognitive abilities.

1.1.3. Cooperation, paternal care and the evolution of hominid social groups

In the previous two sections it has been shown that the social structure of a primate group arises from the cooperative and competitive interactions of the group members. It has been shown that paternal care is also a form of cooperation between males and females, although the units of exchange may be rather different for each sex. In fact, as Strum and Mitchell discovered in their observations on baboons, cooperation is a part of primate life for individuals of all ages and sexes (Strum and Mitchell 1987 p.101):

“A big male, although built as a fighting machine, needs the cooperation of the small infant or the female that he uses as an agonistic buffer if he is to defend himself successfully against the aggression of another male. This same big male needs a female's cooperation to be reproductively successful even if he aggressively claimed her from another male. Females and infants have powerful leverage through the system of social reciprocity created by social relationships. Pumphouse baboons certainly appear to develop and manage social resources in order to gain an advantage in the short and longer term.”

If cooperation underlies the lives of non-human primates, it suggests that the study of cooperation may be fruitful in formulating predictions about the evolution of hominid social structure. Erdal and Whiten believe that cooperation is a unifying theme in modern hunter-gatherer groups (1996 p.140):

“students of hunter-gatherers have discerned a cluster of features which appear to act as the functional core of the societies: egalitarianism, cooperation, and sharing, on a scale unprecedented in primate evolution.”

Why should Erdal and Whiten state that human cooperation occurs on an “unprecedented” scale? They point out that there is almost no hierarchy or dominance in hunter-gatherer groups, and that food sharing, especially of meat is universal. While there are exceptions among the callitrichids (Brown and Mack 1978; Feistner and Price 1990, 1991) food sharing between adults and young is very rare in primates. Food-sharing has been observed in chimpanzees (de Waal 1989) and capuchin monkeys (Perry and Rose 1994; de Waal 1997; de Waal *et al.* 1993), however, these instances are more akin to ‘tolerated theft’ (Blurton-Jones 1987) than active sharing. Humans do not only share food, but they also cooperate in capturing food. Again this is unusual rather than unknown primate behaviour: cooperative hunting is known in baboons (Strum and Mitchell 1987) and chimpanzees (Boesch and Boesch 1989).

We have seen already that different researchers have focused on different aspects of human cooperation: Foley, Lee and Wrangham on male-male kin associations; Knight, Power and Watts on kin-based female coalitions; Lovejoy and Isaac on male-female bonds. I would contend that all of these different types of cooperative relationships in humans are important. Furthermore, there are other types of cooperative relationships found in humans that are not considered by these authors. In some societies, such as the Hadza, senior post-menopausal women play an important role in provisioning their daughter’s offspring (Hawkes *et al.* 1997a, b, c). Furthermore, humans do not restrict their friendly interactions to relatives. Non-relatives and even total strangers participate in cooperative exchanges. Nettle and Dunbar (1997) suggest that dialects and other “social markers” may have evolved to help us determine the honest or dishonest tendencies, and hence cooperativeness, of people we meet on an infrequent basis. In short, unlike any other single primate

species, human cooperative relationships span all combinations of age, sex and relatedness.

Why are humans so cooperative? When and why did human patterns of cooperation evolve? Answers to these questions may only be found when we can answer the more general question: under what conditions do different types of cooperative relationships evolve? Most of this thesis is dedicated to exploring this latter question. Rather than concentrate on any particular primate species, this research looks for underlying mechanisms that could be applied to any primate group. The advantage of this type of model is that it can be tested on data from extant species, before being applied to extinct ones. The first stage in this process is to find, and develop, a good model of cooperation.

1.2: Modelling the Evolution of Cooperation

In the previous section it was argued that an appropriate approach to understanding social organisation is to study patterns of cooperation and competition. This could be done using referential modelling, where extant species are used as analogues for extinct hominids. This is a common approach, and several candidate species have been proposed: chimpanzees (Tanner 1981, 1987), baboons (Strum and Mitchell 1987), the social carnivores (Thompson 1975, 1976) and humans (Isaac 1978). These models stress the similarities between the analogue species and hominids. However, because little attention is paid to differences, it is very difficult to falsify even widely divergent theories. For instance, Washburn and DeVore's (1961) baboon model emphasises the importance of male dominance relationships, while Erdal and Whiten's (1996) hunter-gather model stresses the importance of cooperation and lack of a dominance hierarchy. It is very difficult to falsify either of these models, since they are both correct with respect to their chosen analogue species. Furthermore, most referential models entirely ignore those features which are unique to hominid evolution: exponential brain expansion, language, extensive tool use and culture. As Tooby and DeVore state (1987 p.187):

“Only uniqueness can explain uniqueness; one cannot invoke the features species have in common to explain their differences. By their nature, referential models tend to ignore or obscure the most important question in human evolution: where did our most crucial and novel adaptations come from?”

Tooby and DeVore (1987) promote, instead, the use of “conceptual modelling”. This approach uses extant species to derive fundamental principles that are applicable to any species, at any time. It is this second approach that is followed here. Models will be generated based upon general principles, that can then be applied to specific species. However, Tooby and Devore warn that (1987 p.186):

“At its worst, a conceptual model is highly artificial and obscure; it rests on unstated, unrealistic, or shifting assumptions; it leaves unintegrated, or absent, factors known to be important; it yields conclusions that are trivial, obvious, or absurd.”

A model is only as good as the assumptions upon which it rests. It is crucially important to make explicit these assumptions so that they are open for criticism and debate. It is to this end that the following sections are written.

1.2.1 Assumption 1: Social structure is the emergent outcome of the cooperative and competitive interactions of group members.

This first assumption has already been explored in the previous section, and no time will be wasted re-justifying it here. However, it is important because it defines the form of the model. Viewing a system in this way demands a “bottom-up” approach. It is the decisions of individual animals that determines how the system will develop. The strategic decisions made by any single agent are based upon the actions of other members of the group, which in turn are contingent upon the behaviour of the original agent. This means that this is a dynamic system, in which the actions of all of its parts are essentially inter-connected. Such “complex adaptive systems” (Holland 1992a) are certainly not restricted to primate social groups. Any system which is produced from the actions of smaller components may be described in such a way. For example cells consist of proteins and DNA; organs consist of interacting cells; brains consist of neurons; people consist of interacting organs. One of the interesting things about these systems is that the basic component may only be capable of very simple behaviours and decision making processes, yet the patterns of interaction of these components creates complex and often unexpected overall structures (for reviews see Waldrop 1992; Lewin 1993).

Because complex adaptive systems contain many agents, each of which is making individual decisions about strategy, the most practical way of modelling them is by using computer simulations. That is, by creating an “artificial world” or a “computer ecosystem” (Conrad and Rizki 1989). Conrad and Rizki describe the important features of such a simulation (1989 p.248):

“The chief ground rule is that an artificial world’s ecosystem should be a self-contained microcosm, capable of autonomously generating its own evolutionary development. In principle it could be closed to the modeller after its creation in the same way that a real microecosystem enclosed in a laboratory flask might be. The population and ecosystem dynamics should emerge from simple rules of interaction governing the behaviour of organisms rather than being imposed by fiat by the modeller. These rules should themselves be under genetic control and subject to evolution to a degree that approaches as near as practical to the genetic control exerted by organisms in nature. Constructs such as fitness should not enter into the model. They should emerge in the same way that fitness emerges in nature.”

All of these rules are followed in this research. However, many other requirements identified by Conrad and Rizki are not. For instance, they specify that artificial worlds should include a detailed spatial environment, which is graded with respect to energy and mass which flows through the system in a well defined manner. Furthermore, they prescribe that the physical environment should be “multifaceted” including attributes such as temperature, light intensity and spatial boundaries (1989 p.248). These, and many other features, have been incorporated into a set of models called EVOLVE. These models, and others like them (for example SFI Echo (Holland 1992; Jones and Forrest 1993)) are typically created and then set in motion “as a means of predicting and discovering new features of the natural world” (Conrad and Rizki 1989). These models certainly have resonances with processes that occur in real world populations, for example co-evolution and population expansions and contractions. But, for all their computational sophistication, it is debatable whether these models have told us anything new about natural systems. In fact, these models contain within them so many different variables that it is difficult to discern which of them are important determinants of the observed phenomena. I would contend that these projects have been overly concerned with creating realistic models, and have failed to identify interesting research questions to which these models should be applied. These simulations are, after all, only models; they can never approach the rich variety of forms and processes found in the real world. Rather, the purpose of models should be to create abstract forms of the real world, in which isolated processes can be studied in the absence of many other confounding factors. This is not to say that the resulting models will not be complex, rather that we should be able to clearly identify the processes from which this complexity arises.

Hogeweg and Hesper (1985; see also Hogeweg 1988, 1989) have shown that the complex adaptive systems approach can be fruitful in modelling social structure. They used bottom-up models of individual decision making to simulate the social world of bumble bees and dominance relationships in monkeys. These models can be particularly useful in testing hypotheses about individual processes within larger social structures. As far as I am aware, these types of models have not been used before to predict the social structure of extinct groups.

1.2.2. Assumption 2: The Prisoner's Dilemma is an appropriate model of cooperation.

“Game theory has great potential. Perhaps it is not too much to say that, unless and until major advances are made in game theory, the social sciences are doomed to remain but a poor relation of the physical sciences. On the other hand, our current state of ignorance on so many relevant subjects imposes heavy limitations on the extent to which game theory as it stands at present can be applied.”

(Binmore 1990 p.6)

The basis of the computer simulations used in this thesis is taken from game theory. Binmore (1990) notes how difficult it is to apply game theory to real life situations. This is because we have imperfect knowledge of the important variables within the system of interest. But, the purpose here is to extract from complex scenarios the important variables of interest, and it is to this end that game theory is most useful, as Binmore notes (1990 p.9):

“A game-theoretic study based on hypothetical data about the institutional framework may be useful, for example, as a guide to an empirical worker who is bewildered by the richness of the available data and needs assistance in making judgements about what is likely to be significant and hence worthy of close attention and what is likely to be of only secondary importance.”

Primate social groups are, indeed, “bewildering” in complexity. We require a model which will allow us to focus only on cooperative interactions in the absence of other confounding variables. It will be argued here that a game known as the Prisoner's Dilemma is ideal for this purpose. But first it is important to understand

why cooperation is such an interesting problem. From our peculiarly human perspective, cooperation seems quite logical: if everyone in a group cooperates then everyone in that group benefits and is, surely, better off than a group of individuals who act only in self-interest? To illustrate why such a view is fallacious, let us consider a hypothetical example of such a society. Imagine a group who practice extensive food sharing. Each day, every individual in the group goes out to hunt and forage and at the end of the day all of the food is pooled in a communal feast. Everyone benefits, because the quantity and variety of food is greater than any individual could have found on their own and each individual is buffered from fluctuations in foraging success. But, one individual in the group is a cheat who never foragers but still shares in the feast each day. This person gains all the advantages of group cooperation, but pays none of the costs. Since the forces of evolution are more powerful at an individual level than they are at the group level (Soltis *et al.* 1995) the cheat will do better than the rest of his or her companions. It is easy to see how such cheating behaviour, if unchecked, would proliferate and swamp the nice behaviour of the cooperators (see Dugatkin 1997 for a review of group versus individual selection in relation to cooperation).

The model developed here will consider only two-person interactions, in which the individuals concerned must decide whether to cooperate or not. Again, this scenario will be illustrated with a story: Imagine two individuals, Romeo and Juliet, who simultaneously arrive at a particularly rich food source. Both animals have two options open to them: they may either offer to share the food or they can threaten the other individual in the hope of gaining all the food for themselves. If one individual threatens, and the other offers to share (i.e. cooperate) then the aggressive individual will gain everything at the expense of the cooperator. If both individuals threaten then both do badly since they will each be forced to expend time and energy fighting for the food. Finally, if both individuals offer to cooperate, then the food is shared and both animals do quite well. We can assign pay-offs to each possible outcome as follows: the highest pay-off (5 points) applies when an animal threatens against a potential sharer; the next highest (3 points) applies if both animals share; a fairly low pay-off (1 point) applies if both individuals threaten; the lowest payoff (0 points) applies when a cooperator faces a threatener. As long as the pay-offs are ranked in this order of magnitude then this situation is equivalent to a 'Prisoner's Dilemma' (Axelrod and Dion 1988; Axelrod and Hamilton 1981; Binmore 1992, 1994; Trivers

1971). In the Prisoner's Dilemma sharing is known as cooperating, and threatening as defecting. Figure 1.2 shows the relevant pay-offs.

		<i>Romeo</i>	
		C	D
<i>Juliet</i>	C	3 3	5 0
	D	0 5	1 1

Figure 1.2: The pay-off matrix for the Prisoner's Dilemma. Cooperation (C) and defection (D) are equivalent to sharing and threatening respectively (see text).

Juliet	Romeo	Romeo's pay-off
Cooperates	Cooperates	3
	Defects	5
Defects	Cooperates	0
	Defects	1

Figure 1.3: Strategy choice in the Prisoner's Dilemma. The table shows Romeo's possible pay-offs in relation to Juliet's decision to cooperate (share) or defect (threaten). Whatever Romeo assumes Juliet will do, he will always gain a higher pay-off if he defects.

What should Romeo do, cooperate (share) or defect (threaten)? The possible pay-offs of each course of action are shown in figure 1.3. If Romeo assumes that Juliet is going to cooperate (share), then his best course of action is to defect (threaten) and thus gain 5 points (rather than 3). If, on the other hand, Romeo assumes that Juliet will defect (threaten) he should also defect: he will only gain 1 point, but this is at least better than getting nothing. In fact, whatever Romeo assumes Juliet is going to do, it is always better for him to defect (threaten). Here lies the paradox of the game. If we assume that Juliet is as rational as Romeo, then she will also conclude that her best option is to defect (threaten). The inevitable outcome is that they will both defect and gain a pay-off of just 1 point, far worse than the 3 points they would have gained if they had both cooperated.

While in the “one-shot” Prisoner’s Dilemma it is always best to defect, the repeated (or iterated) Prisoner’s Dilemma opens a doorway for cooperation to emerge. The expectation of future interactions makes cooperation an attractive option. If for two players the probability future interactions, w , is high, then there is no single best strategy. Strategy choice depends critically upon the behaviour of the other player, and the stability of a strategy depends upon the frequency of other strategies in the population (there is no evolutionary stable strategy, Boyd and Lorberbaum 1987). None the less, the higher the value of w the better it is to adopt some kind of cooperative strategy. Axelrod and Hamilton ran a series of computer tournaments in order to determine the best, most robust strategies for playing the iterated Prisoner’s Dilemma (Axelrod and Hamilton 1981; Axelrod 1984). One of the simplest and most effective is called “TIT-FOR-TAT” where a player reciprocates the behaviour of the other player in their previous game so that cooperation is rewarded with cooperation and defection is punished with defection.

While TIT-FOR-TAT has become synonymous with the Prisoner’s Dilemma it is not necessarily the best strategy, there are others that can do even better. One of the problems with TIT-FOR-TAT is that if two TIT-FOR-TAT players meet, and one of them makes a mistake, then it can result in a continuous cycle of punishment and thus low pay-offs. This continual recrimination can be avoided by TIT-FOR-TWO-TATS² which is the same as TIT-FOR-TAT but defects only after the other

² Other solutions to this problem are ‘generous’ TIT-FOR-TAT (Nowak and Sigmund 1992) and FIRM-BUT-FAIR (Freen 1996).

player has defected twice. Another problem with TIT-FOR-TAT (and also TIT-FOR-TWO TATS) is that it can be invaded by a population of players who always cooperate (ALLC) whose behaviour is indistinguishable from TIT-FOR-TAT in the absence of more nasty strategies. The problem with this is that ALLC weakens the TIT-FOR-TAT population because ALLC is vulnerable to exploitation by invading defecting strategies. PAVLOV, proposed by Nowak and Sigmund (1993) avoids this problem, as well as the problem of cycles of recrimination. PAVLOV players cooperate only if both players chose the same action in the previous round, hence they can establish cooperative relationships with TIT-FOR-TAT-like players, but will also exploit ALLC players. Even so, TIT-FOR-TAT is still a robust strategy and can be very important in establishing cooperation, in particular Nowak and Sigmund (1992) have found that it can act as a catalyst for other cooperative strategies.

Trivers brought the Prisoner's Dilemma to the attention of biologists in 1971, demonstrating its value as a model of "reciprocal altruism"³. This was particularly important in explaining how cooperation might evolve between non-relatives, following in the footsteps of Hamilton's (1964a,b) earlier work which showed the clear gene-level benefits that could arise from cooperation between kin. Trivers predicted that altruism was most likely to occur when: 1) an animal has a long life-span (i.e. w is potentially large); 2) small numbers of individuals repeatedly interact with each other; and 3) the costs and benefits for a pair of altruists are roughly similar, or if there is a high degree of mutual dependence (e.g. for avoidance of predators). As Trivers noted, most primate species fulfil all of these criteria, and thus "primates are almost an ideal species in which to search for reciprocal altruism" (Trivers 1971 p.37). Trivers' paper stimulated an enormous amount of research, both practical and theoretical. While many instances of cooperation have been observed in the field, relatively few of these obey the rules of TIT-FOR-TAT, or are clear cut cases of reciprocal altruism (these will be discussed in chapter 2). This has led to some criticism of the Prisoner's Dilemma as a model of cooperation.

Connor (1995) and Connor and Curry (1995) argue that many cases that look like altruism are actually pseudo-reciprocal since the 'altruist' also gains a benefit from the altruistic act. For instance, food calls in cliff swallows (*Hirundo*

³ Outside of the biological community, the Prisoner's Dilemma was a well known, and well studied, game well before this time. According to Binmore (1994) the game was first formulated by Dresher and Flood in 1950. It is also very similar to Maynard-Smith and Price's (1973) Hawk-Dove game.

pyrrhonota) which appear to be altruistic since they alert other birds to a food source, actually serve to increase the caller's foraging efficiency. Dugatkin *et al.* (1992) call this by-product mutualism, where selfishness results in cooperation because the environment, or some agent within it, is so adverse that it forms a common enemy. At the crux of this argument are two factors. Firstly, for an exchange to be truly reciprocal there should be a net loser and a net winner whose roles are exchanged in future interactions (Noë 1990). To clarify this issue, Nunney (1985) draws attention to the difference between strong and weak altruism. A weakly altruistic, or 'benevolent', act is one that increase the fitness of an individual but also increases the fitness of its neighbours, whilst in strong altruism there is a direct cost to the altruist. However, in practice it may be very difficult to distinguish the two, since repeated rounds of reciprocal altruism look like mutualism (Boyd 1988).

The second argument in favour of mutualism as an explanation of cooperation is that in reciprocal altruism there should be a time delay between exchange of favours (Trivers 1971 p.39):

" Reciprocal altruism can also be viewed as a symbiosis, each partner helping the other while he helps himself. The symbiosis has a time lag, however; one partner helps the other and then must wait a period of time before he is helped in turn."

Although in the Prisoner's Dilemma players appear to make their decision to cooperate or defect simultaneously, the opportunity to reward cooperation or punish defection does not present itself until the players meet again in the next game (Boyd 1988). Cooperation is contingent on the other players past behaviour and in that sense there is a time delay. Mesterton-Gibbons and Dugatkin suggest that the consideration of time scale may be a useful way of distinguishing by-product mutualism from reciprocal altruism (Mesterton-Gibbons and Dugatkin 1997 p.553):

“The importance of two time scales, a shorter one on which cooperation is perceived as a problem and a longer one in which it is perceived as the solution, is hard to overemphasise. An important difference between reciprocal altruism and by-product mutualism is that the first category always invokes a long time scale to resolve a problem of cooperation perceived on an intermediate time scale, whereas the second category often invokes an intermediate time scale to resolve a problem perceived on a short time scale.”

At the bottom line, whether a particular situation is by-product mutualism or reciprocal altruism in the longer term, in the short term, the behaviour of each player should be regarded with respect to the alternative behaviour i.e. defection. It will always pay in the short term to defect (Boyd 1988). In fact, the Prisoner's Dilemma is neither mutualistic or antagonistic but some where in-between (Sigmund 1995 p.186):

"The interests of the players are neither diametrically opposed, or identical Most social and biological interactions are closer to the Prisoner's Dilemma than to poker. Even if the interests conflict, they usually do not clash head on."

Dugatkin *et al.* (1992) believe that the major weakness of the Prisoner's Dilemma is that it does not permit communication. They argue that cooperation requires explicit signalling of intentions, such as the wish to collaborate or the threat of terminating the collaboration. Yet, the Prisoner's Dilemma model implicitly implies communication. Willingness to cooperate, forgiveness and punishment are communicated through actions rather than signals. The addition of more complex signalling to Prisoner's Dilemma models is often accompanied by partner choice and other more elaborate behaviours (Casti 1994). The addition of communication to the Prisoner's Dilemma certainly refines the game, but it does not dramatically change the nature of the results. For instance, communication allows more associative patterns of behaviour so that cooperators can avoid defectors, whilst defectors can home in on and exploit suckers (Casti 1994; Nettle and Dunbar 1997).

Noë (1990, 1992) also points out that the lack of communication in the Prisoner's Dilemma is a major short-falling, but believes that communication is not appropriate to a Prisoner's Dilemma type model. The reason for this is that cheats could send out false signals, indicating a willingness to cooperate, but would defect as soon as the other decided to cooperate. There is clearly a risk associated with communication that affects many different species in many different contexts besides cooperation. Warning signals in insects, which indicate that they are poisonous or carry a sting, are constantly evolving and changing due to mimics diluting the power of the signal. This effect has not prevented the evolution of communication, but has made its evolution a dynamic ever changing process as the signaller, the signalled and the cheaters compete in an evolutionary arms race (Dawkins, 1989). Nettle and Dunbar (1997) argue that human dialects may have emerged from just such a process.

The first primate study into reciprocal altruism was done by Packer (1977) with olive baboons. Male olive baboons, when in conflict with another male, will often solicit aid from a third, previously uninvolved, male. This action often results in support from the solicited male. Packer found that such situations arise over access to estrous females, and that on those occasions when coalitions 'won' the female, it was always the soliciting male that gained reproductive access. In other words, helping males gain no immediate benefit from the interaction, but risk substantial costs. Packer postulated that these coalitions must be reciprocal and found that individual males gave support most often to those that supported them. These results were also found by Smuts (1985) but are disputed by Noë (1990) on the grounds that the sample sizes are too small to show a reciprocal effect.

Noë (1986, 1992; see also Noë and Hammerstein 1994) argues that reciprocal altruism is not a good model of baboon coalitions because: 1) the division of benefits can range from symmetrical to very asymmetrical; 2) bargaining is crucial to the transfer of pay-offs; and 3) no two allies are likely to have the same options, moreover, the more options that you have the more power you can yield. Generally, there is considerable disagreement over whether baboons are exhibiting reciprocal altruism or not. Bercovitch (1988) has looked at coalitions in male savannah baboons, who also form alliances to gain access to estrous females. He found that whilst males had preferred allies, this preference was not necessarily reciprocal (although there were individual cases where it clearly was). While male coalitions are indubitable examples of cooperation, reciprocal altruism may be too simple to explain the complex patterns of coalition formation especially in cases where individuals can differ dramatically in their aid-giving potential.

It is, in retrospect, not surprising that the evidence for reciprocal altruism is scant and controversial (but see discussion in chapter 2). Reciprocity is expected in the same contexts as kin selection and tit-for-tat behaviour looks identical to unconditional altruism (Boyd 1992). Furthermore, reciprocal altruism becomes difficult to monitor in the wild when it involves the exchange of different cooperative acts. For example, grooming may be rewarded by help during an agonistic dispute as happens in vervets (Seyfarth and Cheney 1984) and macaques (Hemelrijk 1990, 1994). In these cases assessment of costs, benefits and fitness effects becomes difficult.

Problems in applying the Prisoner's Dilemma are further magnified when we recognise that different individuals have different abilities to give and receive aid,

depending on their sex, age and rank. For instance, a high ranking individual has the capacity to confer significant benefits to a subordinate by helping them, at a relatively small cost to themselves. On the other hand, the dominant individual may actually receive very little benefit from cooperation by the subordinate, although the costs to that individual may be great. Boyd (1992) has found that when the costs and benefits of cooperation vary in this way unbalanced reciprocity may result, where some individuals cooperate more often than others. For example, a dominant animal may cooperate infrequently with a subordinate, while the subordinate cooperates at every opportunity. In primates age, rank and sex are likely to affect fundamentally cooperative strategies. For instance, Hemelrijk and Ek (1991) found that female chimpanzees use different cooperative strategies to males. Both males and females are good reciprocal altruists when it comes to exchanging grooming. Females also exchanged grooming for support. However, the coalitionary behaviour of males was dependent upon the social context. Males only reciprocated support during periods when the dominance hierarchy was unstable. Hemelrijk and Ek suggest that contradictory results on reciprocal altruism in baboons (described above) may be caused by different social contexts.

Finally, it may be too much to expect that animals will behave exactly as game theorists predict. Binmore *et al.* (1991 p.314) note that even humans are not “natural gamblers”, capable of computing all the possible repercussions of a behaviour, and perfectly predicting the behaviours of others. Yet, humans and other animals regularly find themselves in situations that mirror the Prisoner’s Dilemma. Therefore, it is reasonable to suppose that evolution⁴ has equipped them with rules of thumb, or predispositions to behaviours, that enable them to cope with these situations. It is in predicting which ‘rules of thumb’ will confer the greatest benefits to the animal or person concerned that game theory comes into its own. Game theory looks at what people (and/or animals) ought to do, not what they actually do. However, evolution pushes organisms towards the behaviours that game theory predicts (Binmore 1990).

In sum: the Prisoner’s Dilemma encapsulates the problem of cooperation: that is, that the long term benefits of cooperation are outweighed by the short term advantages of cheating or defecting. In the iterated Prisoner’s Dilemma, cooperation can emerge if the expectation of future interactions is high. The Prisoner’s Dilemma model is usually associated with reciprocal altruism, however, there are many other

⁴ Social learning may also be important in this respect. This will be discussed further in chapter 6.

possible strategies. This fact has not been well recognised in field studies and has therefore led to rather mixed results. Social context is likely to affect the kinds of cooperative strategies that individuals employ: sex, age, status and the stability of the dominance hierarchy are likely to be especially important in primates. However, despite a vast literature exploring many different refinements to the Prisoner's Dilemma (see Dugatkin 1997 for a summary) this particular problem has received very little attention. For this reason, this research uses the Prisoner's Dilemma game to explore a particularly important social factor that is likely to affect an individual's strategy choice: gender. What kinds of cooperative strategies are best in groups of mixed sex?

1.2.3. Assumption 3: Sex differences in behaviour arise from sex differences in the energetic cost of reproduction

Trivers' parental investment theory was introduced in section 1.1. To recap, Trivers (1972) showed that breeding systems could best be understood in terms of the relative reproductive effort of both sexes. Reproductive effort measures the cost of reproduction as the extent to which a single reproductive event detracts from an individual's ability to invest in future offspring. It consists of two components, parental investment and mating costs. Because of the constraints of gestation and lactation, mammalian females are likely to invest most heavily in parental care. In contrast, males are not biologically obliged to invest heavily in offspring, and are more likely to incur costs that are related to finding, attracting and defending a mate. In short, sex differences in reproductive effort translate into sex differences in behaviour.

Reproductive effort is not an easy quantity to measure (as we shall see in chapter 4), especially since it can involve many different types of behaviour. However, there are two common currencies that cross all categories of behaviour: time and energy. Since different activities may take equivalent amounts of time, but involve very different amounts of energy (fighting, for instance, is more energetically costly than grooming) energetic costs may provide a closer approximation to the true costs of reproduction. In reality, the true cost of reproduction is impossible to measure, since it includes potential as well as actual events. For instance, a male

baboon that defends an infant from another individual may incur rather low energetic costs, but risks the potentially high costs of injury. It is, however, impossible to measure potential costs, and energetic costs may provide a meaningful estimate of reproductive effort. In fact, energetic costs associated with reproduction can be quite substantial, and influence the behaviour and reproductive success of both males and females.

The energetic cost of reproduction is rarely measured directly, however, there are many indirect indications that energetic costs are substantial. There is a considerable body of evidence suggesting that access to resources is an important factor in determining female reproductive success. McFarland (1997) found that both time to conception and infant survivorship were influenced by female body condition in pigtail macaques. Females with higher percentages of body fat conceived after a shorter time consorting with males than those females with less fat. What is more, still births, abortions and infant deaths were reduced in those females that were heavier and fatter. Improved nutrition has been found to increase infant survivorship in a number of other primate species. Among provisioned Japanese macaques at Koshima, infant survivorship to one year of age was 85.1%, compared to 31.2% when this group was not provisioned (Mori 1979; Watanabe *et al.* 1992). In vervets at Amboseli 61% of infants in the highest quality environment survived their first year, compared with just 42% in the group in the lowest quality habitat (Cheney *et al.* 1988). It is possible that availability of resources limits a mother's ability to produce milk for her offspring, for instance in baboons milk production is reduced in underfed mothers (Roberts and Coward 1985). Furthermore, a mother's ability to feed her offspring may be crucial in the long as well as short term. A ten year study on baboons by Altmann (1991) showed a correlation between an individual's diet at weaning and the number of surviving offspring born to that individual. This suggests the intriguing possibility that diet during weaning may affect lifetime reproductive success.

McFarland (1997) found that in pigtail macaques fluctuations in female body weight correspond with different reproductive stages. On this basis, McFarland concluded that lactation is the most demanding phase of the reproductive cycle. Lactation imposes enormous energetic demands on the female, and females lose weight during lactation in most wild populations (Altmann 1980; Bercovitch 1987). Muruthi *et al.* (1991) found that in baboons female energy intake increases by 57%

when pregnant or lactating. Gittleman and Thompson (1988) estimate that across all mammalian species calorific intake during lactation is between 66% and 188% greater than at other times. Increased energy intake during the reproductive cycle can minimise the impact of lactation and gestation on a female's energy reserves, allowing her to reproduce again sooner. Improved access to resources has been shown to reduce inter-birth interval in Japanese macaques (Fedigan 1997), baboons (Bercovitch 1987; Strum and Western 1982) and vervets (Lee 1987). For example, Strum and Western (1982) found that inter-birth intervals almost doubled in baboons over a five year period of declining food availability, from 17.4 months to 30.3 months. Humans are no exception; in Guatemalan and Gambian women diet supplements have the effect of shortening inter-birth interval (Chavez and Martinez 1973; Delgado *et al.* 1978; Prentice *et al.* 1986).

Availability of food and physical condition also influence age of sexual maturity and age of first reproduction (McFarland 1997). Captive primates reach sexual maturity and conceive earlier than those in the wild. For instance captive baboons (Altmann *et al.* 1977; Altmann and Alberts 1987) and chimpanzees (Coe *et al.* 1973; Goodall 1986) conceive around two years earlier than their wild counterparts. In free-ranging baboons at Amboseli, females of a group that had access to a garbage pit achieved estrous at just 3.3 years of age, around two years earlier than females in all other wild groups (Altmann and Muruthi 1988). In wild vervets, groups living in higher quality habitats have a mean age at first reproduction more than one year younger than those females in the lowest quality habitat (Cheney *et al.* 1988).

Female primates may adjust either their behaviour or their energy intake to compensate for increased energetic demands of reproduction. Lactating howler monkeys spend more time feeding than other females (C.C. Smith 1977) and in baboons feeding time increases during the later stages of pregnancy (Silk 1986). Other baboon studies have found that lactating females sacrifice either social or resting time in favour of longer feeding bouts (Altmann 1980; Dunbar and Dunbar 1988). Captive galagos and wild guenons eat food of higher protein content during pregnancy and lactation (Sauther and Nash 1987; Gautier-Hion 1980).

Taken together, the evidence clearly suggests that females incur considerable energetic costs associated with reproduction, especially gestation and lactation. Energetic costs incurred by males are likely to arise from rather different activities

but may be substantial none the less. Males in multi-male mating systems tend to have larger testes, both in primates (Harcourt *et al.* (1981) and mammals in general (Kenagy and Trombulak 1986). The energetic costs of maintaining mature-sized testes is more demanding than the energetic costs of growth (Kenagy and Trombulak 1986) and in humans sperm production ceases following dramatic weight loss (Frisch 1984). This implies that at least in some instances, males will have relatively high energetic costs associated with the production of sperm.

Males will also incur energetic costs due to the demands of courtship, mate-guarding and male-male competition. Salsbury and Armitage (1995) found that variation in energy expenditure in male yellow-bellied marmots was best explained by the number and dispersion of the females defended by males. In male red deer, grazing time is reduced to 5% during the breeding season, as compared with 44% at other times (Clutton-Brock *et al.* 1988) and male elephant seals do not feed at all during the two to three month breeding season and hence lose around a third of their body mass (Reiter 1997). In polygynous species such as red deer and elephant seals, larger males gain greater reproductive success.

In primates larger males do not necessarily have a reproductive advantage (Bercovitch 1989). Rather, factors such as age, duration of residency, coalitions with other males, friendships with females and other social skills may have a greater influence on a male primate's reproductive success than size alone. The energetic costs of these activities have not been studied. But, while male body size *per se* may not be as important in primates as in other mammals, body fat and body condition may be as important for primate males as it is for primate females. Male squirrel monkeys show seasonal fluctuations in weight, gaining at least 20% of their body weight during the reproductive period (Kinzey 1997). Bercovitch and Nürnberg (1996) found that only 8 out of 21 male vervets in their study group sired offspring. While sires and non-sires did not differ in body size, sires began the mating season with considerably more body fat than non-sires. This excess fat was lost during mating so that, by the end of the mating season, sires had the same amount of body fat as non-sires. Bercovitch and Nürnberg suggest that as with females, body fat provides males with a buffer against the energetic stress associated with reproduction. Observations on baboons support this conclusion. Alberts *et al.* (1996) found that in savannah baboons mate-guarding compromised male feeding efficiency. Packer (1977) noted a similar phenomena, commenting that consorting

males would often appear exhausted due to lack of food and sleep. Rasmussen (1985) has shown that the amount of time male baboons (*Papio cynocephalus*) spend feeding increases with rank, and that during consortships higher ranking males suffer a greater decrease in feeding time compared with low ranking males. Similar energetic costs are likely to apply to other primate genera. In gold lion tamarins male body mass decreases by 12% during June, when male aggression chasing and mate guarding is greatest (Dietz *et al.* 1993).

In the light of these studies it would be fair to suggest that males, as well as females, must meet the energetic costs of reproduction if they are to reproduce successfully. There are very few studies that have compared male and female energetic costs although there are a handful of observations that suggest that they may be greater for females. Hiraiwa-Hasegawa (1997) observes that in many species adult females feed for longer than males, and that they prefer higher-calorie foods, and suggests that “this is probably due to their higher calorific need for maintaining pregnancy and lactation” (Hiraiwa-Hasegawa, 1997 p.72). Female siamangs feed for longer periods and at a faster rate than males (Chivers 1977), and female mangabeys spend a greater proportion of time feeding than males (Waser 1977). It has been suggested that female vervets (Baldellou and Adan 1997; Lee 1984) and baboons (Dunbar and Dunbar 1988) spend more time feeding in the mating season in order to outweigh the costs of reproduction.

Human women are consistently found to be fatter than men (McFarland 1997). For instance Forbes (1987) found that between the ages of 16 and 18 the body composition of a well-nourished woman is 26-28% fat, whilst that of a man is about 14% fat. It is likely that in human females a certain minimal level of body fat is required for successful ovarian function (Frisch and Revelle 1970; Frisch 1988) and lactation (McFarland 1997) although the exact nature of this relationship may be quite complex (McFarland 1997; Pond 1997). Sex differences in the amount of fat in non-human primates have also been found (e.g. baboons, Rutenberg *et al.* 1987; pigtail macaques, Walike *et al.* 1977; orangutans, Morbeck and Zihlman 1988) although not to the same magnitude as is found in humans. Again, these studies suggest that energetic demands of reproduction are greater for females. However, none of this evidence is conclusive since each study focuses on only a single aspect of reproduction whereas a true measure of energetic costs should account for all activities that contribute to reproductive success.

In sum, there is a growing body of evidence demonstrating that both males and females incur an energetic cost of reproduction. Since the ability to pay this cost can have a serious effect on reproductive success it is surprising that there has been very little research that explores either how energetic costs for males and females compare, or how sex differences in energetic costs can affect behaviour. In part, this is because energetic costs are very difficult to measure in practice and in this respect modelling is a particularly valuable means of formulating predictions. Therefore, my third and final assumption, that “sex differences in behaviour arise from sex differences in the energetic cost of reproduction”, is a hypothesis rather than a fact. It is this hypothesis that lies at the heart of this research and from which its central question arises: How do sex differences in the energetic cost of reproduction affect the evolution of cooperation, and ultimately the structure of social groups.

1.3. From Theory to Practice

In this thesis models will be developed, based on the Prisoner's Dilemma, which examine how the energetic costs of reproduction for males and females affect the evolution of cooperation. In doing so, a framework will be built from which we can begin to understand how sex differences in energetic costs affect the structure of social groups. This work is particularly relevant with respect to the evolution of hominid social groups, which are in many ways so different from those of other primates because of the great changes in energetic costs that have arisen during hominid evolution.

Since the energetic cost of reproduction is an abstract and universal variable there is no reason why these models could not be applied to other, non-primate species. Indeed, since many of the ideas dealt with here are new, it will be necessary on occasion to use data from the non-primate literature for additional support. In some cases my choice of examples may appear rather *ad hoc*, and arguments developed should certainly be taken as suggestions or predictions, rather than conclusions. My only claim is that this work is an attempt to create a general model, and its application to particular situations awaits further testing.

The thesis will proceed as follows. In chapters 2 and 3 computer models are used to examine the conditions under which different cooperative strategies emerge. It will be shown that differences in the energetic cost of reproduction for males and females affect cooperative strategies both between members of the same sex, and of different sex. In the fourth chapter data from living primates will be used to estimate energetic costs of reproduction for each sex for a wide variety of species. These estimates will then be used to test the predictions that arise from the previous chapters. Of particular interest will be the conditions under which male care giving occurs. Chapter 5 is, again, largely theoretical and explores the robusticity of the model under different environmental conditions. In particular, how environment quality and seasonality affect cooperative strategies. Finally, in chapter 6, we will return to the evolution of hominid social groups.

CHAPTER 2

The Evolution of Cooperation in Groups of Mixed Sex

The Prisoner's Dilemma is an excellent tool for modelling the evolution of cooperation as it reflects both the long term benefits of cooperation and the short term benefits of defection. However, its weakness is that it assumes that all individuals are identical, while in the real world differences in rank, age and sex are likely to affect an individual's capacity both to give and receive aid (see chapter 1). This chapter examines how sex differences affect the evolution of cooperation, where it is assumed that the fundamental difference between males and females is in their energetic cost of reproduction. This assumption has been discussed in chapter 1, and will be examined in detail in chapter 4.

A model of cooperation will be developed for a population of mixed sex, where individuals interact regularly, and have a memory of the outcomes of these interactions. The model, as described below, forms the basis of most of the experiments presented in this thesis. All experiments use the principal of natural selection to find the fittest strategies within a population of individuals. Every individual has the programming equivalent of a genetic code which not only determines its behaviour, but is also passed onto its offspring through a process analogous to sexual reproduction. Over thousands of generations those individuals with the fittest genetic codes have the most offspring, so that the model evolves over time.

2.1 The Basic Model

Every model in this thesis has the same general format, which is described here. They are all evolutionary models in which a population of agents is created, and the most successful agents are those that produce the most offspring. In order to reproduce agents must pay a reproductive cost, RC, and the only way to pay this cost is to gain points by playing the iterated Prisoner's Dilemma with other members of the population. When an agent has accumulated enough points it is able to reproduce with an agent of the opposite sex who also has enough points. Hence the players with the best strategies for playing the Prisoner's Dilemma will have the most offspring. Each agent has a set of chromosomes or 'strategy strings' which dictate its strategy for playing the game. During reproduction the strategy strings of each parent are 'crossed over' (see fig. 2.1) and may mutate (with a chance of 1/5000). In this way each offspring inherits a combination of its parents strategy strings and strategies evolve over time. The model is, in effect, a genetic algorithm (Goldberg 1989; Holland, 1992a, 1992b) to determine the best strategies for playing the Prisoner's Dilemma in groups of mixed sex.

A player's strategy is determined by two factors: 1) the history of interactions between the players, and 2) the sex of the players. Ikegami (1993) has found that robust and unexploitable strategies for playing the iterated Prisoner's Dilemma ideally require a memory of the outcomes of the last two games played (strategies with longer memory lengths were often too specific and thus inflexible). Since this involves recording two moves (a play of cooperate or defect) for each player it is called a memory length of size 4. Following Lindgren (1991), the strategy string provides a response for every possible situation that could arise from a memory length of 4, i.e. 16 possible situations, where a response is encoded as '1' for cooperate and '0' for defect. For example, if the point on the strategy string labelled 'CCCC' reads '1', this is interpreted to mean "if both players cooperated on their last two moves, then cooperate on the next move" (fig. 2.2). Aside from these 16 alleles or bits, the strategy string must also provide one allele for when an agent meets a new player for the first time (either 'always cooperate on first move' or 'always defect on first move'), and four alleles for the second game (responses to histories CC, DD, CD and

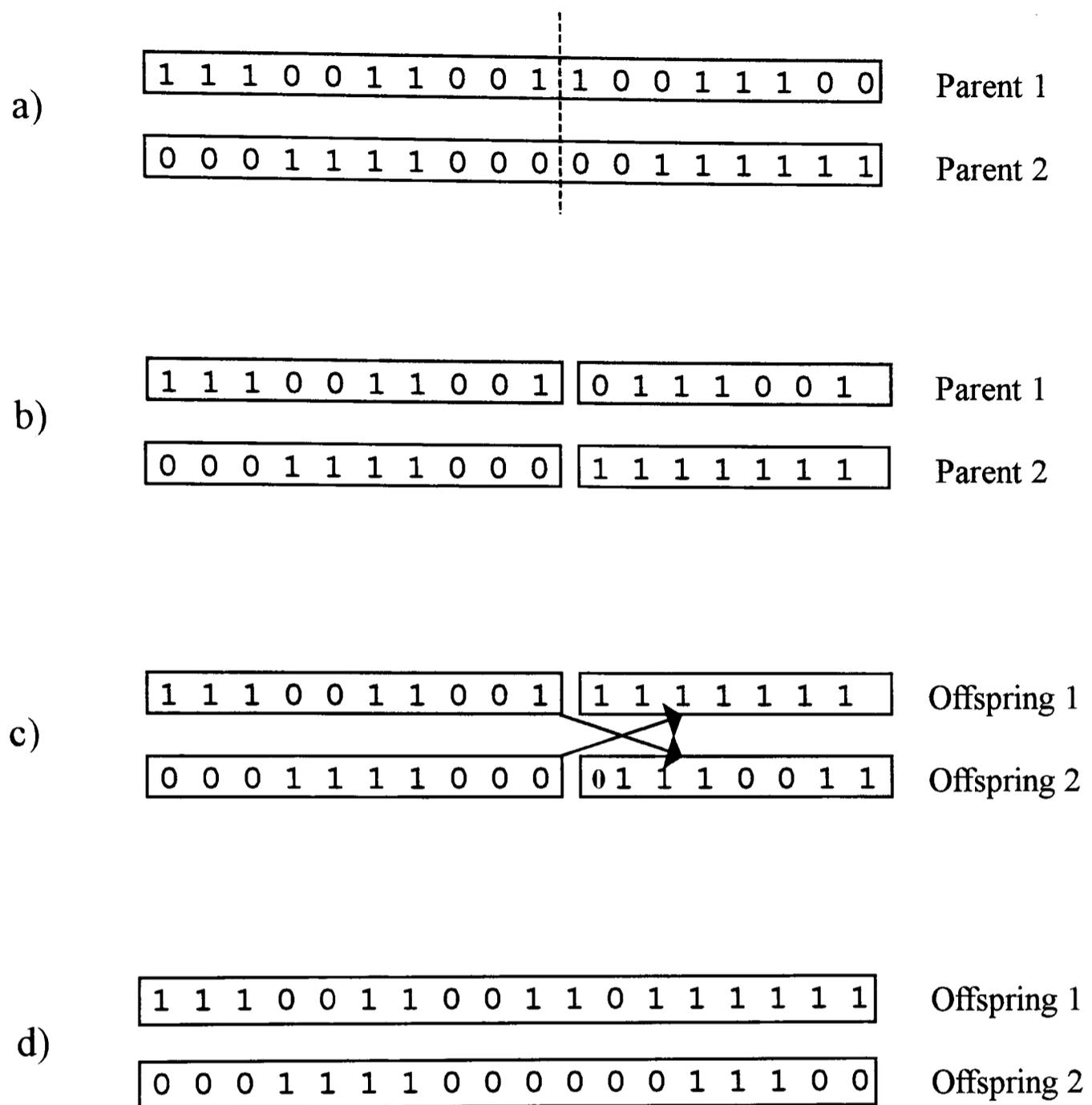


Figure 2.1: Reproduction by crossover

Reproduction involves crossover of the parent's strategy strings. A random point is chosen at the same point on each string (a), and the parent strings are cut (b). The two parts of the parent strings are swapped (c) to produce two new offspring (d).

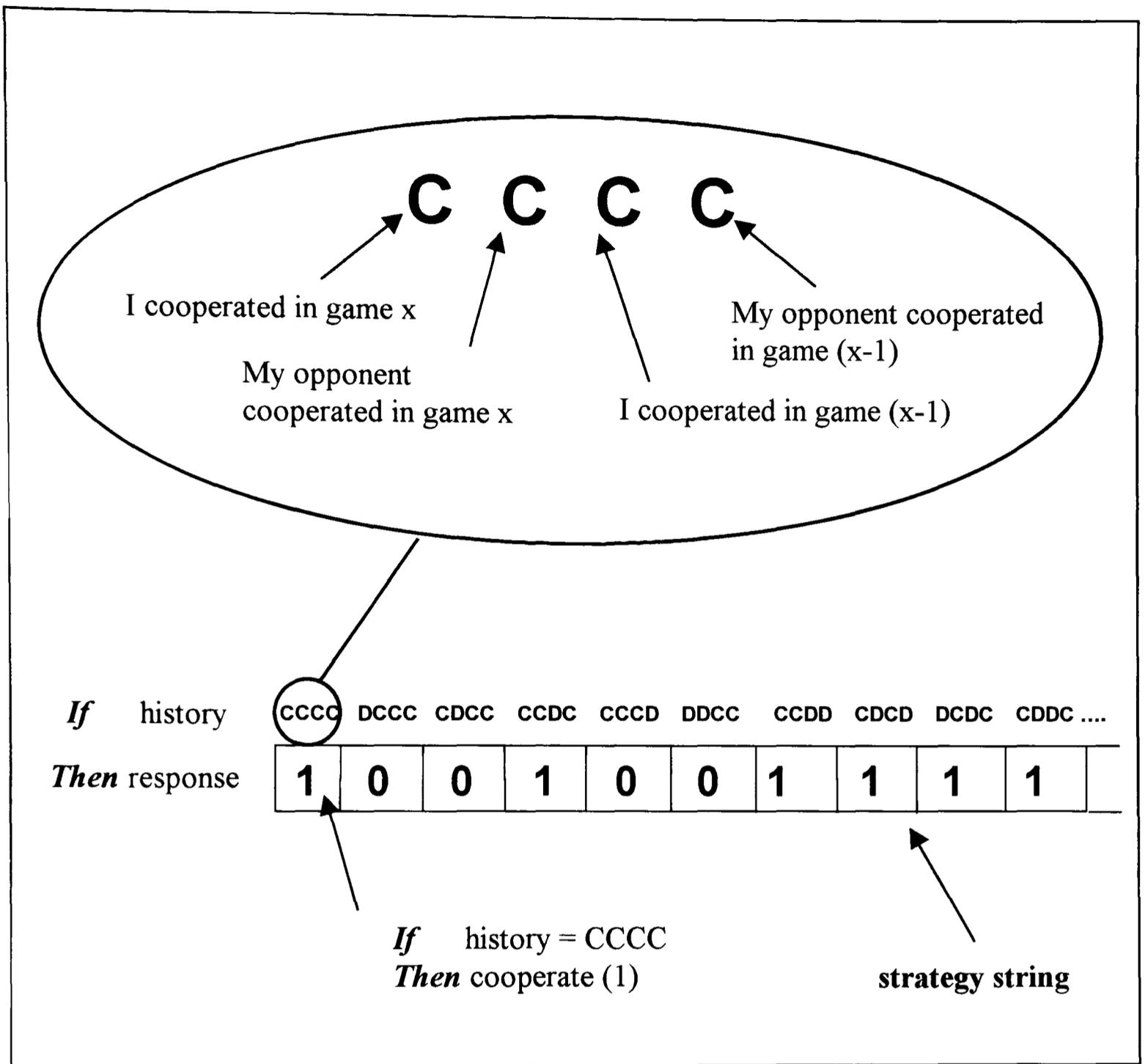


Figure 2.2 The strategy string

The strategy string must provide a response for every possible situation that can arise during a game, where 1 codes for cooperate and 0 codes for defect. The strategy string is essentially a look-up table. In this case the rule 'If there has been a history of CCCC then cooperate' is being activated.

DC). In total the strategy string must be 21 bits long ($16 + 1 + 4$) to cover all possible situations.

The other important factor is the gender of each player. It cannot be assumed that a female will behave in the same way with another female as she would with a male. Four possible situations could arise, which from the point of view of the agent are:

- (1) I am male, my opponent is male
- (2) I am female, my opponent is female
- (3) I am male, my opponent is female
- (4) I am female, my opponent is male

Each player carries four strategy strings, one for each of these possible situations. Although a male, for instance, only requires strategy strings 1 and 3, his daughters will require information from strings 2 and 4. By carrying all 4 strategy strings a player contributes to the behaviour of all its children regardless of their sex.

Reproduction occurs through crossover and mutation of the strategy strings. Crossover is an important part of this process as it creates new strategies through combination of other, previously successful strategies. During reproduction there is also a chance that one of the alleles on the strategy strings will mutate, that is switch from cooperate to defect or visa versa. These mutations create “noise” in the model which prevents strategies becoming fixed at sub-optimum equilibrium. This means that the model converges on good strategies more quickly (Binmore and Samuelson 1997). In a population of 650 agents, each of which is comprised of 84 (4×21) different alleles, a mutation rate of $1/5000$ yields around 11 mutations per generation.

The program, written in C programming language, is summarised in fig. 2.3. At the start of each experiment 650 agents are created randomly, i.e. their strategy strings are generated at random and they are assigned a sex. Each agent also has a score, which at the start of the experiment is 0. Also at the start of the experiment the cost of reproduction is set for males and females (MRC and FRC respectively). Two agents are then selected at random to play 100 rounds of the Prisoner's Dilemma. They gain points according to the pay-off matrix in fig. 1.2 and these are added to

```

Start
User sets female cost of reproduction (FRC).
User sets male cost of reproduction (MRC).
Generate 650 agents at random, where each agent has:
    - 4 strategy strings.
    - sex (male/female).
    - score = 0.

set generation counter = 0

While generation counter < 20,000 do this:
{
    set offspring counter = 0
    while offspring counter < 650 do this:
    {
        1. Pick two agents at random.
        2. These agents play 100 games of the Prisoner's Dilemma
           according to their strategy strings. Each game is scored
           according to the pay-off matrix in fig. 1.2. Points gained are
           added to the each agent's score.
        3. Pick two new agents at random.
        4. If agents are of opposite sex, and each have enough points
           to reproduce (FRC or MRC) they reproduce by crossover
           and mutation of their strategy strings.
           Two new offspring are added to a separate offspring array
           (randomly assign offspring sex).
           FRC or MRC is subtracted from each player's score.
           The offspring counter is increased by +2.
    }
    if offspring counter >= 650 do this:
    {
        Replace adult population with offspring.
        Set offspring counter = 0.
        Set all scores = 0.
        Generation counter is increased by +1.
    }
}
If generation counter = 20,000 do this:
{
    Collate and print results.
    End.
}

```

Figure 2.3: The basic model

The outline for the basic program, used in most of the models described.

their score. Two *new*¹ agents are then selected, and if they are of opposite sex, and each have enough points they reproduce to create two new offspring. The cost of reproduction (MRC or FRC) is deducted from each player's score according to their sex and they are returned to the pool of agents. The offspring are randomly assigned a sex and put into an offspring array. Any single agent may reproduce several times, provided it has accumulated enough points during games of the Prisoner's Dilemma. This process of interaction and reproduction continues until 650 new offspring have been created. At this point the first generation is complete, and the offspring become the new parent population who begin a new cycle. This continues for 20,000 generations.

It is important to understand that in this model, the cost of reproduction is the minimum amount of energy required to produce an offspring. Investment below the minimum value would result in the death of the infant, and it is assumed that agents do not waste energy (points) in this way. Agents could invest more than the minimum amount of energy. Instead it is assumed here that any excess energy is conserved and contributes to the production of the next offspring. For example, if the cost of reproduction is 500 and an agent has 700 points, after reproduction its score will be reduced to 200 points and it must gain only another 300 points (through games of the Prisoner's Dilemma) in order to reproduce again.

The programs were run on 486 PCs. Simulations would take anywhere from a few hours to a few days to complete. Each program was extensively tested by fixing strategy strings to values in which there were known outcomes, and by meticulously following through each stage of interaction and reproduction when strategy strings were randomly generated.

¹ It is important to note that in this experiment agents are likely to interact with, and reproduce with, different partners.

2.2 The Control Experiment

2.2.1 Method

The experiment was first run with male reproductive cost (MRC) equal to female reproductive cost (FRC). Since this makes males indistinguishable from females the program was simplified. Agents were not assigned a sex, and were given only one strategy string which they used in all situations. This means that strategies are based solely on the history of the interactions, not the sexes of the players. This functioned to reduce the running times of the programs², and also to simplify the processing of results. The program code and outline are given in Appendix 1.

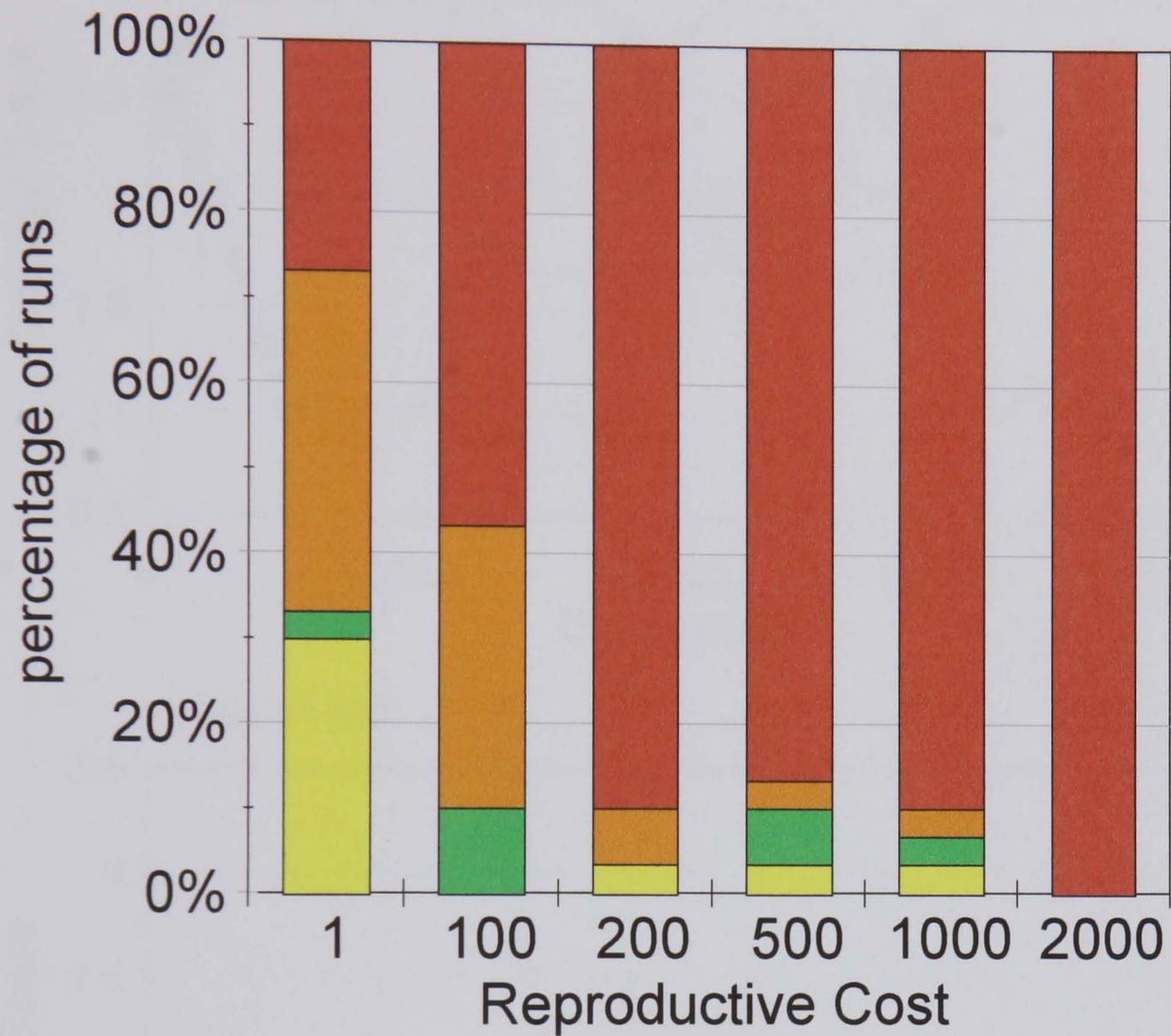
The simulation was run for reproductive costs of 1, 100, 200, 500, 1000 and 2000. The results are analysed using the average score per player per game of Prisoner's Dilemma over the entire experiment. For example, an average score of 3.00 would indicate that players are cooperating, while an average score of 1.00 would show that players are defecting (see the payoff matrix in fig. 1.2). Intermediate scores represent intermediate behaviours. Each control experiment was run 30 times.

2.2.2 Results and discussion

The results are presented as a percentage bar chart (fig. 2.4) showing the percentage of simulations where individuals evolved to be “defectors” (average score = 1.00 - 1.49), “weak defectors” (average score = 1.5 - 1.99), “weak cooperators” (average score = 2.00 - 2.49) and “cooperators” (average score = 2.5 - 3.00) for different costs of reproduction. These categorisations are used throughout this thesis, along with two further categories: “suckers” (average score < 1.00) and “exploiters” (average score > 3.00). For brevity these average scores are summarised as <1.00, 1.25, 1.75, 2.25, 2.75 and > 3.00. Note that some of these scores are not obvious outcomes of the Prisoner's Dilemma pay-off matrix, and this is because over repeated games many different average scores are possible. For example if on the first turn each player cooperated, and on the second each player defected, and on the third each player cooperated and so on, after 100 games they would have scored 200 points each, or an average of 2.00 points per game.

² In general, each experiment was run for 20,000 generations at least 150 times. Each run lasts from four hours to two days depending on the model and the parameters used.

		Opponent	
		C	D
Player	C	3	0
	D	5	1



Average score per player, per game:

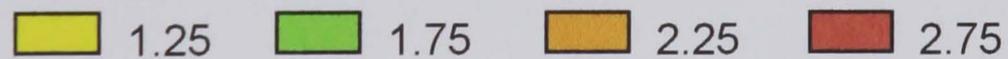


Figure 2.4: The Control Experiment

Each bar represents a summary of the average scores over 30 simulations. An average score of 1.25 (interval 1.00 - 1.49) indicates most individuals were defectors, 1.75 (1.50 - 1.99) indicates weak defection, 2.25 (2.00 - 2.49) indicates weak cooperation and 2.75 (1.50 - 3.00) indicates cooperation. For example, at RC = 1, in 30% of experiments the average score per agent per game was 1.25, which means that in most of these games players were playing a strategy of defection.

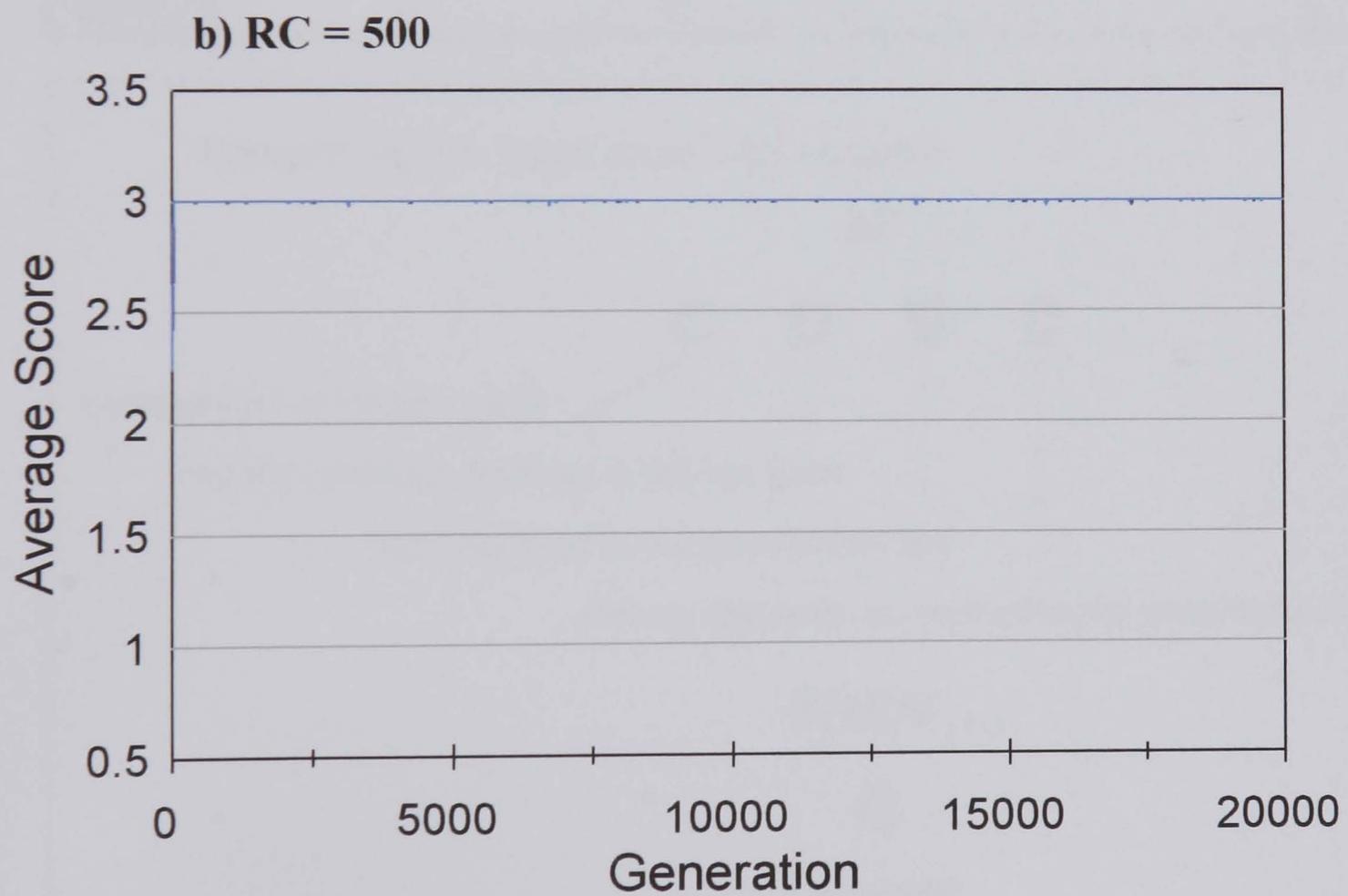
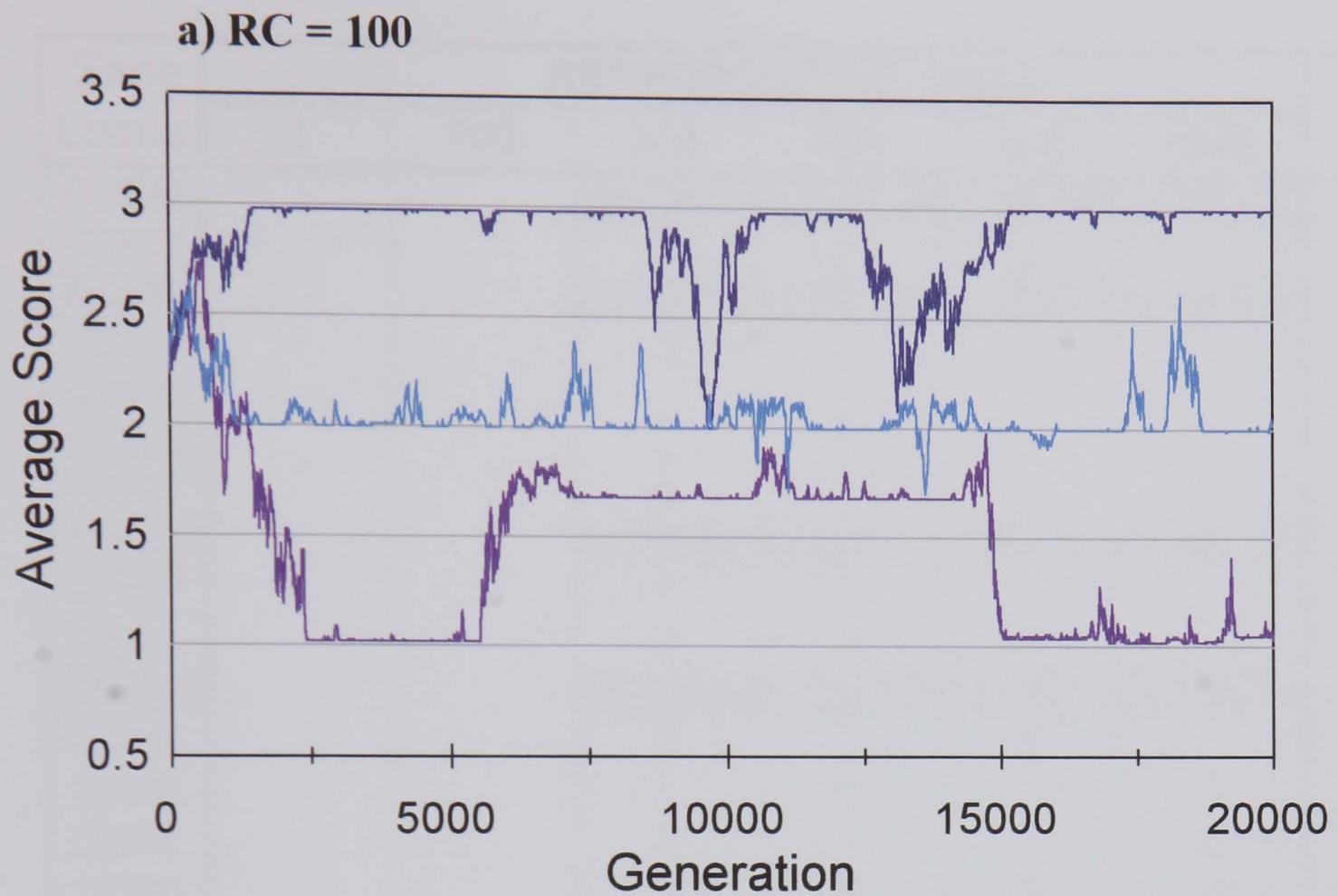


Figure 2.5: Fluctuations in average score over the course of an experiment.

Each graph shows three examples of how the average scores change over 20,000 generations when scores are: (a) low $RC = 100$; and (b) high $RC = 500$.

Gene Locus	REPRODUCTIVE COST						TFT
	1	100	200	500	1000	2000	
CCCC			C	C	C	C	C
DCCC			C	C	C		C
CDCC			D	D	D	D	D
CCDC			C				C
CCCD							C
CCDD			C	C		C	C
DDCC			C				D
CDDC			D	D	D	D	D
DCCD			C	C			C
DCDC			C	C			C
CDCD			D	D	D	D	D
CDDD			C		D		D
DCDD			C	C		D	C
DDCD			D		D	D	D
DDDC			C	C	D	D	D
DDDD			C	C	C	D	D

Interpreting the 'gene locus', an example:

IF

C D D C
 I cooperated in the last game / | | |
 and my opponent defected in the last game | | |
 and I defected in the game before last | | |
 and my opponent cooperated in the game before last | | |

THEN

C
 cooperate

Table 2.1: The most common alleles on the strategy string

A gene locus is described as cooperative (C), or defective (D), if cooperation or defection is the most common allele at that locus in at least 60% of experiments. The columns for RC = 1 and RC = 100 are blank because there was no strong selection for either allele at any locus. The shaded rows indicate those cases where there is strong selection for a particular allele at reproductive costs greater than, or equal to 200. TFT shows the alleles expected for a TIT-FOR-TAT strategist.

A reproductive cost of 1 is practically no cost at all, and as would be expected no particular strategy is selected at this cost. Around 25% of simulations resulted in the evolution of defection strategies, while a similar number evolved cooperative strategies. At a reproductive cost of 100, cooperation is more common, evolving in around 50% of experiments. At higher reproductive costs there is strong selection for cooperation. When the reproductive cost is greater than or equal to 200, in almost every case some kind of cooperative strategy evolved. This clearly indicates that a reproductive cost of 200 marks the threshold, at or beyond which cooperation is strongly selected.

Fig. 2.5 shows how typical simulations progress over 20,000 generations. Fig. 2.5a gives 3 examples of how the average scores fluctuate when reproductive cost is low ($RC=100$). The graphs are erratic, indicating that the populations never fully stabilise onto any one strategy, and new mutations can easily invade the population. In contrast, at high RC (e.g. $RC = 500$, fig. 2.5b), all experiments quickly stabilise on a strategy of cooperation which is very hard to invade. This suggests that as the selection pressure on agents increases (as the cost of reproduction increases) the model stabilises more quickly onto good equilibrium.

Given that cooperative strategies are being selected as the cost of reproduction increases, what kinds of cooperation are being favoured? Are the agents reciprocal altruists? Does TIT-FOR-TAT evolve? In order to answer these questions, for each experiment, the frequency of cooperate alleles, averaged over the whole experiment (i.e. 20,000 generations) was calculated for each of the 21 gene-bits on the strategy string. For instance, if every individual in every generation in every experiment had a cooperate allele at the gene CCDD, the frequency of cooperate alleles at CCDD would be 100% indicating strong selection for cooperation at this locus. The null hypothesis is that there is no selection pressure, which would mean we would expect 50% of alleles at this locus to be cooperate, and 50% to be defect. The results are summarised in table 2.1. If the frequency of cooperate alleles is greater than 60%, then that locus is described as being selected for cooperation (C). If the frequency is less than 40%, then that locus is described as being selected for defection (D).

When reproductive costs are low ($RC=1$, $RC = 100$) there is no consistent selection for either cooperation or defection, at any locus, across the experiments (indicated by the blank columns in table 2.1). This does not mean there is no selection

within a simulation. Rather, because each run is unique and there are many different possible strategies, no single strategy is emerging as the best. When reproductive costs are high, that is greater than 200, strong general patterns do emerge. Cooperation is strongly selected at the locus CCCC, i.e. runs of cooperation are being rewarded with cooperation. Defect alleles are dominant at loci CDCC, CDDC and CDCD, i.e. if an agent cooperates and its opponent defects it will reply with defection. It appears that players are rewarding co-operators and punishing defectors, which is consistent with a strategy of TIT-FOR-TAT (see table 2.1).

There is an interesting way in which the strategies appear to differ from TIT-FOR-TAT. In three out of four cases at high cost, cooperation is the dominant allele at the DDDD loci. This means that if both players have played defect for the previous two rounds they will cooperate. If they were playing TIT-FOR-TAT we would expect defection after a run of defection. This result was also found by Lindgren (1992), and indicates a capacity for 'forgiveness'. Its principle advantage is that two TIT-FOR-TAT players do not become locked into a cycle of punishing defection with defection following a mistake (or mutation). This is a very interesting result. One of the very few strategies that is known to beat TIT-FOR-TAT is generous TIT-FOR-TAT (Nowak and Sigmund 1993) which occasionally forgives defections. Nowak and Sigmund (1993) found that in a world where players occasionally make mistakes generous TIT-FOR-TAT out-competes TIT-FOR-TAT. It appears that this model is very good at discovering successful strategies.

Although the strategies that evolve for reproductive costs between 200 and 2000 are broadly similar, there are some subtle differences. Defect alleles are far more common when $RC = 1000$ and $RC = 2000$ as compared with lower reproductive costs. As reproductive cost increases players become much tougher on defectors and more likely to exploit potential suckers. This is reminiscent of another strategy called Pavlov, or 'win-stay/lose-shift' (Nowak and Sigmund 1993). Pavlov is a nice strategy that reciprocates cooperation, punishes defectors and is forgiving like generous TIT-FOR-TAT. However, if Pavlov finds a sucker that will always cooperate, it will keep on defecting and exploit that player. It seems that the higher the cost of reproduction, the greater the incentive to find winning strategies.

2.2.3 Summary: Control experiment

The results above show that as the cost of reproduction increases players are more likely to behave cooperatively during the iterated Prisoner's Dilemma. Furthermore, increasing the cost of reproduction effectively strengthens the selection pressure to find good strategies: populations fix on good solutions in fewer generations, and are more resistant to new mutations. Variations on the theme of TIT-FOR-TAT dominate over nastier strategies. At high reproductive costs players are likely to forgive runs of defection, although as reproductive cost increases players are also more likely to exploit suckers. The emergence of forgiveness and exploitation in these experiments is an indication of the power of this technique for discovering good strategies.

The results provide a benchmark for looking at a population where there is an imbalance in male and female reproductive cost, and indicate that $RC=200$ is the cut-off value, at or beyond which, reciprocal altruism is expected.

2.3: The Evolution of Cooperation in Groups of Mixed Sex (Model 1)

2.3.1 Method

This model follows exactly the format described in section 2.2 (the basic model). An outline of the program, and the program code, is given in appendix 2. In these experiments male and female costs differ, and the cooperative and competitive strategies that emerge are compared with the control experiment. The results are very surprising: strategies deviate greatly from expectations, not only when males play females but also in games between members of the same sex. In all of these experiments female cost (FRC) is kept constant at $FRC = 1000$, while male cost (MRC) is varied between $MRC = 1$ and $MRC = 600$. As in the control experiment, results are summarised as the average score per player per game recorded over the entire simulation (see section 2.1). The most common strategies have also been determined using the same methodology as used in the control experiment (again, see section 2.1). Results will be described by interaction type.

Note that the experiments were also repeated for different population sizes, numbers of interactions (i.e. the number of rounds of the Prisoner's Dilemma that a pair play) and mutation rates. None of these factors were found to affect the results in any important way. At smaller population sizes the time it takes to produce a new generation is less and so the simulation runs much more quickly. At higher mutation rates new strategies are generated more quickly, and this speeds up the rate at which new strategies are selected. However, the types of strategies that evolve are similar regardless of mutation rate. Also, the affects of mutation rate and population size interact: small populations with high mutation rates will have similar numbers of mutations per generation as large populations with low mutation rates.

2.3.2 Female-female interactions

Interactions between two females evolve in exactly the way expected from the control study at $FRC = 1000$. Fig. 2.6 compares the distribution of average scores from the control experiment ($RC = 1000$) with this experiment when MRC is at its highest and lowest values (1 and 600). These graphs show that female-female interactions are unaffected by the level of male reproductive cost, and that when female cost is high females almost always adopt a strategy of TIT-FOR-TAT against other females.

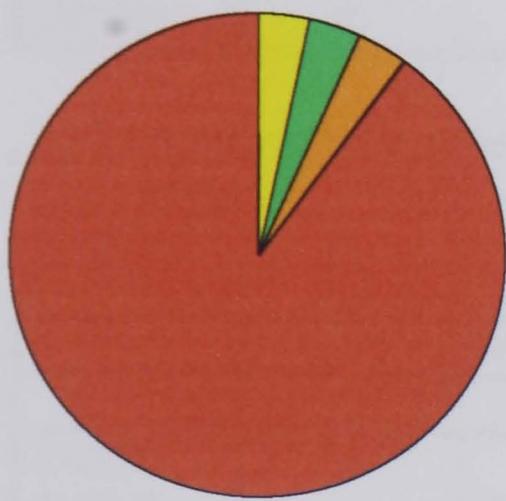
The strategies used by females are very similar to TIT-FOR-TAT, as would be expected from the control experiment at $RC = 1000$ (see table 2.2a). Note that in this instance the capacity for “forgiveness”, that is, cooperating after runs of defection, does not evolve as it did in the control experiment.

2.3.3 Male-male interactions

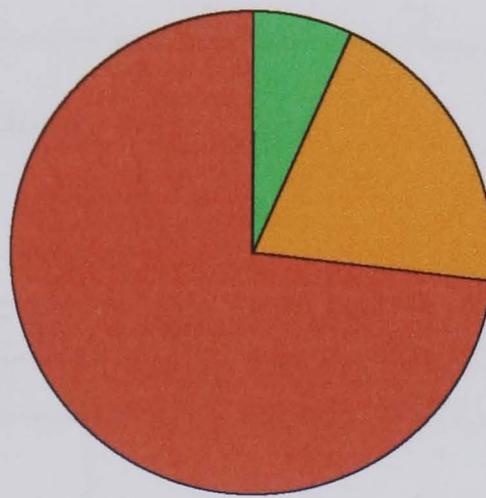
Interactions between males are considerably different from those expected on the basis of the control study and are indicative of considerable competition between males (fig. 2.7 and table 2.2b). When $MRC = 1$ (2.7a), the expected and observed results are similar, however at $MRC = 100$ and above the observed scores are much lower than those expected from the control experiment. For instance, at $MRC = 100$ (fig. 2.7b), cooperation is expected in more than half of the experiments, but actually evolved in less than a quarter. The control experiment strongly predicts cooperation when $MRC \geq 200$, yet in the mixed sex environment when $MRC = 200$ (fig. 2.7c) reciprocal altruism was the dominant strategy in just 27% of the experiments. Referring to table 2.2b, cooperation is not strongly selected at any gene-locus when $MRC = 200$, not even after runs of cooperation (gene locus CCCC).

Even at $MRC = 400$ (fig. 2.7d) males cooperated in less than half of the runs and adopt nastier strategies than TIT-FOR-TAT (table 2.2b). While these males are likely to cooperate after runs of cooperation (CCCC), there is strong selection for defection at the gene loci CCDC, CCCD and CCDD. That is, males are obeying the rule “if both players cooperated in the last game then defect”. This strategy is quite opposite to how a TIT-FOR-TAT player would react. Only at very high reproductive

		Opponent	
		C	D
Player	C	3	0
	D	5	1



Expected



**FRC = 1000
MRC = 1**



**FRC = 1000
MRC = 600**

Average score per player, per game:



Figure 2.6: Female-female interactions (FRC = 1000)

Each pi-chart summarises 30 experiments in terms of the average score per player per game of Prisoner's Dilemma. In nearly every experiment females were reciprocal altruists.

	MALE REPRODUCTIVE COST					TFT
	1	100	200	400	600	
CCCC	C	C	C	C	C	C
DCCC	C	D	C	C	C	C
CDCC	D	C	D	D	D	D
CCDC	D	D	D		D	D
CCCD		C				C
CCDD		C	D			C
DDCC		C				C
CDDC	D	D	D	D	D	D
DCCD		D	C	C		C
DCDC	D		D	D	D	C
CDCD	D	D	D	D	D	D
CDDD	D	D	D	D	D	D
DCDD		C				D
DDCD	D	D	D	D	D	D
DDDC	D	D	D	D	D	D
DDDD	D	D	D	D	D	D

a) Female-female interactions

	MALE REPRODUCTIVE COST					TFT
	1	100	200	400	600	
CCCC				C	C	C
DCCC	D	D				C
CDCC		D	D		D	D
CCDC				D		C
CCCD			D	D	D	C
CCDD		D		D		C
DDCC					D	D
CDDC		D	D	D	D	D
DCCD						C
DCDC	D			D		C
CDCD		D	D	D	D	D
CDDD			D	D		D
DCDD	C				D	C
DDCD			D	D	D	D
DDDC					D	D
DDDD	D			D	D	D

b) Male-male interactions

Table 2.2: The most common alleles on the (a) female-female and (b) male-male strategy strings.

The tables show the most common alleles for different values of male reproductive costs where female reproductive costs are constant at FRC = 1000. The table should be interpreted in the same way as table 2.1.

		Opponent	
		C	D
Player	C	3	0
	D	5	1

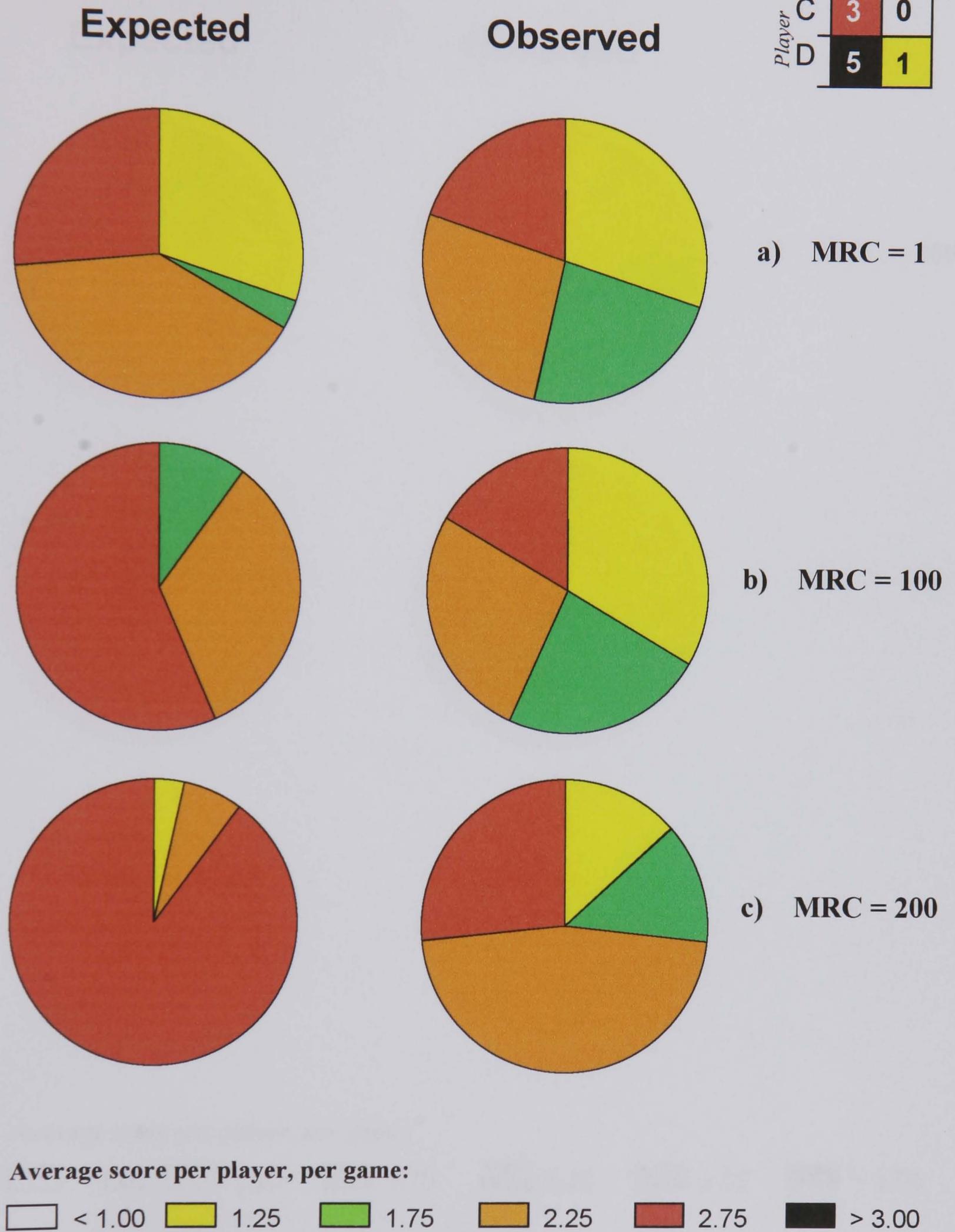


Figure 2.7: Male-male interactions (FRC = 1000)

Expected results are derived from the control experiment.

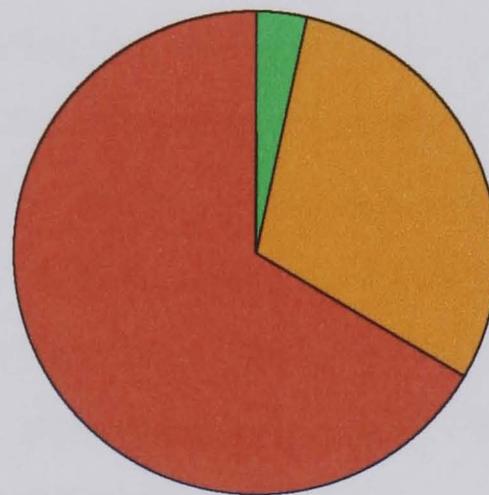
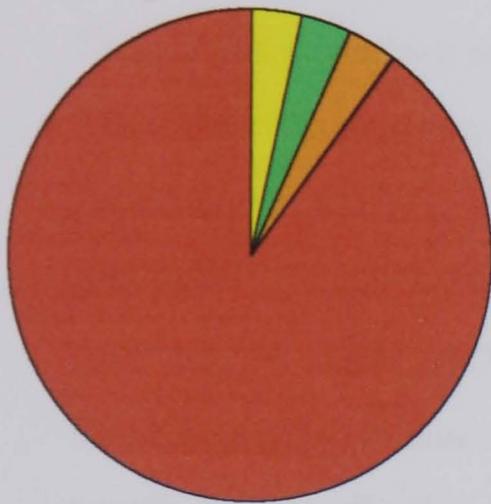
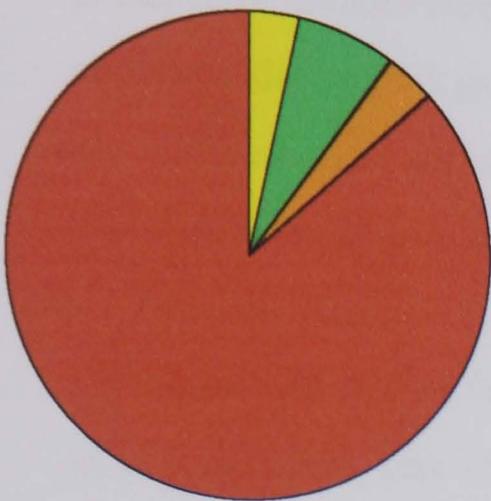
		Opponent	
		C	D
Player	C	3	0
	D	5	1

Expected

Observed

d) MRC = 400

e) MRC = 600



Average score per player, per game:



Figure 2.7: Male-male interactions (FRC = 1000) continued

Expected results are derived from the control experiment.

costs do males tend to cooperate. At $MRC = 600$ males evolved cooperative strategies in around two thirds of the experiments.

Overall these results indicate that males behave much less cooperatively in the presence of females than they would in a single sex population. Even in this relatively simple model there is greater competition between males than between females due to sex differences in the energetic cost of reproduction. For females, gaining enough points to reproduce is the primary concern. Males also have to acquire enough points to meet the male cost of reproduction by the time that the females are ready to reproduce. But, if the female cost of reproduction is much higher than the male cost of reproduction, this should be a relatively simple task. Males may stand a better chance of maximising their fitness if they prevent other males from acquiring points. This means that males may be defecting in order to minimise their opponent's fitness, rather than to maximise their own. Another factor is that at lower values of MRC the selection pressures on male strategy strings are considerably weaker than those acting on female strategy strings. Whether or not a male scores 100 points or 300 points in each bout of male-male interactions may make little difference if it takes females 3 or 4 bouts of interactions to gain the 1000 points required to reproduce. Thus, males may be able to afford more risky, competitive strategies.

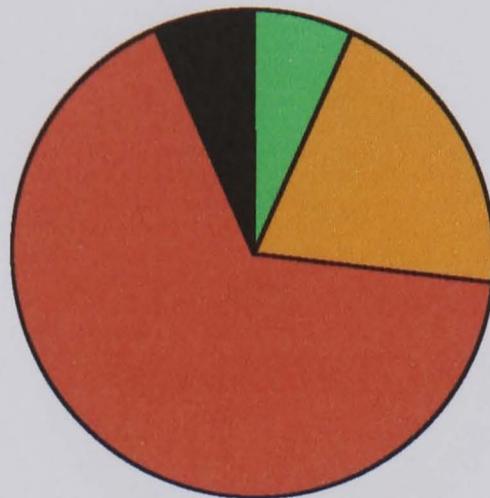
2.3.4 Mixed sex interactions

Interactions between males and females are far more complex than those of single sex interactions and are crucially dependent on the ratio of male and female reproductive costs. Depending on the ratio of FRC to MRC three different patterns of behaviour emerge (fig. 2.8). Reciprocal altruism evolves when MRC approaches FRC, for example when $MRC = 600$ both males and females participate in a reciprocally cooperative relationship in two-thirds of the experiments (fig. 2.8a). The second pattern occurs when MRC is greater than 100, but less than 600. There is considerable variation between these experiments indicating a wide variety of behaviour patterns and in many cases high levels of competition (figs 2.8b & c). At $MRC = 400$ (fig. 2.8b) while the overall level of cooperation is quite high, males consistently score more highly than females. At $MRC = 200$ (fig. 2.8c), cooperative relationships are established in only a third of cases. These results may reflect the fact

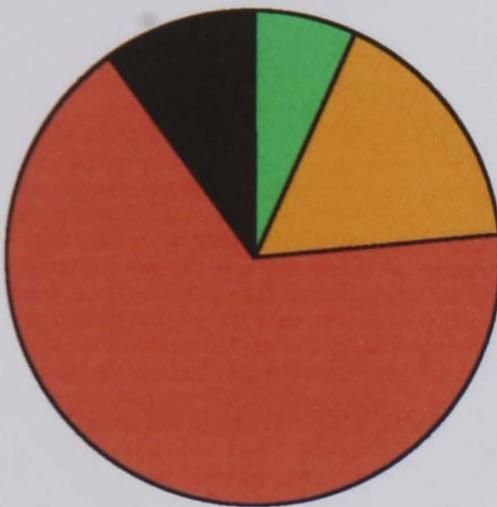
		Opponent	
		C	D
Player	C	3	0
	D	5	1

Expected

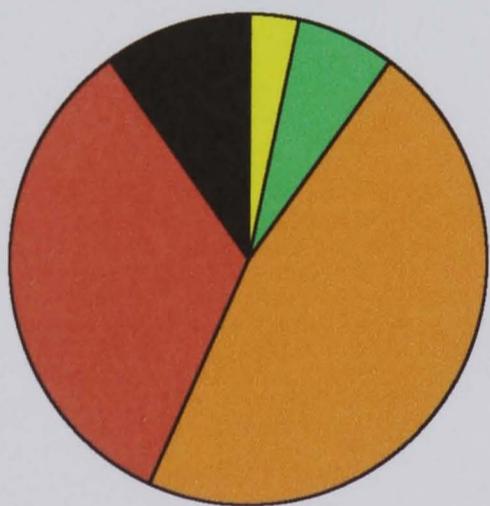
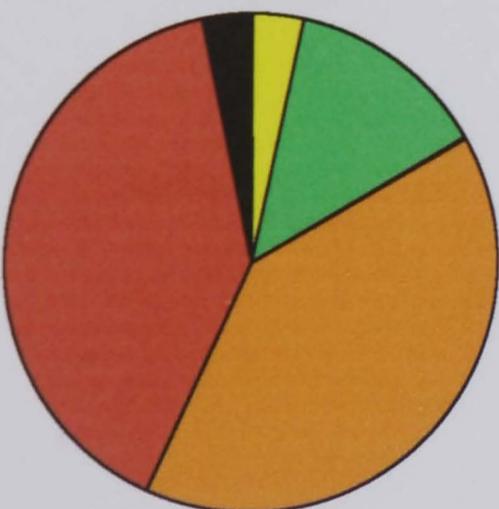
Observed



a) FRC = 1000
MRC = 600



b) FRC = 1000
MRC = 400



c) FRC = 1000
MRC = 200

Average score per player, per game:

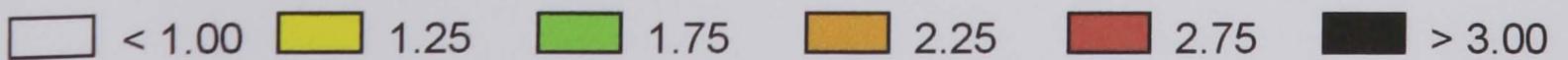


Figure 2.8: Mixed sex interactions (FRC = 1000)

		Opponent	
		C	D
Player	C	3	0
	D	5	1

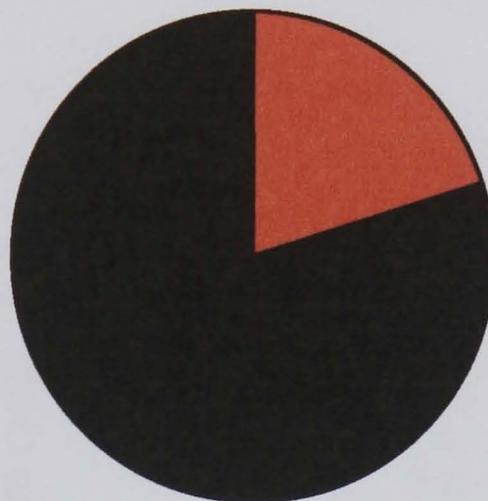
Expected

Observed



d) FRC = 1000

MRC = 100



e) FRC = 1000

MRC = 1

Average score per player, per game:



Figure 2.8: Mixed sex interactions (FRC = 1000) continued

	MALE REPRODUCTIVE COST					TFT
	1	100	200	400	600	
CCCC					C	C
DCCC					C	C
CDCC			D	D	D	D
CCDC			D	D	D	D
CCCD					D	C
CCDD					D	C
DDCC	C		D		D	D
CDDC		D	D	D	D	D
DCCD	D			C	C	C
DCDC	C	D		D	D	C
CDCD	D	D	D	D	D	D
CDDD					D	D
DCDD			D		D	D
DDCD		D	D	D	D	C
DDDC		D	D	D	D	D
DDDD		D	D	D	D	D

a) Males

	MALE REPRODUCTIVE COST					TFT
	1	100	200	400	600	
CCCC	D		C	C	C	C
DCCC		C	C	C	C	C
CDCC	D	D	D	D	D	D
CCDC	D	D	D	D	D	C
CCCD	D	D				C
CCDD	D	D	D	D	D	C
DDCC	D	D	D	D		D
CDDC	D	D	D	D	D	D
DCCD	D	D		C	C	C
DCDC	D	D	D	D	D	C
CDCD	D	D	D	D	D	D
CDDD		D				D
DCDD	D	D	D		D	C
DDCD	D	D	D	D	D	D
DDDC	D	D	D	D		D
DDDD	C	C				D

b) Females

Table 2.3: The most common alleles used during male-female interactions

The tables show the most common alleles for different values of male reproductive costs where female reproductive costs are constant at FRC = 1000. Table (a) shows the strategies males most commonly use against females, and (b) shows those that females use against males. The table should be interpreted in the same way as table 2.1.

that males, because of their lower reproductive cost, are more able to take the risk of defecting.

The third pattern of male-female behaviour is very distinctive. When male costs are much lower than female costs, pay-offs become skewed in favour of females (figs 2.8.d & e). When $MRC = 100$, females consistently achieve higher scores than males. In nearly 75% of experiments females receive an average pay-off of 2.75 or more points, often scoring more than 3.00 points per game. Males, on the other hand, receive low scores in most of the runs. This situation is particularly marked when $MRC = 1$, when females attain a score greater than 3.00 in 80% of cases, while the majority of males get very low scores in return (1.00, or less than 1.00). These scores reflect a behaviour pattern where males always cooperate with females even though the females do not return the same level of cooperation i.e. females are exploiting male “suckers”. Because males do not get an equal pay-back for their cooperation, this behaviour cannot be described as reciprocal altruism. It would be more accurate to describe males as non-reciprocal altruists³.

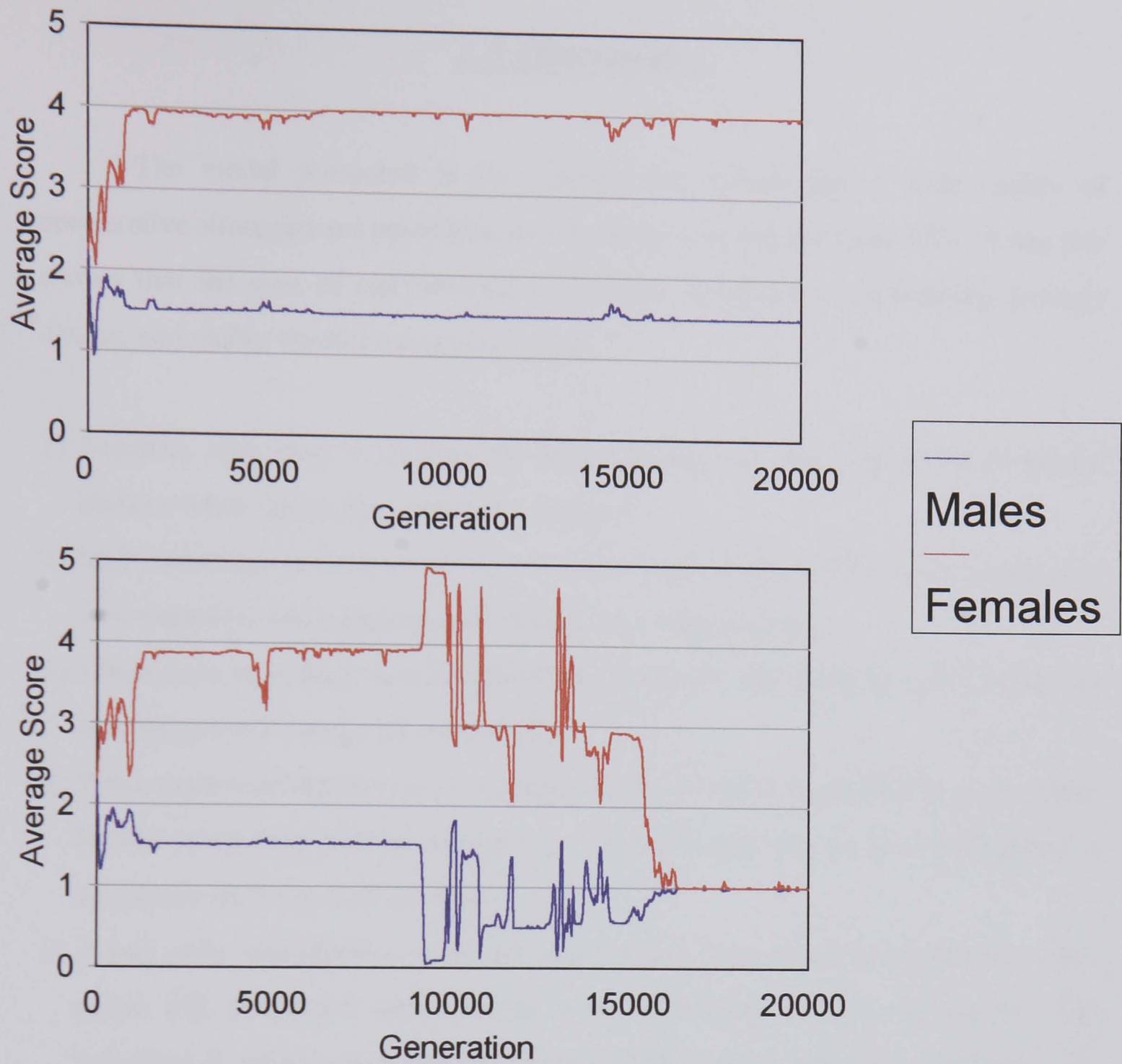
What strategies are males using against females and visa versa? Again, this is dependent upon reproductive costs, and the strategy strings that evolve reflect the three patterns of behaviour described above (table 2.3). When $MRC = 600$ both males and females tend to follow TIT-FOR-TAT like strategies. However, there are considerable sex differences in strategy when $MRC = 200$ and $MRC = 400$. Females appear to try to follow some kind of cooperative strategy, with strong selection for cooperation at the CCCC and DCCC loci. Males, on the other hand, are distinctly uncooperative with no strong selection for cooperation at any of the gene-loci except DCCD when $MRC = 400$. This does not mean that males never cooperate, rather that there is no typical situation after which males always cooperate, such as after CCCC. This is reminiscent of male-male strategies at this level of reproductive costs, indicating that males are generally more competitive.

The difference between male and female strategies at low male reproductive costs ($MRC \leq 100$) is quite distinct (table 2.3). There is very strong selection for

³ Note that even at high reproductive costs, in some cases one sex will get more than three points a game, that is, occasionally one sex will be exploited by the other. The difference is that while at high reproductive costs both sexes are exploited equally, when $MRC \leq 100$ it is always the males that are exploited to the advantage of the females.

defect alleles on the female strategy string, in fact defect alleles dominate 81% of the gene-loci. As already described, females consistently score more highly than males at low male reproductive costs. In many cases males appear to be non-reciprocal altruists, cooperating with females even when their cooperation is not reciprocated. For $MRC = 100$ the strategy strings for those runs where non-reciprocal altruism (NRA) evolved were compared with the strategy strings for all other runs (at this level of MRC). This showed that while males in NRA populations are slightly more cooperative, the deciding factor is the behaviour of the females. Females in NRA populations alternate cooperation and defection while the male always cooperates, leading to an average payoff of 1.50 to the male and 4.00 to the female (figure 2.9). For males, the pay-off of 1.5 points is slightly better than the 1.00 point they would receive if both parties defected all of the time. In order for females to maintain this strategy of alternating cooperation and defection, they should cooperate after DCCC. This is exactly what happened in 84% of simulations in which NRA evolved (as opposed to 61% of simulations in which it did not). However the distinguishing characteristic of females in NRA populations is that they will defect following CCCC, while females in other populations cooperate in this situation.

In short, the evolution of non-reciprocal altruism is driven by female behaviour. Males who behave as non-reciprocal altruists are making the best of a bad situation, gaining 1.5 points per interaction rather than 1.00 point. However, females cannot afford to be totally nasty: they will often cooperate following a string of defections (DDDD in table 2.3b) rather than get stuck on a very low scoring strategy.



ROUND	MALE	FEMALE	MALE SCORE	FEMALE SCORE
1	C	C	3	3
2	C	D	0	5
3	C	C	3	3
4	C	D	0	5
5	C	C	3	3
..... 100	C	D	0	5
Average score			1.5	4.0

Figure 2.9: Examples of non-reciprocal altruism

Two examples of runs at $MRC = 100$, $FRC = 1000$, in which non-reciprocal altruism evolved. Females gain an average score of approximately 4.00 points per game, whilst males score only 1.5 points. The table below shows how these average scores result from a strategy of alternating cooperation and defection by the female and continual cooperation by the male. The second graph illustrates what can happen if a female is too greedy and attempts to earn 5.00 points per game: there is a period of instability which ultimately results in lower pay-offs (just 1.00 point) for both sexes.

2.4 Discussion

The model presented in this chapter has shown that a wide variety of cooperative strategies are possible in social groups where individuals differ. It has also shown that the cost of reproduction is crucially important in determining strategy choice, and makes the following predictions:

- 1) Females, who have a consistently high reproductive cost, should be reciprocal altruists when interacting with other females.
- 2) Male behaviour is likely to be mixed. On average, males will be more competitive than expected, and certainly more competitive than females.
- 3) When male reproductive costs are similar to female reproductive costs, mixed sex interactions will usually be cooperative.
- 4) When male reproductive costs are around half of female reproductive costs, male-female interactions will be competitive. This is largely due to an unwillingness to cooperate on the part of the male.
- 5) When male reproductive costs are much lower than female reproductive costs, males will cooperate with females, even if females do not reciprocate. This behaviour is called non-reciprocal altruism. This result is partially the outcome of a female strategy to always defect against males, unless they behave as non-reciprocal altruists in which case they will cooperate half of the time.

Each of these conclusions is discussed below, in the context of cooperative strategies observed in the wild. This discussion will introduce ideas which will be developed as the thesis progresses: the evolution of communal care, the interplay between kin selection and reciprocity, the evolution of paternal care and the importance of paternity certainty. Wherever possible examples from the primate literature will be used although there is no reason why this model should not also apply to non-primates. Throughout this thesis examples from other mammals, fish, birds and even insects will be used to supplement the primate data.

2.4.1. Female-female interactions

Trivers (1972) and Wrangham (1980) predicts that females should be more cooperative than males. High female energetic costs mean that females can best maximise their fitness by maximising their access to resources, and since food resources are easily shared and better defended as a group, female cooperation is expected. The model presented here also uses high female costs as a basis, and confirms the conclusion that if females have high energetic costs relative to males, then they will be predisposed to cooperate. Given these conclusions, it should not be a surprise to find that the most well known and undisputed case of reciprocal altruism in the wild, blood sharing in vampire bats, occurs between females (Wilkinson 1984, 1985, 1990). Without food, vampire bats will starve to death in just 60 hours, hence a regular food supply is essential. Wilkinson found that females who have successfully fed will regurgitate blood to other female bats who have not been so lucky. What is more, the bats appear to recognise cheats and do not give blood to those who have refused to donate a meal on a previous occasion. These females are reciprocal altruists.

Blood sharing in bats occurs between unrelated females. Wilkinson (1984) estimates that the average relatedness between the females is somewhere between 0.02 and 0.11. However, very often cooperation occurs between relatives. Trivers (1971) points out that reciprocal altruism could operate between related, as well as unrelated individuals and this makes it very difficult to distinguish between reciprocal altruism and kin selection. According to Ligon (1991 p.43), kin selection and reciprocal altruism are in fact impossible to separate, and “pure reciprocal altruism and pure kin selection may be viewed as opposite and rarely realised ends of a continuum.” For instance, in the white-nosed coati, *Nasua narica*, females and their immature offspring live together in groups composed of 30 or more adult females (males are solitary). These groups tend to be extended families, but often contain unrelated females and reciprocal altruism may play an important role in female-female relationships (Gompper *et al.* 1997). Coalition formation is central to the group’s social structure, especially when there is feeding competition, agonistic encounters with males, or attacks from predators. While kin are usually supported over non-kin, unrelated females do gain some support. In the brown hyena, young males and

females help in provisioning and guarding the younger cubs. Provisioning by males appears to be determined by kin selection, males will not provision any individual more distantly related than half sib (Owens and Owens 1984). Females, on the other hand, provision all young, no matter how distantly related they are. This behaviour is likely to be based on reciprocity, since most females remain in the clan and can thus gain aid from the infants that they help, no matter what the relatedness. In both the coati and the hyena kinship effects may support, but do not seem to determine, reciprocity.

Several species have evolved high levels of female cooperation in infant care. In elephants, lactating females feed infants other than their own (Douglas-Hamilton and Douglas-Hamilton 1975). In lions, adult females rear their young together, allowing any cub to suckle (Schaller, 1972). Notably, in lions, a major cause of infant mortality is starvation, hence the benefits of sharing the burden of lactation are high. In the red fox, sisters or mother-daughter pairs may den together and suckle each others young (Ewer 1973). In each of these cases females are likely to be related. Given high reproductive costs and strong selection for cooperation, it may pay an individual to cooperate with relatives and in doing so reap *additional* inclusive fitness benefits. In many other species non-offspring nursing is provided to non-kin as well as kin (Packer et al. 1992). Packer *et al.*, in a review of non-offspring nursing across the mammalia, were unable to determine whether or not it was reciprocal. They suggest that in many cases females may be unable to distinguish their own young and non-offspring nursing is actually 'milk-theft'.

Baby-sitting is an effective form of female cooperation in many species including African wild dogs, gray wolves, golden jackals, coyotes, lions, mongooses, coatis, vespertilionid bats, elk, bison, pronghorns, mountain sheep and dolphins (Riedman 1982). In the vespertilionid bats *Myotis thysanodes* and *Antrozous pallidus*, O'Farrell and Studier (1973) found that baby-sitting was such a successful strategy that postnatal mortality was only one per cent.

Female cooperation in infant care between unrelated individuals is taken to almost ridiculous extremes in the free-tailed bat, *Tadarida brasiliensis* (Davis *et al.* 1962). Millions of females may live in a single enormous cavern and females nurse young bats indiscriminatingly. Females are unable to identify their own offspring and form a "dairy herd" where each female produces up to 16% of her own weight in milk

each day (Davis *et al.* 1962). It seems incredible that given the huge cost of nursing, females do not 'defect' and minimise their milk output, or even cease nursing altogether. Indiscriminate nursing can also occur with infant recognition. Wilkinson (1992a) found that around 20% of nursing bouts in the evening bat (*Nycticeius humeralis*) were between a female and unrelated offspring. In this case offspring recognition is not a problem, and the females on first sight appear to be altruists. However, females are not indiscriminate in their donations and favour unrelated females over unrelated males, presumably to maximise opportunities for reciprocation since males disperse when they reach maturity. This is especially significant since Wilkinson (1992b) reports that females of the species exchange information about foraging sites.

As can be seen from the discussions above, bats have provided a fruitful hunting ground for altruism between females. A further case has been reported by Kunz *et al.* (1994) for the Rodrigues fruit bat, *Pteropus radricencis*. They witnessed female bats assisting in the birth of other, unrelated, females. The assisting bat encourages the expectant mother to take the feet down posture, necessary for birthing, by taking this position herself. Furthermore, the midwife grooms the pregnant female's anovaginal region, grasps her with her wings, grooms the newborn infant, and helps to place the pup in suckling position. Midwives appear to be particularly important during difficult births, and Kunz *et al.* (1994) suggest that they may be particularly valuable to inexperienced mothers. Furthermore, familiarity, rather than kinship, seems to govern these altruistic acts.

A common theme unites reports of cooperation in the non-primate literature. In almost every case, female cooperation is manifested in behaviours that directly benefit reproduction (baby-sitting, indiscriminate lactation, feeding of offspring). The only examples of cooperative behaviours that do not directly impact on reproduction are food-sharing in vampire bats and coalitionary support in coatis. In primates, cooperative mothering would be expected by virtue of their delayed maturity, low fecundity, long life span and relatively long period of offspring dependency (Reidman 1982). However, unlike almost any other non-primate, female-female cooperation is also widespread in social contexts. This is especially true in matrilineal groups such as vervets, macaques and baboons where kinship reinforces the value of female-female cooperation.

Several primate studies have found cooperation between unrelated females. De Waal (1984) describes how (unrelated) chimpanzee females band together to protect themselves from overly aggressive males, and in bonobos unrelated females partake in food-sharing and genito-genital rubbing (Parish 1994). In the latter case, strong female bonds appear to serve as a defence against coalitions of related males. Seyfarth and Cheney (1984) used play-back experiments to show that vervet females will respond to the calls of help from unrelated individuals who have recently groomed them. In contrast they would respond to the calls of relatives regardless of prior grooming activity. Similarly, Hunte and Horrocks (1987) found that related vervet females aided kin unconditionally during disputes, but that aid provided by non-relatives was based upon reciprocal exchange.

While examples of cooperation between non-relatives could be found for most primate groups, cooperation is usually kin directed. The prevalence of female philopatry in Old World monkeys means that once again, hypotheses based on kin selection are more parsimonious than those based on reciprocal cooperation. Few studies have attempted to disentangle the effects of kin selection and reciprocity. Perry and Rose (1994) tested for differences in food sharing between kin and non-kin in capuchin monkeys. Their results were ambiguous: In one year (1992) they found that food transfer was more common between kin, but in the following year there was no kin-related effect. Schaub (1996) has explored food sharing in long-tailed macaques by constructing an apparatus in which the animals could either monopolise a food source, or share it with a partner. Out of 11 donors, 8 did not discriminate between relatives (sisters or daughters) and non-relatives. Schaub concludes that kin selection cannot explain the cooperation observed in this case. More studies of this type are required before firm conclusions can be drawn, although it seems likely that kin selection will turn out to be important in reinforcing, rather than causing, cooperation.

In many primate species females will help each other in the care of offspring. While these females may be related, as in marmosets and tamarins⁴ (Goldizen 1987a,b; Yamamoto *et al.* 1996) this is not always the case. For instance, in langurs adult females will help other unrelated females in infant care (Stanford 1992). This

⁴ Male care in these species is discussed in chapter 3.

behaviour, called allomothering, may provide substantial benefits to the recipient. In langurs, Stanford found that female helpers usually have offspring of their own and the mothers whose offspring are being cared for benefit by being able to spend more time feeding. Stanford suggests that (1992 p.29) “allomothering may have adaptive significance as altruistic behaviour among group females, in that it enables lactating females to increase feeding time.” He concludes that (Stanford 1992 pp.32-33):

“Allomaternal behaviour in capped langurs is best viewed as cooperative alliances among group females, not necessarily close kin..... The adaptive significance of allomothering in at least some nonhuman primates thus may lie in a reciprocal altruistic relationship between the adult females of a group. Such intragroup cooperative behaviour would add an additional benefit to the female-female bonding that is now seen as the most important element of some primate species’ social systems.”

However, in other cases allomothering may be detrimental to the mother and her offspring. Several studies suggest that allomaternal care may be a way for young females to acquire mothering skills, thus side stepping the potentially high cost of mistakes when it comes to the real thing (Hrady 1976, 1977; Nishida 1983). If this is the case then allomothering is far from altruistic. Rather, mothers should be wary of inexperienced female ‘carers’ who may harm their offspring (e.g. vervets, Lancaster 1971; hanuman langurs, Hrady 1977; chimpanzees, Nishida 1983).

As in other animals, baby-sitting is another form of cooperative infant care in primates. Baby-sitting has been reported for patas monkeys (Hall and Mayer 1967), rhesus macaques (Rowell 1963), vervets (Lancaster 1971), Nilgiri langurs (Poirier 1968), hanuman langurs (Hrady 1977), mantled howlers (Glander 1974) and squirrel monkeys (Rosenblum 1971). In the ring-tailed lemur, *Lemur catta*, Klopfer and Boskoff (1979) suggest that baby-sitters may be particularly important in providing protection for the infant during terrestrial feeding. The relatedness of the baby-sitters to the mothers is usually unknown.

Mitani and Watts (1997) conducted a cross-species analysis of allomaternal care in primates. They found that this type of cooperation has very clear benefits to the recipient in terms of rapid infant growth and shortened inter-birth intervals. But if the advantages of allocare are so great, why is this behaviour not more common? Or, as Mitani and Watts ask (1997 p.217):

“If uniform benefits in terms of infant growth and female reproduction are derived through allocare taking, why does non-maternal care occur infrequently in those species in which (a) maternal costs are low due to egalitarian female dominance relationships and reduced feeding competition and (b) interest in infants and attempts to handle them are high, e.g. in gorillas?”

Mitani and Watts point out that in many species which practise allocare predation pressure is high (e.g. tamarins and squirrel monkeys). Furthermore, the only Old World monkeys in which allocare occurs are vervets and patas monkeys which are both terrestrial savanna-dwelling species in which predation risks are also high. High predation risks may translate into increased costs to the female in guarding and protecting her vulnerable infant. Furthermore, the potential costs to a female are very high indeed since she risks the injury or death of herself or her infant. Allocare is a mechanism by which both actual and potential costs can be limited.

A wide variety of animals have been covered here, and some very persuasive examples of female-female altruism have been described. For behaviours to be altruistic they must involve a cost to the giver, and a benefit to the receiver. The costs and benefits of foodsharing, indiscriminate lactation, baby-sitting, allomothering, coalitionary support and food sharing are in most cases quite clear (with the possible exception of allomothering by juvenile primates). Given the benefits of cooperation it is perhaps surprising that intra-female cooperation is not more common. The model presented here suggests that only when females have very high reproductive costs can the short-term temptation to defect be overcome. In most non-primates female-female cooperation is manifest as care of young, where kinship effects can maximise the benefits of cooperation. In primates, cooperation also occurs in contexts not directly related to reproduction, such as coalitionary support.

2.4.2. Male-male interactions

The model predicts that intra-male interactions should be very competitive, or at least much more competitive than we would expect from the control scenario. In most animals, competition is the most common form of intra-male interaction, and primates are no exception. Regardless of social system or ecological context it is a basic tenet that males in the vast majority of species compete with each other for access to females. In fact, our whole understanding of male behaviour is based upon this principle. It is, therefore, very satisfying to find that this model accords so well with biological expectations. This is not to say that males never cooperate. The model suggests that male-male strategies are mixed and can range from out-right defection to reciprocal altruism. This means that if male costs are lower than female costs, a mix of competitive and cooperative strategies are to be expected.

In primates, while male-male competition is always evident, cooperation between males is not unusual. Reciprocal altruism was first reported in male baboons, who use coalitions to gain access to estrous females (Packer 1977). Packer found that males would enlist the help of another, unrelated male and that the pair would attempt to steal a female away from a third, usually more dominant, male. If successful, the soliciting male would mate with the female. While the solicited male gains no immediate pay-off, Packer (1977) argues that those males who give support are most likely to receive support in the future. Packer's findings, while supported by a subsequent study by Smuts (1985), have been disputed by Bercovitch (1988) who failed to find reciprocity in his study of olive baboons, although he did find strong reciprocity between certain pairs of males. As discussed in chapter 1 (section 1.2.2), Hemelrijk and Ek (1991) suggest that these contradictory results may be due to differing social contexts. They found that in chimpanzees males only behaved as reciprocal altruists during times when the alpha male position was in dispute. If baboon males are affected in a similar way this could explain the discrepancy in Packer and Bercovitch's results.

Male bonding in chimpanzees is well known (e.g. de Waal 1982, 1992). Chimpanzees live in multi-male groups, where the alpha male can dominate, but not monopolise, matings. Male chimpanzees navigate the social hierarchy by manipulation of social relationships, rather than physical competition, and de Waal paints a vivid picture of

the importance of male-male coalitions. Male chimpanzees appear to trade support, and de Waal concludes (1992, p.234):

“ There can be little doubt that these close alliances of male chimpanzees are reciprocal in the sense that both parties invest in and benefit from the relationship, although the nature of the investment and the pay-offs may be different for each party.”

Male chimpanzees groom each other, form alliances and cooperate in hunting and group aggression. Males will even tolerate sexual promiscuity, at least in some circumstances (e.g. Goodall 1965; Tutin 1979). De Waal (1982) describes how an alpha male re-paid coalitionary support from another male by allowing him reproductive access to females. This high level of male cooperation, as well as female philopatry, has led many authors to suggest that male bonding in chimpanzees is an outcome of relatedness. For example van Hooff and van Schaik state that “to achieve tolerance and cooperation, the conflict over reproductive interests has to become subordinate to other interests. One of these, indeed, can be the inclusive fitness interest” (van Hooff and van Schaik, 1994 p.317). A link between male cooperation and relatedness has been found in hamadryas baboons (Stammbach 1987), and male bonnet macaques (Silk 1992a). Furthermore, in species associated with male philopatry and female dispersal, such as red colobus monkeys, gorillas, spider monkeys and hamadryas baboons, males tend to associate more closely and form affiliations (Silk 1992a). For example, in a Costa Rican group of squirrel monkeys, Boinski (1994) concluded that low rates of intra-male aggression and male cooperation over estrous females were due to male philopatry. However, strong inter-male affiliations should not be automatically associated with male philopatry. Gould (1997) found inter-male affiliations in the setting of female philopatry and male dispersal in ringtailed lemurs, and Starin (1994) reported weak male bonding with male philopatry in red colobus.

Almost every study that reports male affiliations between kin in monkeys and apes, also reports support between unrelated individuals (Silk 1992b). In the case of chimpanzees, inclusive fitness benefits may only partially contribute to male-male cooperation. In fact, van Hoof and van Schaik (1994) note that relatedness between males may be rather lower than usually assumed. Many male group members will have emigrated into the group with their mothers, furthermore, sexual promiscuity will counter high levels

of relatedness. Male cooperation in chimpanzees is more likely to be mediated by reciprocal altruism, and strengthened by kin selection.

Hill (1994), in a review of alliances between male macaques, found that alliance formation was “not rare” in 7 out of 11 species. Male cooperation was most common in the bonnet macaque, and virtually absent in the pig-tailed macaque with other species showing intermediate levels of intra-male affiliations. In these cases, female philopatry indicates that relatedness between males is unlikely, and male-male relationships are based on familiarity. Bonnet macaque males sit together, groom, huddle, greet, and support each other (Silk 1994), directing support to those with whom they generally associate. Silk found that (1992b p.319):

“males selectively support those who support and groom them, intervene most often against those who most often intervene against them, and are most loyal to their relatives and those who are most loyal to them.”

This type of cooperation between males is very unusual in non-primates. Coalitions of male lions participate in joint defence of territories, and individuals in larger coalitions father more offspring (Packer *et al.* 1988). However, these coalitions are usually between relatives, and when coalitions between non-relatives do occur they are usually formed by a pair of lions rather than a larger pack (Packer *et al.* 1991).

Cooperation between males is a more complicated issue than cooperation between females. Cooperation between females may be easier to establish because of the nature of the most valued resources: food is more easily shared than mates are. While the model predicts that males ought to be more competitive than females, it also predicts both cooperation and competition between males at the same level of reproductive costs. This means that for males, decisions about when to cooperate and when to compete are likely to be more complex than for females. Therefore, we should expect greater variability in the cooperative behaviours of males. Furthermore, this discussion indicates that social context may be a critical factor in determining when males cooperate, and with whom.

2.4.3. Mixed sex interactions

The mixed sex interactions produced some very interesting results. Three very different types of interaction arose: reciprocal altruism, competition and non-reciprocal altruism. The latter two categories are the most intriguing. Competition occurs when male reproductive cost is greater than 100, but less than 600. Both sexes gain lower scores than expected, and there appears to be a high temptation to defect. Males appear to be less willing to cooperate than females, mirroring their more competitive strategies in intra-male interactions. In the iterated Prisoners Dilemma, defection may be viewed as a more risky strategy than cooperation (in sharp contrast to the 'one shot' game). In a well established population of cooperators, a defector gambles on being able to achieve the maximum pay-off of 5 points, at the risk of ending up consistently scoring just 1 point per game. Males, by virtue of their lower reproductive costs, may be more likely to take a risk on defection. Females, on the other hand, are likely to be more conservative, favouring the long-term assurance of cooperation over the short term benefits of defection. At the same time, of course, they must ensure that they are well defended against potential male exploiters. In short, females ought to behave as TIT-FOR-TAT strategists, seeking out cooperation where possible but guarding against exploitation. Males, on the other hand, can afford to opt for more risky strategies and are more likely to pursue the short-term advantages of defection.

In many primate groups where there are high levels of male competition (and hence fairly high male reproductive costs), interactions between males and females can be quite nasty. Infanticide by males who have recently taken over a reproductive group has been reported in langurs (Hrdy 1974), macaques (Wolf and Fleagle 1977), colobus monkeys (Marsh 1979), guenons (Struhsaker 1977) and howler monkeys (Sekulic 1983) in the wild. In other species, such as Barbary macaques (Deag and Crook 1971) and baboons (Packer 1980), males may use infants as agonistic buffers during confrontations to reduce tension (but see below for an alternative interpretation of this behaviour). On the other hand, while male-female aggression is one pattern of behaviour in harem groups, in many cases the alpha male is dependent on female cooperation to maintain his position. Dunbar (1988) describes how gelada females effectively vote for their favourite male during contests by grooming him. In

these cases males have two possible ways of attracting female support, aggressive cohesion or friendly attraction. The first solution is adopted in rhesus macaques and hamadryas baboons, while gorilla males generally opt for the friendly approach.

This is not to say that the model can explain the evolution of behaviours such as infanticide, agonistic buffering or complex patterns of male-female cooperation. Rather, it predicts that when male reproductive effort is fairly high, there will exist strongly opposing forces of cooperation and competition which will result in a wide variety of patterns of behaviour. Ecological and demographic variables will determine how these behaviours manifest themselves.

The most surprising result from these models is that when MRC is equal to, or less than 100, males will behave as non-reciprocal altruists. That is, they will invest in females and their offspring at a cost to themselves in terms of time, energy and (implicitly) lost mating opportunities. This behaviour seems very like paternal care for a female and her offspring. If this is the case, then this model implies that paternal care could evolve as a response to relatively high female energetic costs, in the absence of a genetic link between the male and the female's offspring.

It is generally assumed that whenever paternal investment occurs, the likelihood that the caring male is the father of the offspring should be high (Trivers 1972). In recent years, DNA fingerprinting has allowed us to test this logic directly, and has provided mixed results. At one extreme, in the rodent *peromyscus polionotus*, a monogamous mating system ensures 100% paternity certainty to the male (Foltz 1981). At the other extreme, Dixon *et al.* (1994) found that in reed buntings (*Emberiza schoeniclus*) 86% of nests contained extra pair young, and 55% of offspring were being looked after by males other than the father. In some cases males fed whole broods entirely unrelated to them. In Savannah sparrows, monogamous males have only a 40% likelihood of being fathers to their brood, while polygynous males have a 75% chance of paternity (Freeman-Gallant 1997). Male dunnocks, who live in polyandrous or polygynandrous breeding groups, invest in all offspring, regardless of the proportion of the brood that are their own, even if this proportion is zero (Burke *et al.* 1989).

Given the finding that cuckoldry is widespread, it is possible that males adjust their levels of parental care in response to probability of parentage. Again, the evidence for this is mixed. Møller and Birkhead (1993), in a cross species analysis of

paternal investment in birds, found that the most energetically expensive paternal activity, male feeding of offspring, was highly associated with paternity certainty. However, other activities associated with costly male investment, such as nest building, courtship feeding and incubation were unaffected by the frequency of extra-pair matings by the females. Westneat *et al.* (1995) used DNA fingerprinting to show that nestling red-winged blackbirds do not provide paternal care on the basis of paternity. Male house martins invest heavily in females and their young, providing food for the offspring, courtship feeding, incubation and brooding (Whittingham and Lifjeld 1995b) even though extra-pair paternity occurs in 35% of broods (Whittingham and Lifjeld 1995a). Whittingham and Lifjeld (1995b) found that male house martins do not adjust their investment with their likelihood of paternity, which means that in many cases males were labouring for the benefit of another male's offspring. Whittingham and Lifjeld (1995b, p.106) conclude that "any effect of paternity on male parental care is likely to be very small, at best." It is quite likely that birds are, in fact, unable to identify their own offspring (Beecher 1988). While it would be in a male's best interests to be able to care preferentially for his own offspring, Kempenaers and Sheldon (1996 p.1165) point out that males may be unable to do so "because of conflicts between the male, female and offspring over signalling identity." A newly born chick has no way to ascertain whether it is a product of an extra-pair fertilisation, so in order to extract the maximum amount of care from the male it should hide its identity. Pagel (1997) suggests that human infants may be selected not to resemble their parents for the same reason.

Heterosexual cooperation has been most thoroughly studied in birds, particularly with respect to the occurrence of paternal care. Two studies seem to demonstrate male non-reciprocal altruism even when males are aware of their non-paternity. In bell miners, individuals help at the nests of several neighbours, only some of which are relatives, while maintaining their own brood (Clarke 1984). Clarke found that while both males and females would act as helpers, only males reciprocated cooperation. Males reciprocated on more than 50% of the occasions when reciprocation could have taken place. In the pied kingfisher, *Ceryle rudis*, Reyer (1980, 1984) identified two types of male helpers. Primary care-givers are sons of breeding pairs and provide extensive, energetically expensive care. In this case, cooperation is clearly best explained in terms of inclusive fitness. Primary care givers

are directly aiding their own genes. Secondary care-givers, on the other hand, are unrelated to the breeding pair. The secondary helper provides energetically expensive care (although not to the same extent as either the primary care-giver or the parents) with a high benefit to the breeding pair in terms of offspring survival. The secondary male probably has good selfish reasons for cooperation. Care giving allows him to develop a bond with the breeding female, and he may eventually become accepted on the territory. Secondary helpers are only tolerated by the primary-males when conditions are poor.

The prediction that male care can occur without genetic paternity is not new. Maynard Smith (1977) and Werren *et al.* (1980) claim that paternity certainty is only an issue in the evolution of paternal care if care giving is costly to the male in terms of missed mating opportunities. For example, in fish, males who establish spawning territories actually have very few opportunities for promiscuous mating and hence should provide care regardless of paternity (Werren *et al.* 1980). Similarly Busse, in a review of paternal care in primates, suggests that (1985 p.878):

“males might profit from caring for young even when confidence of paternity is relatively low, if there are few or no opportunities for mating. Conversely, males might forego caring for young, even when confidence of paternity is high, if there are opportunities for siring further offspring.”

The relationship between the model presented here, and the mating opportunity hypothesis is explored in the next chapter (section 3.4).

In primates, there is considerable confusion over what constitutes male care, let alone who does the caring. For instance, male chacma baboons appear to protect infants from aggressive, potentially infanticidal, immigrant males (Busse and Hamilton, 1981). However Deag and Crook (1971) interpret this behaviour as ‘agonistic buffering’, claiming that males are using infants to defuse potentially violent incidents, putting the infant involved at great risk. One of the most controversial species in the male-caretaking debate is the Barbary macaque (*Macaca sylvanus*) in which male carrying of infants during interactions with other males has been described both as agonistic buffering (Deag and Crook, 1971) and as a side-effect of male caretaking (Taub 1980). Taub (1980 p.196) believes that agonistic buffering is a “special, ritualised subset of a comprehensive system of male-infant caretaking so

characteristic in this species.” Paul *et al.* (1992) used DNA fingerprinting to show that males are usually unrelated to the infants that they carry. This lack of paternity could be taken as support for the agonistic buffering hypothesis. Alternatively, if this behaviour is care-taking in the absence of paternal relatedness, this is a clear example of non-reciprocal altruism. Zhao (1996) studies male-infant relationships in Tibetan macaques (*Macaca thibetana*). He notes that interactions between two males that involve an infant occur in a predictable and standardised manner. Infants involved in these interactions, while excited, show no sign of fear or distress. Zhao compares Barbary with Tibetan macaques and concludes (1996 p.135):

“Considering that the two triad-species *M.sylvanus* and *M.thibetana*, had different levels of paternity, but shared similar foraging conditions, and showed similar intensities of male-infant caretaking, the triad was very likely a by-product of male-infant caretaking, which was probably shaped to compensate heavy maternal investment to young offspring in harsh conditions.”

If Zhao’s conclusions are correct, then we have the first clear evidence for non-reciprocal altruism in primates: (1) male care-taking, (2) high energetic costs for the female, and (3) absence of a genetic relationship between male care-taker and his charge (Paul *et al.* 1992).

Baboons are also well studied with respect to triadic interactions involving two adult males and an infant. Again, adult male behaviour is variously interpreted as exploitative or protective. Alternatively, males may be trying to develop a relationship with the infant’s mother. As with macaques, it is likely that all three explanations apply, even within a single population. Numerous baboon studies have concluded that males will both care for and exploit the same infants (e.g. in *Papio anubis*, Smuts 1985; chacma baboons, Collins 1986; yellow baboons, Klein 1983). Different adult-infant pairs will have different characteristics and Ransom and Ransom (1971) found that male-infant relationships arose in both friendly and antagonistic contexts. They conclude that in both situations “these relationships appear to be highly influential in directing the processes of social development and ultimately, adult bond formation” (Ransom and Ransom, 1971 p.179). That is, even agonistic encounters are an important part of an infants social development within a group.

As with macaques, male-infant bonding in baboons occurs in the absence of paternity. Smuts (1985) estimated that the carrying male was the likely father of the infant in less than half of the observed relationships. Packer and Pusey (1985) found that the carrying male was the probable father in only 40% of cases. However, other studies have reached the opposite conclusion. For instance, Klein (1983) suggests that in his study group, baboon males interacted primarily with their own offspring. To date, no genetic studies have been published, and in most cases the genetic relatedness between males and infants can only be guessed.

Relationships between males and infants may be an extension of a pair bond between an adult male and female (Ransom and Ransom 1971). Ransom and Ransom even suggest that relationships between adult males and infant females may develop into an adult friendship when the female matures. No long term studies have tested this hypothesis, but male-female friendships are common in both baboons and macaques. Byrne *et al.* (1990) describe baboons as “cross-sex bonded” on the basis of strong male-female affiliations and Takahata (1982) and Chapais (1983) report male-female social relationships in some groups of macaques which endure beyond the period of female sexual receptivity.

As discussed in section 1.1.1, male care taking, in the context of a “friendship” with a particular female, may be viewed as a long term mating strategy (Smuts and Gubernick 1992). Palombit *et al.* (1997) have found that in baboons the major benefit that females derive from these friendships is protection of their infants from infanticide. Males may also reap substantial rewards from their relationships with females and their offspring, including cooperation from the infant when used as an agonistic buffer, support from the female and, most importantly, mating access to the female (Smuts and Gubernick 1992). However, while some male friends may benefit in this way, these benefits are not always guaranteed. Manson (1994) looked at male-female relationships between non-kin in adult rhesus macaques. Nearly all females had at least one “friendship” with a male, and the males would lend their friends support during fights. Because male aggression is potentially a great cost to females, these relationships are of great benefit to them. On the other hand, Manson (1994) found that the benefits to the male friends were minimal. Females do not provide support for males during aggressive encounters, nor is there a strong association between friendship and mating. A third of friendships were between partners who had mated in

the preceding season, and just 10.5% were between pairs who would mate in the following season. Furthermore, males directed courtship signals at a lower rate towards friends than towards other females. A similar result was found for Japanese macaques (Takahata 1982), where mating rarely follows the formation of a friendship. In this case male-female affiliations, with their associated benefits for both the female and her offspring, could be interpreted as non-reciprocal altruism.

De Waal and colleagues used food-sharing experiments with capuchins to examine cooperative relationships (de Waal *et al.* 1993; de Waal 1997). Capuchins feed on animal and plant foods of high energetic value, and adult males are noted for their tolerance and food-sharing, especially where infants and juveniles are involved (de Waal *et al.* 1993). Vocalisations are sometimes used to advertise the presence of food, and food transfers between individuals are common and are not necessarily associated with either rank or relatedness. Pairs of subjects were placed in adjacent cages, separated by wire mesh, where only one individual had access to food which could be transferred to the other through the mesh. De Waal found that food sharing occurred between all levels in the hierarchy, in both directions and between both sexes. The most common food transfers were between partners of opposite sex. Intrigued by these results, de Waal (1997) conducted a longer series of experiments in which there was greater opportunity for food sharing to be reciprocated. In this study it was found that, in comparison with females, adult males shared food more readily and less discriminately. While females based their food sharing on principals of reciprocal altruism, for males there was no correlation between amount of food received in the first phase of the experiment, and food transferred in the second. De Waal (1997 p.376) states that:

“If we accept food transfer rate as an indicator of the possessor’s sharing tendency, the best way to put this is that males share more generously and less discriminately than females, and that their sharing is not necessarily mutual.”

De Waal goes on to consider the possibility that this food sharing is a paternal investment strategy. In the absence of genetic data he suggests that food sharing by males must be the result of kin selection, although since capuchins live in multi-male groups there is no reason to suppose that this is true. Non-reciprocal altruism may be

a more accurate model for this behaviour. This is an exciting possibility given that capuchins have relatively large brain sizes (Aiello and Wheeler 1995). Furthermore, Fedigan and Rose (1995) have shown that capuchins invest more time into the lactation and cycling phases of their reproductive cycle when compared with other primates, even when corrected for body size, brain size and brain/body weight ratio. This suggests that capuchin females have high reproductive costs. Male cooperation may have evolved to help offset these costs.

2.4.4 Summary discussion

In this chapter computer simulations have been used to show that sex differences in the cost of reproduction affect the kinds of cooperative strategies that individuals employ. A wide variety of examples from the primate and non-primate literature support this supposition. Females are more cooperative than males, particularly in their interactions with each other, and this is likely to be due to a number of factors. Firstly, female energetic costs are often very high due to a high investment in gestation, lactation and offspring care. This fact in itself predisposes females to cooperate. Furthermore, females can cooperate in a wide variety of contexts, such as infant care, grooming and coalitionary support which can be reciprocated in kind. Male-male cooperation is far less likely because there is often a direct conflict of interest: access to mates is not a resource that is easily shared, and it is not in a male's interests to help his rivals in any way. It has been hypothesised that lower male energetic costs mean that males may be able to afford to take more risks in their cooperative relationships both with males and with females. Male-female cooperative relationships are perhaps the most complex of all, since they rarely involve the exchange of similar commodities. The complexities of male-female associations are reflected in the literature on male-female friendships which seems unable to decide whether or not male care giving in species such as baboons is exploitation, paternal care, a male mating strategy, or part of a wider cooperative relationship between the individuals involved.

In both same-sex and inter-sex interactions primates can be distinguished from non-primates in terms of the types of cooperative relationships in which they are

involved. In non-primates cooperation most commonly occurs in the context of infant care. In primates high levels of cooperation also occurs in social contexts not directly related to reproduction. Primates endeavour to form alliances with animals of the highest competitive ability, compete over allies and prevent the formation of rival alliances. Harcourt (1992) argues that primates differ from nonprimates in that coalitions are a goal in themselves, rather than a means to an end. Harcourt suggests that this may reflect the different cognitive abilities of primates. Reciprocal altruism between non relatives involves complex cognitive processes such as individual recognition, memory, calculation of the costs and benefits of different behaviours, and the ability to detect non-reciprocators (Seyfarth and Cheney 1988). The implication is that reciprocal altruism is only possible in animals with higher order mental abilities (Harcourt 1992).

De Waal (1992) compares reciprocity in macaques and chimpanzees, and concluded that while both species reciprocated good deeds, only chimpanzees punished those individuals that did not cooperate with them. He concludes that the more complex and flexible patterns of alliance formation in chimpanzees may be the result of higher cognitive capabilities. Complex cooperative strategies in other large-brained animals, such as dolphins, also suggests that brain size may limit the evolution of cooperation. Bottlenose dolphins live in fission-fusion societies, comparable in structure to chimpanzee social groups (Connor 1992). Groups of two or three males form 'first order' alliances in order to herd and mate with females. Males may take it in turns to mate with the captured female, although in many cases they will mate with her simultaneously. The most interesting feature of dolphin alliance systems is that they are the only known species other than humans that form 'second order' alliances. A coalition group will enlist the support of a second coalition group in order to steal a female that is being guarded by a third group. These encounters between groups can be quite dangerous and involve high levels of risk to the enlisted group, who often have a female of their own to guard and will not gain anything from the attack. Connor found evidence of reciprocal cooperation between first order alliances and argues that this level of cooperation requires higher level cognitive abilities than those of chimpanzees.

Research into the cognitive requirements of cooperation is only just beginning. However, it is likely that different types of cooperative relationships will require different types of cognitive mechanisms. Relationships with relatives may be mentally less challenging than those with non-relatives whose activities must be carefully monitored and

remembered. Interactions between males, females and their offspring may be especially tricky since they involve a wide range of activities each of which may have very different costs and benefits to those involved. Cooperation between females, involving the direct reciprocation of similar altruistic acts, may be simpler to monitor than cooperation between males. De Waal (1984) found that while female chimpanzees consistently chose the same cooperative partners, males were rather more fickle. Males would choose their alliances on the basis of the current social situation and would change allies if they thought it would gain them a social advantage. Hemelrijk and Ek (1991) also found that males were 'opportunistic' in their cooperative strategies. However, Hemelrijk and Ek suggest that since males are totally selfish in their choice of alliance partners, this may not in fact involve particularly sophisticated mental processes (1991 p.932):

“ When support is a selfish act, it is unnecessary to keep track of support given and received, but reciprocity and cooperation may be a side-effect of directly selfish behaviour displayed by animals with the same aim. Nevertheless, the animals may well have the capacity to keep mental records of support given and received, but this ability is not required to direct selfish acts.”

Even if Hemelrijk and Ek are correct, other cognitive skills are involved in these relationships: individuals must keep track of who is related to whom and who will support whom; furthermore they must be able to recognise when the social hierarchy is liable to disruption, and when it is best to maintain the status quo. In short, group-living primates require a sophisticated social intelligence. The cognitive requirements of cooperation will be further explored in chapter 6.

Probably the most surprising and interesting cooperative strategy discussed here is non-reciprocal altruism. It has been proposed that non-reciprocal altruism evolves when male energetic costs of reproduction are much less than female energetic costs of reproduction. In this situation males will cooperate with females even when females do not cooperate in return. Non-reciprocal altruism may provide an interesting new way of viewing the evolution of paternal care and several possible examples of non-reciprocal altruism have been suggested. Since non-reciprocal altruism does not involve reproduction between the male and female it provides a mechanism by which paternal care could evolve without paternity certainty. A review of the literature suggests that paternal care can and does occur in the absence of

paternity in a number of species. But a number of questions remain unanswered: Exactly when can we expect non-reciprocal altruism? Why does it occur? How does it affect male reproductive success? In order to address these questions the next chapter focuses solely on non-reciprocal altruism. The details of the model will be examined and checked and finally the model will be expanded to provide a more complete scenario for the evolution of paternal care.

CHAPTER 3

The Evolution of Non-Reciprocal Altruism

3.1: Introduction

In the previous chapter it was shown that when males and females differ in their energetic cost of reproduction, many different cooperative strategies emerge. Perhaps the most interesting of these is non-reciprocal altruism, where males cooperate with females even when this cooperation is not reciprocated. This strategy is only observed when male reproductive costs (MRC) are considerably less than female reproductive costs (FRC). It was postulated that non-reciprocal altruism could be involved in the evolution of paternal investment. Since many of the conclusions of this thesis rest on this result, the first part of this chapter examines in greater detail the conditions under which non-reciprocal altruism evolves. Firstly, in section 3.2 it will be shown that non-reciprocal altruism is advantageous to both males and females in terms of reducing generation time (the time it takes to create enough offspring to replace the adult population). This means that non-reciprocal altruism can be selected for at both an individual and a group level. Given this advantage it is surprising that non-reciprocal altruism only evolves when $MRC=100$. For instance, why does it not evolve when $MRC = 200$? In section 3.3 it is shown that it is not the *absolute* value of MRC that is important, but rather its *relative* value compared with FRC. Having established experimentally that non-reciprocal altruism occurs when $MRC \leq 0.1 \times FRC$, section 3.4 explores the reasons for this threshold.

By exploring these questions the first aim of this chapter is to establish how robust predictions generated in the previous chapter regarding non-reciprocal altruism are. Its second aim is to expand these results to create a model of the evolution of paternal investment that may have wider applicability. This is done by focusing on the issue of paternity certainty. A model is developed where males have a much greater likelihood of mating with females with whom they have formerly interacted (section 3.5). In this case, if males behave as non-reciprocal altruists they have a high chance that they are investing in the mother of their future offspring. As might be expected, in this case non-reciprocal altruism occurs at much higher levels

of MRC. The results are discussed in terms of a general model of the evolution of paternal care.

3.2 Non-Reciprocal Altruism vs. Reciprocal Altruism: **Generation Times Model**

3.2.1 Method

To differentiate it from the models developed here, the model presented in chapter 2 will be called “model 1” (see section 2.3). In model 1, while non-reciprocal altruism evolved in the majority of cases when $MRC = 1$, it was the dominant strategy in only a quarter of cases when $MRC = 100$ (fig. 2.8 d&e). Even so, this may be a very significant result if selection can occur at the group level. Imagine the following scenario: in a species of primates there has been strong selection for an increase in body size which has put considerable strain on the females during the lactation period. The females cannot wean their infants until they have reached a certain body weight and, because the mothers cannot increase either the quality or quantity of their food intake, the infants are weaned at a later age than they would have been at a smaller body size. This late age at weaning has, in turn, increased the inter-birth interval. The males must dedicate a certain amount of energy each day to maintaining their body weight, and to competing with other males for access to females, although they are under no energetic stress. In most groups the males and females interact very little, however, in one group, one of the males begins carrying the infants for the females, regardless of whether or not they are his own offspring. This is of great benefit to the females because it reduces their energetic output, but is a very small cost to the male who has energy to spare. In fact, the male is better off than the other males in his group because now the females occasionally will help him by supporting him in fights and grooming him. This behaviour spreads amongst the males in the group and reduces the inter-birth interval by two months. This group now has a competitive advantage over other groups in which non-reciprocal altruism has not evolved.

This scenario is not unrealistic. Hamilton (1984) in an analysis of the costs and benefits of male care in primates, found that benefits to the mother could be

substantial while the costs to the male may be low. Mothers receiving male help can reduce the costs of locomotion, temperature regulation and avoiding and threatening others, and as a result divert more energy to infant growth and future reproduction. Hamilton calculated that the energy cost to the male would be very small, around 2-3% of his daily energy budget. Furthermore, Anderson (1992) points out that in baboons there may be considerable advantages to an investing male in terms of improved social position and reduced aggression from other troop members. These advantages are independent of paternity issues. If non-reciprocal altruism reduces the time that it takes for females to become fertile this means that the population as a whole can reproduce more quickly. There is then, a group level advantage that amplifies the selection pressure for this trait at an individual level. To investigate the extent to which non-reciprocal altruism speeds up the reproductive rate of a population a simplified set of simulations were run, based on model 1. These simulations examine the effect of different strategies on the time it takes to create a new generation.

Just like model 1, a population of 650 agents is created which is made up of males and females who interact and can only reproduce when they have gained enough points to meet the cost of reproduction (MRC or FRC). Agents are chosen at random and interact by playing 100 rounds of the Prisoner's Dilemma. Different agents are chosen at random to reproduce. To a great extent the model is identical to model 1, the only difference is that the agents do not have strategy strings. Instead simplifying assumptions are made, based on the results from model 1, about what types of strategies different agents employ. It is assumed that in same sex interactions females always cooperate and males always defect. Only interactions between males and females are variable: they can be one of three types, depending on the male strategy (or *male-type*):

- 1) Always defect (both players score 1 point per game)
- 2) Reciprocal altruism (both players score 3 points per game)
- 3) Non-reciprocal altruism (male scores 1.5 points, female scores 4 points per game)

It is assumed that if females meet an ‘always defect’ male, they will also defect. Similarly, if females meet a reciprocal altruist male it is assumed that they will cooperate. At the start of the experiment there are equal numbers of each type of male. Reproduction is very simple, like model 1 it can only occur between a male and female who have enough points, but there is no crossover or mutation. Instead, the offspring is given the same male-type as the father. Once 650 offspring have been created, a new population of adults is generated, where sexes are assigned at random and all males carry the male-type of their father. The program is run for 300 generations, by which time one male-type is usually at 100% frequency. The program then records the final frequency of each male-type and the average generation time. The program is given in full in appendix 3. The experiments were all run at $FRC = 1000$, and repeated 100 times each for $MRC = 1$, $MRC = 100$ and $MRC = 200$.

3.2.2 Results and discussion

In nearly every experiment, the population fixes onto one male-type within the 300 generation run, if it did not it was classified as the male-type that occurred at highest frequency at the end of the experiment. Table 3.1 shows, for each value of MRC , the percentage of runs that evolved into each male type, and the average generation time associated with each male type. Generation time is measured as the number of cycles the model must run to create 650 offspring. A single cycle is defined as one interaction phase (100 games of the Prisoner’s Dilemma between a pair of agents) and one reproduction phase.

		Always Defect	Reciprocal Altruism	Non-reciprocal Altruism
MRC = 1	% of runs	35	33	32
	Average generation time (cycles)	4416	4046	3119
MRC = 100	% of runs	22	54	24
	Average generation time (cycles)	3807	3528	3338
MRC = 200	% of runs	0	100	0
	Average generation time (cycles)	N/A	3502	N/A

Table 3.1: Comparison of the success of different male strategies.

The table shows the percentage of runs in which each male strategy was the most successful. It also shows the average generation time associated with each strategy.

By examining the percentage of runs in which each male strategy (male-type) evolved, it is possible to ascertain which were the most successful strategies. When $MRC = 1$, no particular strategy emerges as best. Each strategy dominated around a third of the runs (table 3.1). When $MRC = 100$, reciprocal altruism evolved in 54% of experiments, while each of the other two strategies dominated around a quarter of the runs. When $MRC = 200$, reciprocal altruism dominated all the experiments. Non-reciprocal altruism only evolved when $MRC = 1$ and $MRC = 100$, confirming the results found in model 1. The defector strategy did as well as non-reciprocal altruism at lower values of MRC , and also failed at $MRC = 200$. This is surprising as in model 1 male-female interactions were very competitive when $MRC = 200$. The simplicity of the experiment means that the defector strategy is unlikely to succeed. Since it is assumed that females will always defect against defecting males the competitive advantage of defection is nullified (the temptation to defect is only relevant if the other player is expected to cooperate).

Generation time is sensitive to population size and the magnitude of MRC and FRC and as well as the strategies of the players. For a constant population size (650), at any given level of reproductive costs, generation times are, as expected, shortest for non-reciprocal altruist populations, and longest for defector populations. For instance, when $MRC = 100$, reciprocal altruism evolved in 54% of experiments with an average generation time of 3528 cycles, as compared to 3338 cycles for non-reciprocal altruism which evolved in just 24% of experiments. This means that, even though non-reciprocal altruism is less likely to evolve than reciprocal altruism, if it does evolve the population can replace itself more quickly. By the time that reciprocal altruists have completed 1000 generations, non-reciprocal altruists will have produced 1057 generations.

These results show that while the male strategy of non-reciprocal altruism is less likely to evolve than reciprocal altruism, at a group level it will out-compete reciprocal altruism because of the advantage it confers in terms of shortened inter-birth intervals. Field studies have shown the importance of male investment for shortening the inter-birth interval. For example, Anderson (1992) found that male help had a stronger effect on infant survivorship and inter-birth interval in chacma baboons than either maternal age or rank. Of course, group level selection is only possible if there are also advantages at an individual level. In this case, the advantages to the females are clear. Males may also be better off as non-reciprocal

altruists if the females refuse to play reciprocal altruism (see section 2.3.4). Finally, this model confirms that males will only behave as non-reciprocal altruists when $MRC \leq 100$. Since the program structure of this model is very different from that of model 1, this indicates that non-reciprocal altruism is a true result rather than a spin-off from a programming querk.

3.3 Absolute Versus Relative Reproductive Costs

Recent studies of paternal investment in primates have focused largely on female costs. For example, Ross (1991) argues that in callitrichids females can only sustain high birth rates, litter weights and high litter growth rates, if males assist in infant transport. Dunbar (1988) also suggests that high energetic costs associated with lactation are likely to determine whether or not males participate in infant care. These theories assume that the magnitude of the cost of reproduction for the male is irrelevant. It is not immediately clear from this model whether non-reciprocal altruism is a response to absolutely or relatively high female costs. Is the threshold below which non-reciprocal altruism can evolve $MRC = 100$, or $MRC = 0.1 \times FRC$? The 'absolute' versus 'relative' hypotheses are tested here.

3.3.1 Method

Female cost was increased to $FRC = 2000$ and male cost was set at values of 100, 200 and 400. These experiments were identical to those described for model 1 (section 2.3), and each was run for 20,000 generations and repeated 30 times. Because only male-female interactions are of interest here, these are the only results described. In fact, the male-male and female-female results are very similar to those for model 1.

3.3.2 Results

When $FRC = 2000$ the ‘absolute’ hypothesis predicts that non-reciprocal altruism will only occur at $MRC \leq 100$. The ‘relative’ hypothesis predicts that when $FRC = 2000$, non-reciprocal altruism will occur at $MRC \leq 200$. Hypotheses and results are presented in table 3.2, and the illustrated in fig. 3.1.

Female cost	Male cost	‘Absolute’ prediction	‘Relative’ prediction	Actual results
2000	100	NRA	NRA	NRA
2000	200	competition	NRA	NRA
2000	400	competition	competition	competition

Table 3.2: Absolute vs. relative reproductive costs.

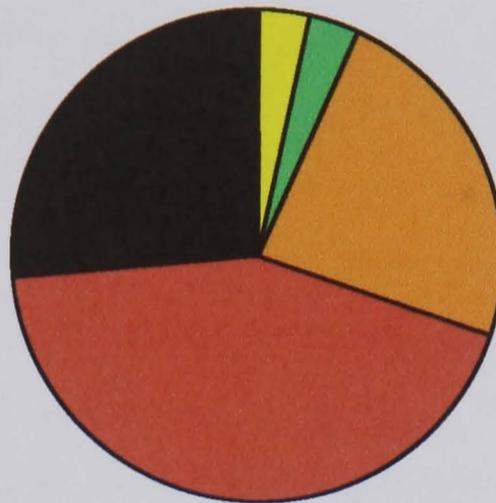
Actual results, compared to predictions, when $FRC = 2000$. NRA is non-reciprocal altruism.

When $MRC = 100$ and $MRC = 200$ (fig 3.1 a & b) there is the heavy imbalance in male and female scores which characterises non-reciprocal altruism (section 2.3.4). Females are consistently scoring more highly than males, and in some cases gaining more than 3.00 points per game. These results are comparable to those when $FRC = 1000$ and $MRC = 100$ (fig. 2.8d). Only at $MRC = 400$ do the male and female scores even out. From these results, and the summary in table 3.2, it is quite clear that the ‘relative’ hypothesis is more accurate and that non-reciprocal altruism is the result of relatively low male reproductive costs. The results from this section indicate that non-reciprocal altruism will only evolve when $MRC \leq 0.1 \times FRC$. This is an important result as it shows it is the relative difference between male and female energetic costs that is relevant. The costs to both males and females must be taken into account in developing theories regarding the evolution of paternal care.

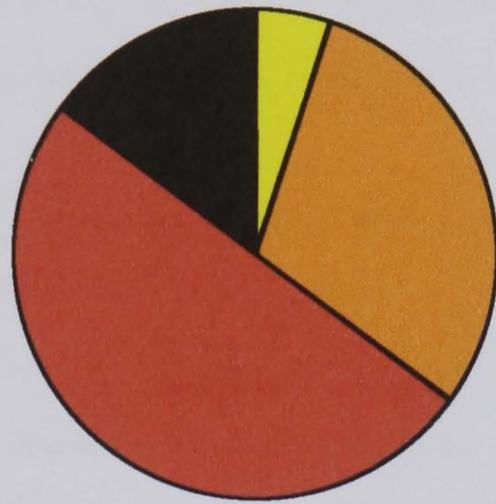
		Opponent	
		C	D
Player	C	3	0
	D	5	1

Expected

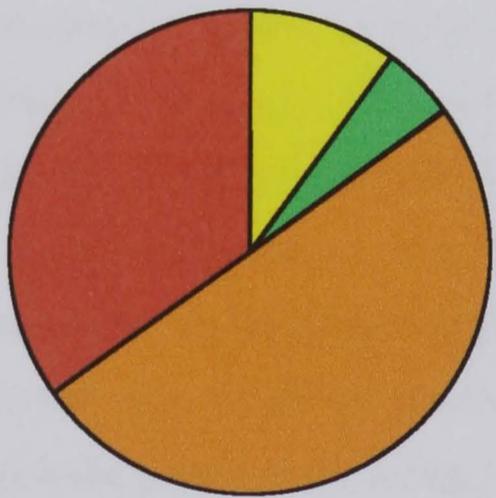
Observed



a) **FRC = 2000**
MRC = 100



b) **FRC = 2000**
MRC = 200



c) **FRC = 2000**
MRC = 400

Average score per player, per game:

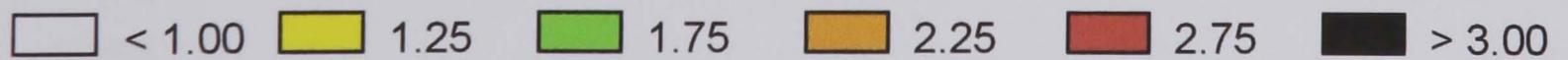


Figure 3.1: Mixed sex interactions (FRC = 2000)

3.4 Exploring the Threshold Value

One of the most interesting things about these models is the clearly defined thresholds between the different behavioural strategies. In the control model, described in section 2.2, there is a definite switch to reciprocal altruism at $RC = 200$. In model 1 and in the model just described in section 3.3, there is a drastic change in male behaviour at the boundary $MRC = 0.1 \times FRC$, from non-reciprocal altruism to great competition with females. Why does the threshold occur here? Why not follow the rule ‘behave as a non-reciprocal altruist when $MRC \leq 0.3 \times FRC$ ’? This is particularly puzzling since it would seem that at male reproductive costs of 300, or even 500, males should have plenty of energy to spare to help the females. As it turns out, in a world where female fertility is unpredictable males have to keep their ‘spare energy’ for themselves.

Imagine a wild population in which there is no birth season so that females may come into estrous at any time. This means that males are unable to predict at what times females will become fertile. Usually about one female comes into estrous each month although sometimes, by chance, two or even three females come into estrous within a short space of time. If this occurs only those males with ‘energy to spare’ will stand any chance of impregnating several females. The same chance effects occur in the model. If the generation time is, say, 3500 cycles in a population of size 650 (see section 3.2), a male can be expected to be selected for reproduction about 11 times¹, however, he will only be allowed to take the opportunity to reproduce if he has enough points (and, of course, his partner is female and also has enough points). In a predictable world the male would be selected once every 325 cycles, which is time enough to replenish the points spent during reproduction. In an unpredictable world there is a chance that the interval between selections may be very small. In which case, the male needs to quickly acquire enough points, not just to reproduce once, but to reproduce twice in quick succession if the opportunity arises.

In a stable population, where population size does not increase, each individual can expect to have, on average, 1 offspring. That is, the mean number of

¹ The population size is 650 and there are assumed to be 3500 cycles per generation. During each cycle two agents are chosen, hence expected number of selections = $2 \times 3500/650 = 11.2$.

offspring per agent must be 1.00. In a probabilistic model it is likely that some individuals will have no offspring, and that others will have more than 1.00 offspring. This is likely to be the case for model 1. Unfortunately, when the model was first run, variation in offspring number was not recorded. So, in order to assess this variation without completely re-running the experiment, Model 1 was run ten times at FRC = 1000, exactly as described in section 2.4, for 5,000 generations. Two new variables were measured: (1) The maximum number of offspring born to a single male and a single female in each generation; (2) The standard deviation in number of offspring born to males and females in each generation.

Every 20 generations, standard deviations and maximum number of offspring born to one parent were measured for males and females, so that after 5,000 generations 250 sets of measurements had been taken. This was done 10 times for each value of MRC, and MRC was varied between 100 and 600 points. Table 3.3 shows the average² standard deviation and average maximum scores for each sex, and each value of MRC. At all values of MRC, there is greater variation in number of offspring born to males than females. While the most successful males can expect to have four or five offspring over a lifetime, the most successful females will have only three or four offspring.

MRC	MALES		FEMALES	
	SD	MAX	SD	MAX
100	1.00	4.85	0.76	3.31
200	0.99	4.82	0.76	3.32
400	0.96	4.55	0.78	3.39
600	0.92	4.23	0.79	3.41

Table 3.3: Sex differences in reproductive success.

Average standard deviation (SD) in, and maximum number of (MAX), offspring born to a single parent.

² Average values were calculated over the 10 experiments for each value of MRC.

In order to examine the range of variation within a single experiment, one experiment was chosen at random for each value of MRC. For these chosen experiments, the distribution of standard deviations and maximum number of offspring were plotted as histograms. Fig. 3.2 illustrates the distribution of standard deviations, and shows that there is more variation in the number of offspring born to males, than to females. As MRC increases, the difference between the males and females decreases, although even at $MRC = 600$ male reproductive success is still the most variable. The histograms for maximum number of offspring born (fig. 3.3) show even more dramatically that males have better opportunities than females to have many offspring. Whatever the value of MRC the maximum number of children that any one female is likely to have is 3, and given the low standard deviation (fig. 3.2) this is likely to be a rare occurrence. The top breeding males, on the other hand, may have five or more offspring, and this is more likely the lower the value of MRC.

Of course, only those players who have good strategies are able to attain enough points to have large numbers of offspring, but it seems likely that chance will also affect an individual's opportunities to realise its potential reproductive output. Given this potential, at what value of MRC does non-reciprocal altruism become a bad strategy? To calculate this easily some assumptions must be made:

- 1) Females always cooperate with each other, scoring 300 points each time they meet (100 rounds at 3.00 points per round).
- 2) Males always defect against each other, scoring 100 points each time they meet (100 rounds at 1.00 points per round).
- 3) Males are non-reciprocal altruists and will score 150 points each time they meet a female (100 rounds at 1.50 points per round), while the female scores 400 points (100 rounds at 4.00 points per round).

The first stage in this calculation is to estimate how many times a female must be chosen to play the Prisoner's Dilemma before she has acquired enough points to reproduce. When $FRC = 1000$, a female must be picked either 3 or 4 times to acquire the necessary points. The exact number of times depends on whether she plays males and/or females. The probabilities of 3 or 4 picks are shown below where M = male partner in game, F = female partner in game.

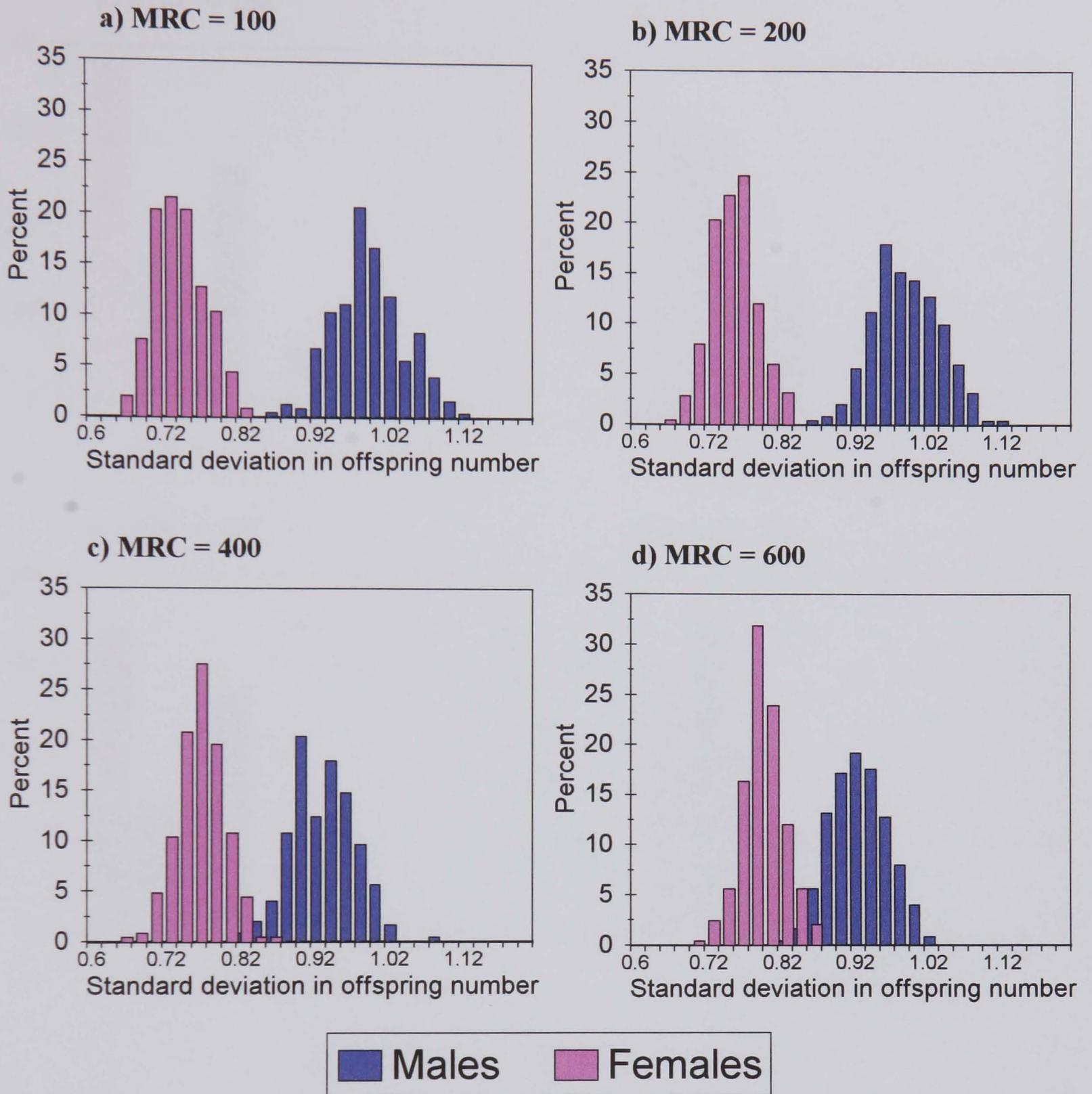


Figure 3.2: Comparison of male and female standard deviation in number of offspring born to a single individual.

Each graph shows the results for just a single run. The standard deviation in number of offspring born to males and females was recorded every 20 generation. Each graph shows the distribution of standard deviations over the 5000 generations of a single experiment. FRC = 1000 in each case.

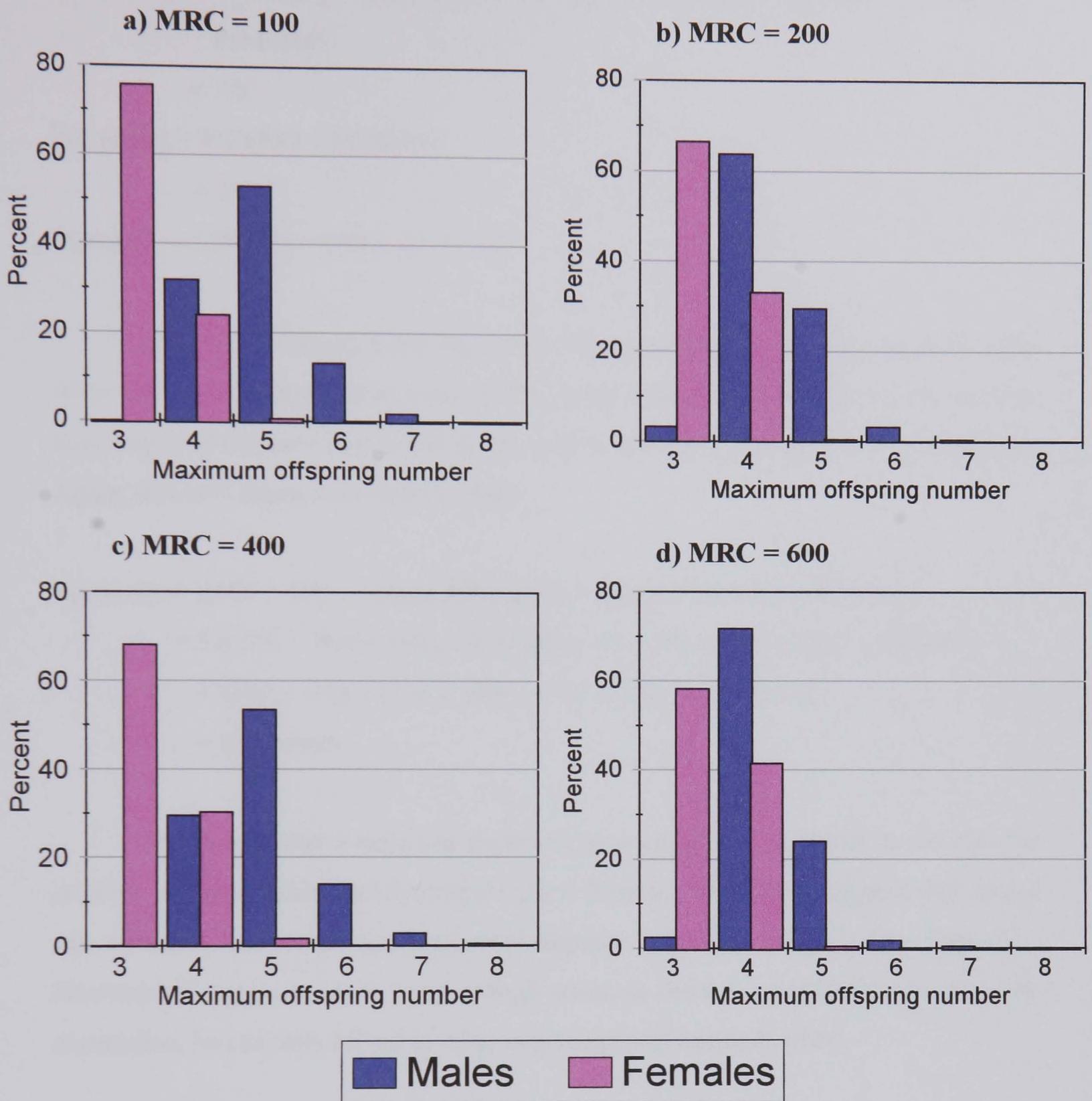


Figure 3.3: Comparison of maximum number of offspring born to a single male or female.

Each graph shows the results for just a single run. The maximum number of offspring born to a single male and a single female over the course of a generation was recorded every 20 generations. The graphs show the distribution of results over the 5000 generations of a single experiment. FRC = 1000 in each case.

$$\begin{aligned}
P(3 \text{ picks})^3 &= P(MMF) + P(MFM) + P(FMM) + P(FFM) + P(FMF) + P(MFF) + \\
&\quad P(MMM) \\
&= 7/8
\end{aligned}$$

$$\begin{aligned}
P(4 \text{ picks}) &= P(FFFF) + P(FFFM) \\
&= 1/8
\end{aligned}$$

$$E(\text{picks})^4 = (7/8 \times 3) + (1/8 \times 4) = 3 \frac{1}{8}$$

These calculations show that most females will be ready to reproduce after three selections, hence males must also be ready to reproduce after 3 selections. The next step is to estimate how many points a male can expect to acquire in 3 selections. Again, this will depend on who he plays:

$$\begin{aligned}
E(\text{points}) &= ((100 + 100 + 100) \times P(MMM)) + ((150+150+150) \times P(FFF)) + \\
&\quad 3 ((100 + 100 + 150) \times P(MMF)) + 3 ((100 + 100 + 150) \times P(FFM)) \\
&= (300 \times 1/8) + (450 \times 1/8) + (350 \times 3/8) + (400 \times 3/8) \\
&= 375 \text{ points}
\end{aligned}$$

This means that a male can expect to have acquired 375 points by the time he is given an opportunity to reproduce with a female. This would suggest that males can afford to behave as non-reciprocal altruists whenever MRC is less than 375. However, if a male needs to keep enough points in hand to reproduce twice in quick succession, he can only afford to play non-reciprocal altruism when:

$$2 \times \text{MRC} \leq 375$$

This means that males should only behave as non-reciprocal altruists when MRC is less than or equal to 187.5. Since these calculations are themselves based on probabilities and are dependent on the strategies played between agents of the same sex, this should be taken as a rough estimate. None the less it is very close to the observed threshold value of 100. This calculation suggests that males can afford to behave as non-reciprocal altruists as long as this strategy allows them to acquire

³ Probability of '3 picks' equals

⁴ Expected number of picks equals

enough points to mate with at least two females. In other words, males will only invest in females when doing so does not jeopardise their potential to mate with other females. This is similar to the conclusion drawn by Maynard Smith (1977) and Werren *et al.* (1980) that paternal investment can occur without paternity certainty as long as the male does not suffer a promiscuity cost.

Two interesting conclusions have arisen from this section. Firstly, because males invest less in each reproductive event, there is greater variation in male reproductive success, than female reproductive success. This conclusion is well known to biologists (Daly and Wilson 1983), and yet it is a surprising outcome from such a simple model. Secondly, because females have the highest reproductive cost they are likely to always be on an energetic knife edge, with very little energy in reserve. Males should easily be able to meet their energetic needs, even when these are quite high, but the most successful males will be those who keep enough energy reserves to mate with multiple females. This means that males will only behave as non-reciprocal altruists when they can aid females without seriously reducing their own energy stores.

For the past 25 years, the received wisdom has been that a male's fitness is limited by the number of females he can inseminate (Trivers 1972). Accordingly he can best maximise his reproductive success by competing with other males for access to females. By implication, access to resources is likely to have little influence on male fitness. Yet, contrary to this, the model presented here suggests that resources may also be very important for male reproductive success. A few recent studies lend support to this conclusion. Bercovitch and Nürnberg (1996) found that in one population of rhesus macaques, only 8 out of 21 males sired a single season's offspring. When they compared sires with non-sires they found that sires were heavier, longer, had bigger testes and higher abdominal skinfolds. As measured by skinfold thickness, sires began the season with twice as much body fat as non-sires. By the end of the season sires and non-sires had the same amount of body fat, indicating high levels of energy expenditure on the part of the sires. Bercovitch and Nürnberg state (1996, p.66):

“Our research has major implications for the view that females augment their reproductive success by concentrating on access to food, whereas males achieve this goal by channelling resources into access to females. Our data confirmed that mating with more females yielded more

offspring, but this outcome was a function of male body condition. If obtaining and maintaining access to females is a consequence of male quality, then male feeding behaviour has a direct, not a secondary, effect on male reproductive success.”

Two studies on birds also support a link between resources and reproductive success. Whittingham and Lifjeld (1995a) found that in house martins the males with the highest body weight gained the most matings. Hannon and Dobush (1997) that in the usually monogamous willow ptarmigan that only those birds with very good body condition and larger territories were among the 20% of males that practised polygny. The energetic costs of reproduction for both sexes will be analysed in detail in chapter 4.

3.5 The Further Evolution of Non-reciprocal Altruism

(Model 2)

In the model that has been developed, when the reproductive effort required by a male to produce an offspring is low in comparison to female reproductive effort, males behave as non-reciprocal altruists, investing in the females of the group and enabling them to reproduce more quickly. So far, this chapter has shown that non-reciprocal altruism benefits females by shortening the inter-birth interval, and that male's will participate in non-reciprocal altruism as long as $MRC \leq 0.1 \times FRC$. It has also been shown that there is more variation in male compared with female reproductive success, and that males should only be non-reciprocal altruists when this behaviour does not result in missed mating opportunities.

Male non-reciprocal altruists are sacrificing energy for the benefit of the female and her offspring. This is akin to male investment in a female and her offspring, and suggests that the evolution of paternal investment could be triggered by a heavy imbalance in the level of reproductive effort between the sexes. Since there is no link between the interaction and reproduction phases of the model it is more than likely that males are investing in the mothers of another male's future offspring. But, if males must invest in the females they would be better off ensuring that they are investing in the mother of their own infant. Once this link between cooperation and reproduction is made, the males may invest even more heavily in the females and their offspring. This hypothesis is explored in the following experiment, 'model 2'.

3.5.1 Method

The basic experiment was repeated with the difference that after a male and female had finished interacting (playing the Prisoner's Dilemma) they were allowed to reproduce, with the proviso that they each have enough points⁵. Remember, in the first model two agents were selected to interact (play the Prisoner's Dilemma) and following this two *different* agents were chosen to reproduce. In this model, the same

⁵ This change was made by removing a single line ("3. select two new agents at random") from the program outlined in fig. 2.3.

pairs are involved in both the interaction and reproduction phases of the simulation. This does not guarantee reproductive access for the male, since if either sex does not have enough points to reproduce after the interaction phase they will not be allowed to reproduce. However, in this model it is much more likely that a pair that have interacted together will also reproduce together. Male-male and female-female interactions proceeded as usual, without reproduction. The simulation was run 30 times for each set of variables. As in model 1, the control experiment was run with male reproductive cost equal to female reproductive cost. The main experiment was run with $FRC = 1000$ and the value of MRC was varied. As with model 1, results were analysed in terms of the average score per player per game of Prisoner's Dilemma.

3.5.2 The control experiment: symmetric reproductive costs

In the control experiment $MRC = FRC$. Figure 3.4 compares the distribution of average scores per player per game for the control experiment for model 1, with the results for this model. Linking interactions and reproduction makes almost no difference to the outcomes. Most importantly, a reproductive cost of 200 is still the threshold at and beyond which reciprocal altruism almost always evolves.

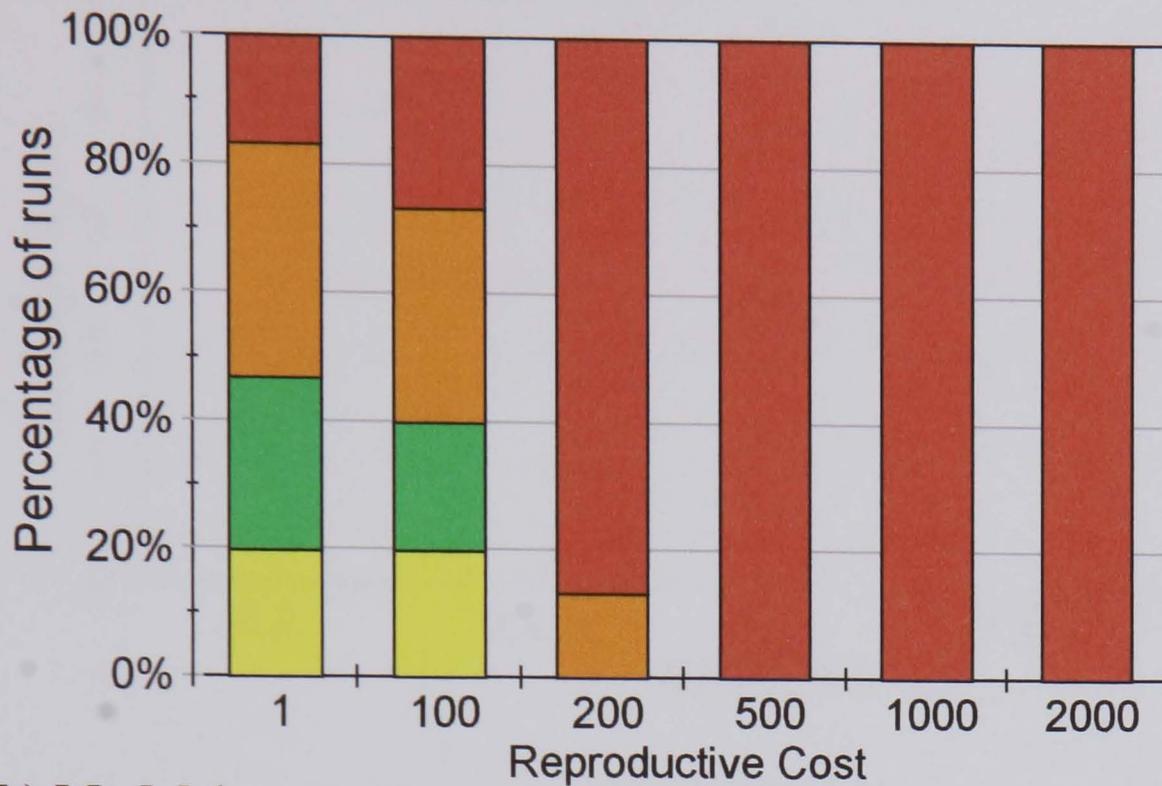
3.5.3 The main experiment: asymmetric reproductive costs

Figure 3.5 shows how the average score for each interaction type (male-male, female-female, male-female and female-male) varies with the ratio of MRC to FRC . The results for male-male and female-female interactions are very similar (fig. 3.5a). Regardless of the value of MRC , both male-male and female-female interactions tend to be cooperative. In same sex interactions players gain, on average, between 2.5 and 3.00 points per game. Intra-female games score slightly higher than intra-male games, but this difference is small. In model 1, female-female interactions were also very cooperative, however, male-male interactions were far more competitive than is the case here. Why the males in this simulation should be so cooperative will become clear after examining the inter-sex interactions.

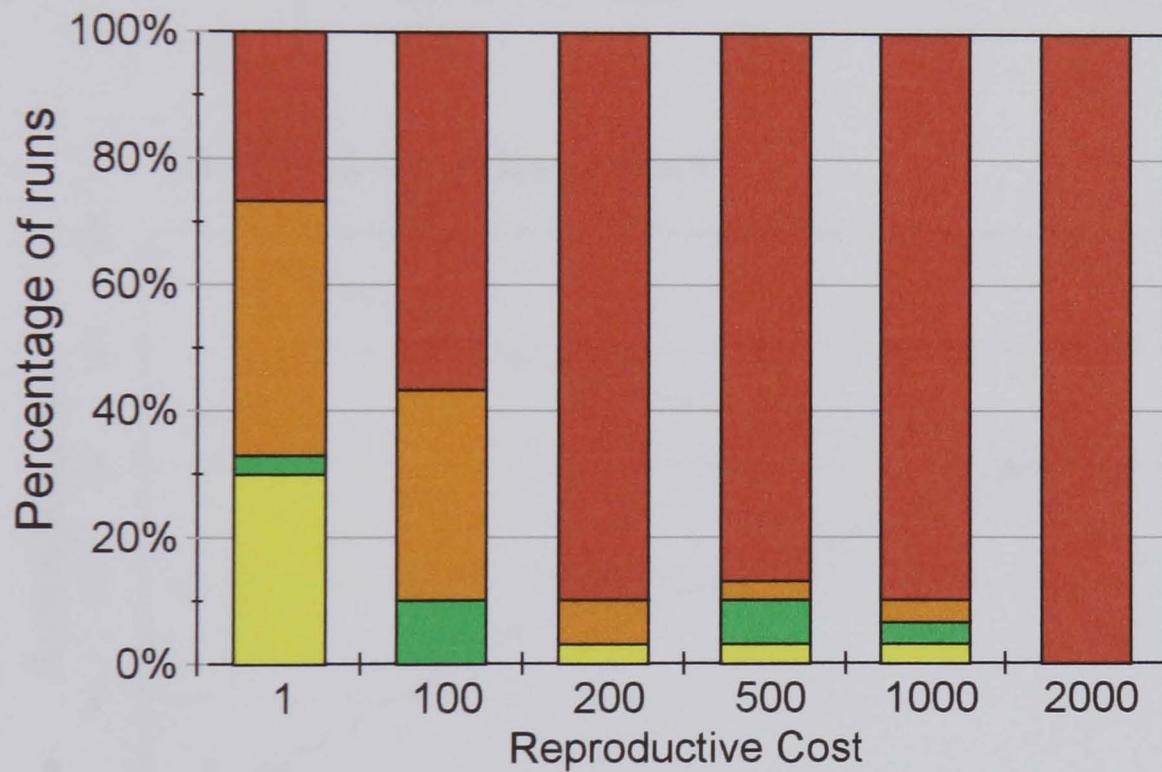
The results for the inter-sex interactions strongly predict the evolution of non-reciprocal altruism under these conditions. The greater the difference in male and female costs the greater the divergence in their average scores. For instance, when

		Opponent	
		C	D
Player	C	3	0
	D	5	1

a) Model 2



b) Model 1

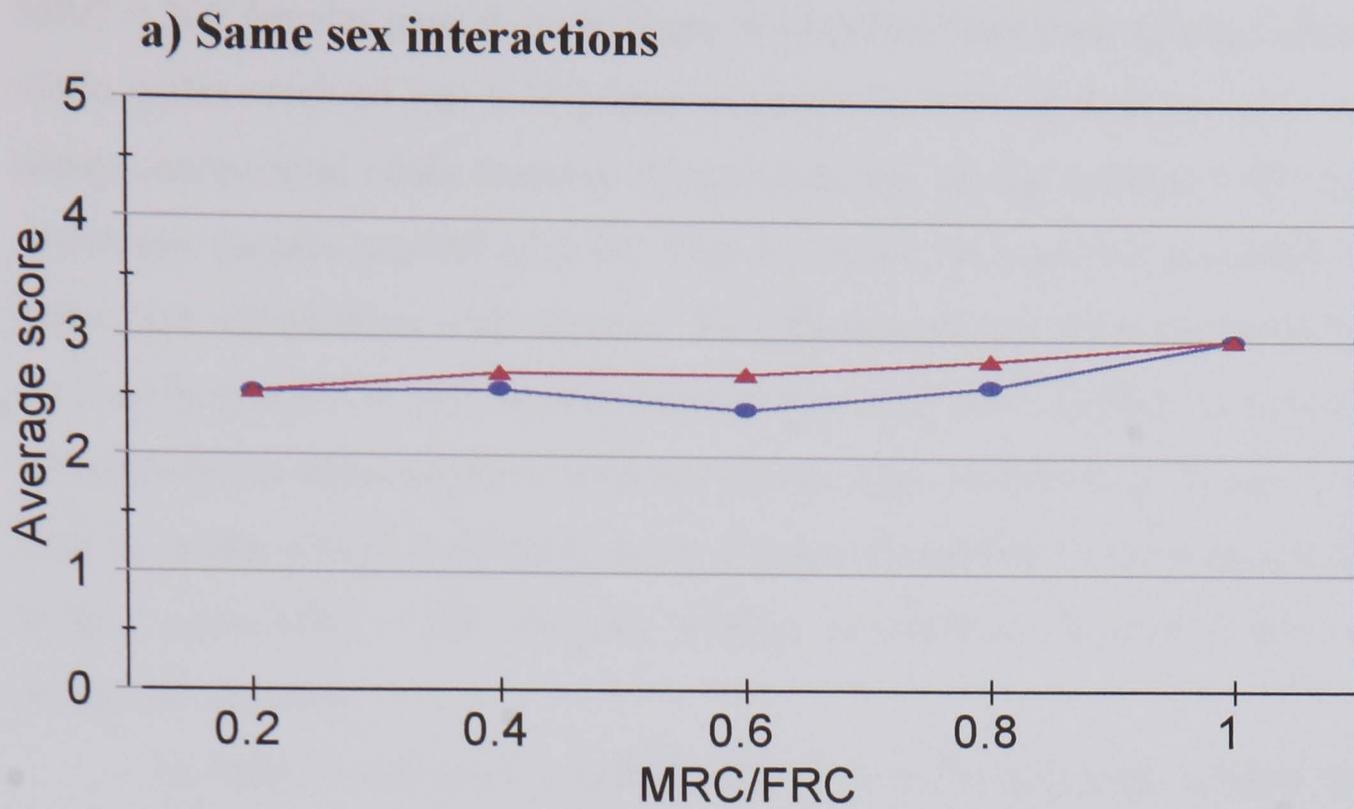


Average score per player, per game:

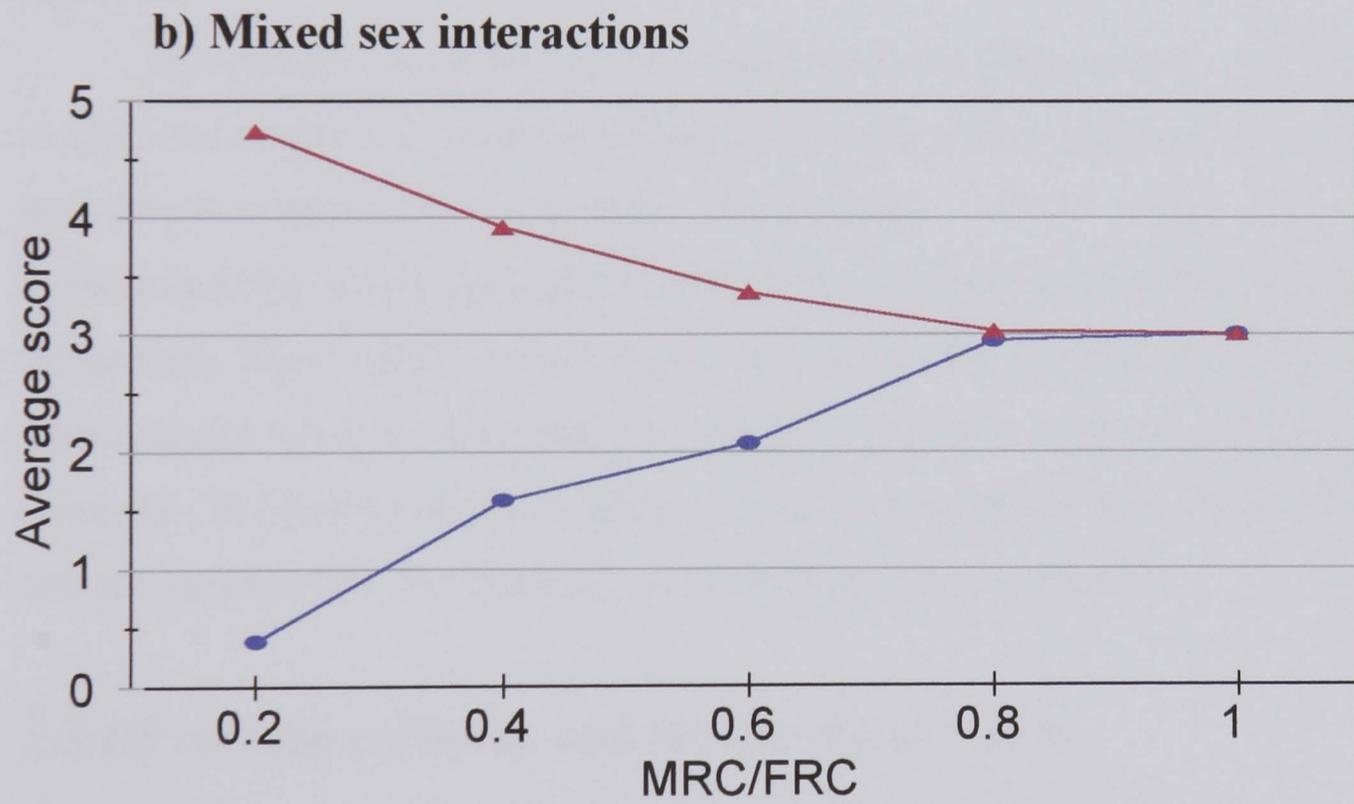


Figure 3.4: The control experiments

Male and female reproductive costs are equal in each case. Each bar represents a summary of the average scores over 30 simulations: (a) shows the distribution of the average scores for model 2 when interactions and reproduction are linked; (b) shows the distribution of average scores for model 1 where there is no connection between the interaction and reproduction phases. The distributions are very similar in each case.



● male vs. male ▲ female vs. female



● male vs. female ▲ female vs. male

Figure 3.5: Variation of average scores with MRC/FRC

The results for model 2 are shown for a) same-sex interactions, and b) mixed sex interactions. Each point on the graph represents the average score per player per game, averaged over 30 separate simulations.

MRC = 200 females gained, on average, 4.74 points from their games against males while males received just 0.38 points in return. In 73% of these simulations males always cooperated while females always defected, giving females 5.00 points and males the suckers pay-off of 0.00. That is, males have gained absolutely nothing from their interactions with females. To differentiate this from the behaviour that evolves in model 1, it will be called strong non-reciprocal altruism. In the other 27% of experiments non-reciprocal altruism of the type described in Model 1 evolved. That is, males always cooperated while females alternately cooperated and defected. In fact, when MRC = 200, the only strategy to evolve in all experiments was non-reciprocal altruism.

At MRC = 400 non-reciprocal altruism was the dominant strategy in all but one simulation, although strong non-reciprocal altruism did not evolve. Even at MRC = 600 males behaved as non-reciprocal altruists in 40% of experiments. Only at MRC = 800 do the scores even out: both sexes played a strategy of reciprocal altruism.

In summary, while linking interactions and reproduction has very little effect on the outcomes of the control experiment, it greatly effects the outcomes when male and female reproductive costs differ. When $MRC \leq 200$, males nearly always behave as strong non-reciprocal altruists, always cooperating with females who never reciprocate. When $MRC \leq 600$ there is strong selection for non-reciprocal altruism, where males always cooperate and females alternate between cooperation and defection. In other words, the quality of male non-reciprocal altruism has increased, and the threshold for this behaviour is much higher than in model 1.

3.5.4 Paternity certainty and the threshold values.

Strong non-reciprocal altruism and non-reciprocal altruism can greatly influence a female's reproductive success. Strong non-reciprocal altruists donate 5.00 points per game to females, and gain nothing in return. This means that the only way that males can gain points is through their intra-sex interactions which explains why male-male cooperation is so high in this model as compared with model 1. Why are males behaving as non-reciprocal altruists, and why are the threshold values 200 and 600 for strong non-reciprocal altruism and non-reciprocal altruism respectively? There are two possible hypotheses. Firstly it is possible that males only behave as

non-reciprocal altruists when they can afford to do so and have enough points to produce two offspring in quick succession. This would be in a accord with model 1, where it was found that males would only behave as non-reciprocal altruists when there were no promiscuity costs (section 3.4). The alternative hypothesis is that males behave in this way in response to high paternity certainty, and will invest in females regardless of lost of mating opportunities. These hypotheses can be tested separately for strong non-reciprocal altruism and non-reciprocal altruism by performing similar calculations to those used in section 3.4. It will be assumed that members of the same sex always cooperate with each other, receiving 300 points per 100 interactions.

a) Strong non-reciprocal altruism

Assuming that males are strong non-reciprocal altruists, females will gain 500 points each time that they interact with a male (5.00 x 100 interactions), and males will get no points in return. Females will be ready to reproduce in either 2, 3 or 4 selections, with the following probabilities:

$$P(2 \text{ picks}) = P(MM) = 1/4$$

$$P(3 \text{ picks}) = P(MFM) + P(FMM) + P(FFM) + P(FMF) + P(MFF) = 5/8$$

$$P(4 \text{ picks}) = P(FFFF) + P(FFFM) = 1/8$$

$$E(\text{picks}) = (1/4 \times 2) + (5/8 \times 3) + (1/8 \times 4) = 2 \frac{7}{8}$$

This means that most females will be ready to reproduce after three selections, and that males must also be ready to reproduce after 3 selections. The next step is to estimate how many points can a male expect to acquire in 3 selections:

$$\begin{aligned} E(\text{points}) &= ((300 + 300 + 300) \times P(MMM)) + ((0 + 0 + 0) \times P(FFF)) + \\ &\quad 3 ((300 + 300 + 0) \times P(MMF)) + 3 ((0 + 0 + 300) \times P(FFM)) \\ &= (900 \times 1/8) + 0 + (600 \times 3/8) + (300 \times 3/8) \\ &= 450 \text{ points} \end{aligned}$$

This result suggests that males can afford to be strong non-reciprocal altruists when $MRC \leq 450$. But, the results show that strong non-reciprocal altruism never evolves at this value of MRC. These calculations and observations seem to support the hypothesis that males are reserving enough points for two possible matings, with

a threshold for non-reciprocal altruism at 225 points. The alternative hypothesis is that at $MRC = 400$, even though males *expect* to score enough points to reproduce, there is a high chance that if they play strong non-reciprocal altruism they will fall short. For instance, if they are picked to play three females in a row, or one male and two females, they will not have enough points to reproduce. The probability of not getting 400 points within 3 selections is:

$$\begin{aligned} P(\text{males do not score 400 points in 3 games}) &= 3 \times P(\text{MFF}) + P(\text{FFF}) \\ &= 3/8 + 1/8 \\ &= 1/2 \end{aligned}$$

This means that males have a 50% chance of not being able to reproduce when they meet a fertile female. Strong non-reciprocal altruism is clearly a risky strategy at a reproductive cost of 400. By not playing strong non-reciprocal altruism at $RC = 400$ males get the double advantage of avoiding the risks of failing to get enough points while at the same time maximising their potential for multiple matings.

b) Non-reciprocal altruism.

The threshold for ordinary non-reciprocal altruism is between 600 and 800 points. With non-reciprocal altruism males gain 150 points each time they meet a female, while the female gains 400 points. The females can expect to be fertile after 3 selections (see section 3.4). How many points can males expect to acquire during this time?

$$\begin{aligned} E(\text{points}) &= ((300 + 300 + 300) \times P(\text{MMM})) + ((150 + 150 + 150) \times P(\text{FFF})) + \\ &\quad 3 ((300 + 300 + 150) \times P(\text{MMF})) + 3 ((150 + 150 + 300) \times P(\text{FFM})) \\ &= (900 \times 1/8) + (450 \times 1/8) + (750 \times 3/8) + (600 \times 3/8) \\ &= 675 \text{ points} \end{aligned}$$

675 is very close to the observed threshold for non-reciprocal altruism. If males were attempting to keep enough points for two matings, the threshold would be half of this value, i.e. 337.5 points. This clearly is not the case. In other words by

playing non-reciprocal altruism males are foregoing opportunities for multiple matings.

These calculations are very revealing. Males will only behave as *strong* non-reciprocal altruists when they can do so without jeopardising their own chances of producing at least one offspring. There is no point in a male investing in a female to the extent that it makes him too weak to reproduce. Non-reciprocal altruism, on the other hand, appears to be a very good strategy even at high male reproductive costs. Males are behaving as non-reciprocal altruists even though this means paying a cost in terms of lost mating opportunities with other females. The likelihood of mating with the female he is investing in is the key factor here. When a male helps a female there is around a 57% chance that he will be the father of her offspring (see figure 3.6). The converse of this, of course, is that there is a 43% chance he will be investing in another male's offspring. None the less it seems that paternity certainty of 57% is enough to promote paternal care.

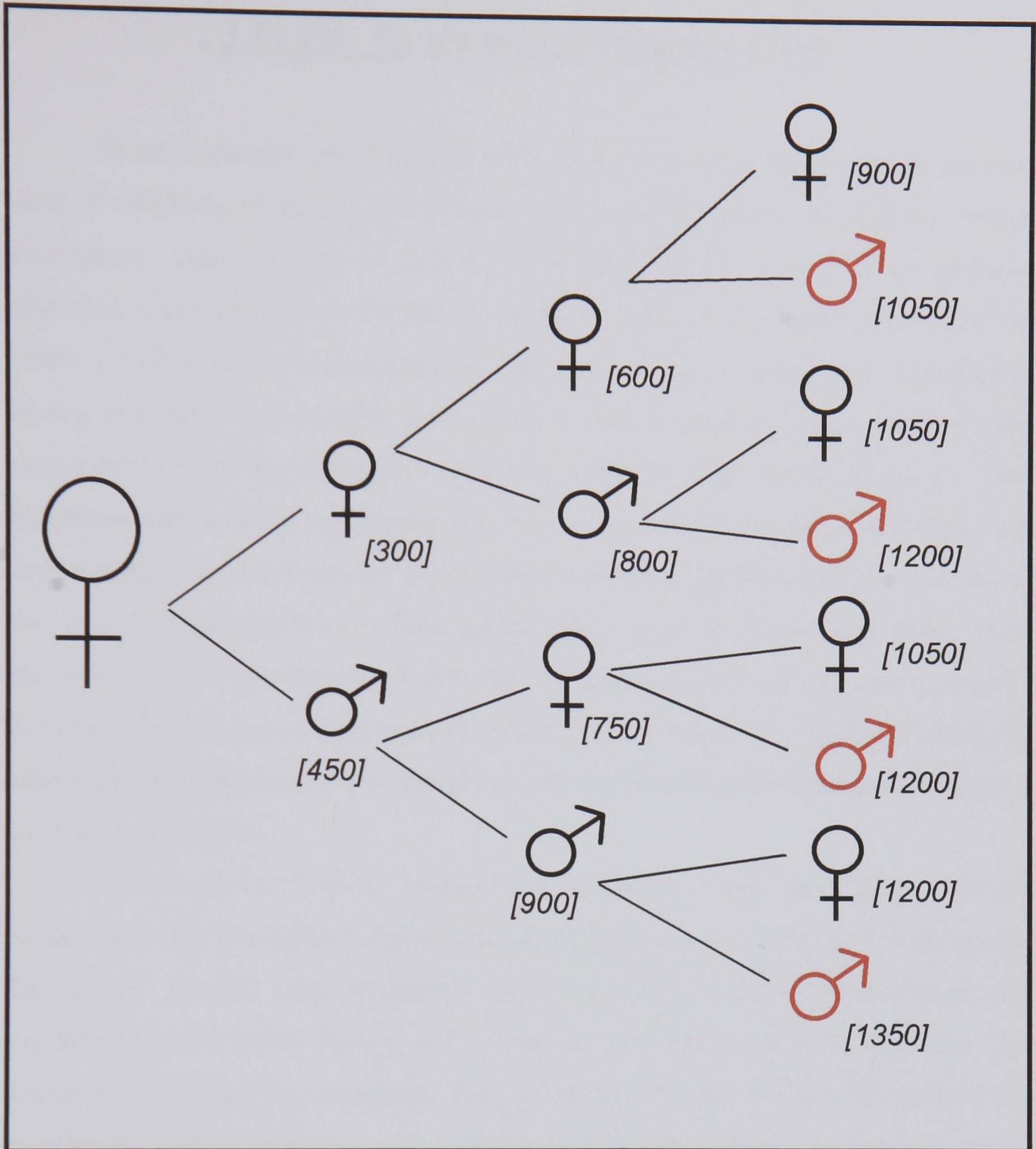


Figure 3.6: Probability tree to estimate probability of paternity.

The tree shows all the possible types of interactions a single female could have over three selections. If she meets a female she gains 300 points, if she meets a male she gains 450 points. Her accumulated score is shown in the square brackets. At 7 different points on the tree she interacts with a male, and if she has enough points they can reproduce. Only four out of the seven males on the diagram would be able to reproduce (shaded in red). This means that whenever a male meets a female, he has a 4/7 or 57% chance of breeding with her.

3.6: The Evolution of Paternal Care

In monogamous social groups, males usually involve themselves in paternal care of offspring (although not always, e.g. in many species of gibbon). While monogamy occurs in 5% of mammals (Kleiman 1977), and 15% of primates (Rutberg 1983) the reasons for its evolution are poorly understood. Clutton-Brock (1989 p.344) describes monogamy as “one of the most puzzling of mammalian mating systems.” One possible explanation is that monogamy occurs when female ranges are so large that males are only able to defend a single female at a time. This hypothesis may explain monogamy in gibbons (van Schaik and van Hooff 1983) but does not appear to have general applicability. Cockburn (1988) found no evidence in rats that monogamous females have larger home ranges. Similarly in primates, once the effect of body size has been controlled for, monogamous and polygynous species have very similar home range sizes (Dunbar 1988). Furthermore, Dunbar (1988) has shown that monogamous males would actually be capable of defending the ranges of three or four females.

Clutton-Brock (1989) favours the hypothesis that monogamy evolves whenever males can achieve higher reproductive success by helping a female to rear the young. In this case monogamy serves the dual function of increasing the reproductive rate of the female, and increasing the male’s paternity certainty. For instance, among canids, monogamy allows females to produce unusually large litters (Gittleman 1986). Gittleman and Oftedal (1987) have shown that communal or biparental care in carnivores is associated with high litter weights and litter growth rates in comparison to species with only maternal care.

Marmosets and tamarin females usually give birth to twins and may produce two litters in a single year. This high reproductive investment may only be possible when females receive male assistance in offspring care (Feistner and Price 1990; Ferrari 1992; Ross 1991). In marmosets, mothers without helpers reduce their nursing frequency, and wean their infants later than those with helpers (Ximenes and Sousa 1996). This means that in callitrichids, males may be better off helping a single female raise twins, than mating polygamously (Dunbar 1988). However, Goldizen (1990) has shown that the common ancestor to the callitrichids while monogamous, only gave birth to a single offspring at a time. The pre-existence of

monogamy and male care would have then allowed the subsequent evolution of twinning. But, if we assume that male care giving evolved before female energetic costs became high (due to twinning) then we can no longer use high female energetic costs alone as our explanation for paternal care. Furthermore, this hypothesis cannot apply to monogamous species such as sakis, titis and night monkeys where twinning does not commonly occur. In these species Clutton-Brock (1989 p.347) describes paternal care and monogamy as “an enigma.”

At present there is no unifying theory to explain the evolution of paternal care. In the next section a new hypothesis will be presented that is based on the models developed in chapters 2 and 3.

3.6.1 Paternal care: evolution at the edge of chaos

This chapter has clarified and expanded the model presented in chapter 2 where it was shown that non-reciprocal altruism is one of a whole range of cooperative strategies that can emerge in populations of mixed sex. Non-reciprocal altruism was compared to paternal care, and it was hypothesised that if female energetic costs of reproduction are very high then male care could occur, even in the absence of genetic paternity. This chapter has shown that the benefits of non-reciprocal altruism, in terms of a shorter inter-birth interval and generation time, could be great (section 3.2). More importantly, it has shown that paternal care is not merely a response to high female energetic costs, but that it will evolve only when female costs are high *relative to* male costs (section 3.3). More specifically, we can only expect the evolution of paternal care when male costs are 10% or less than female costs.

The most worrying aspect of this hypothesis is that it seems very unlikely that male reproductive costs could ever be just 10% of female costs. Male costs of reproduction are not insignificant. In many cases males must meet the energetic costs of male-male competition, maintenance of a larger body size and territorial defence. In macaques, house martins and ptarmigans it has been shown that male body condition is highly related to reproductive success (section 3.4). Given that male reproductive costs are likely to be far greater than 10% of female reproductive costs, is this model inapplicable?

In times of evolutionary change unusual conditions should be expected. An increase in body size, a climatic shift, an increase in lactation time, or an increase in the duration of offspring dependency could all elevate female energetic costs. If female costs become very high, even for a transitory period, the basic model predicts that males would provide care for females and their offspring, regardless of paternity. This is a very unstable situation. In the complexity literature the threshold $MRC = 10\% FRC$ would be called the 'edge of chaos' (Lewin 1993; Waldrop 1993). This is the unstable part of the model, where any small change that affects the value of MRC or FRC will spin the model in one of two directions: no paternal care, or strong paternal care. If male costs increase, or female costs decrease so that MRC is greater than 10% of FRC, then non-reciprocal altruism will no longer be selected and it is unlikely that paternal care will evolve. On the other hand, if female costs remain high relative to male costs then we would expect to see a change in male behaviour. Paternity certainty is not a condition for non-reciprocal altruism. However, in a situation in which non-reciprocal altruism is favoured, males could maximise the benefits to themselves by trying to invest in those females who are likely to become mothers of their own offspring. That is, we would expect males to start to interact with and reproduce with the same females.

This link between interactions and reproduction has been reported in a number of primate species which are not usually monogamous or polyandrous. Stanford *et al.* (1994) have shown that the presence of estrous females is the best predictor of hunting behaviour in male chimpanzees, and bonobo males have been reported to give food to females immediately after, or even in the midst of intercourse (Kuroda 1984; de Waal 1987). Smuts (1985) reports that subordinate males in a harem group often form special friendships with females, helping them in the care and protection of offspring in the expectation of future matings. Females can also actively encourage this link between interaction and reproduction. Anderson (1992) suggests that in chacma baboons, females encourage male investment by limiting mating to a single male and assuring him of a high likelihood of paternity.

Once a link between interactions and reproduction is made, the ground rules change and male care giving can become locked into the system. Model 2, presented in section 3.5, shows that if interactions and reproduction are linked, then males will invest in females as long as male reproductive costs are less than or equal to 60% of female costs. Furthermore, males ought to invest even more heavily. Under this new

scenario male reproductive costs could increase, but as long as they remain below the threshold value of 60% FRC then paternal care will remain a stable strategy. What is more, high levels of paternal care may allow females to invest even more in their offspring, elevating female energetic costs still further. For example, in tamarins male helping is such a successful strategy in overcoming the constraints of high female costs, that female energetic costs have soared and male helpers are now essential (Jennions and Macdonald 1994). Similarly in carnivores, the presence of helpers in some species has released energetic constraints which means that in many cases energetic costs have become so high that reproduction is impossible without helpers (Creel and Creel 1991).

Field studies on the semipalmated sandpiper, *Calidris pusilla*, suggest that comparison of male and female energetic costs is a constructive approach to the evolution of paternal care. In this species, while both males and females engage in care of the offspring, it is not unusual for the female to desert the brood leaving the male to care for the chicks. Two separate studies have looked at this behaviour, one on the coast of Hudson Bay, Manitoba (Gratto-Trevor 1991), the other in North Alaska (Ashkenazie and Safriel 1979). Female desertion was more common in the latter study, and occasional male desertion was reported in the former. Gratto-Trevor suggests that the increased energetic stress in the harsh arctic environment was responsible for the higher male cooperation and increased female desertion in this study. In both studies there was clear evidence of the high energetic demands on the female. In the Alaskan birds Ashkenazie and Safriel calculate that the female's energetic requirement is 15% greater than the males. By the end of the breeding season females are in a much poorer condition than males, and females leave the brood early in order to find better feeding grounds.

This is not the first time that paternal care has been studied within the theoretical framework of the evolution of cooperation. Ligon (1983) suggests that monogamy is a case of reciprocal altruism, where males are trading male care for mating opportunities. Koenig (1987) strongly disagrees with this position. He believes that in the case of monogamy both the male and female are acting in their own self interest. He claims that males who donate aid to females do not incur a lifetime reduction in fitness, hence they cannot be acting altruistically. But, this reasoning misses the point. Cooperation in terms of feeding and aiding a partner involves high *short-term* costs in terms of time, energy and lost mating

opportunities. If these short-term costs are balanced by *long-term* benefits then there will be no cost in terms of lifetime reproductive success (Ligon 1991). The point is that at any given moment a male would be better off not cooperating with the female, but in the long term cooperation pays. Koenig also argues that monogamy cannot be reciprocal altruism because the female does not incur any costs. This is true, even in the short term the female does not seem to lose out by mating with her partner. But, if males are non-reciprocal altruists then this objection is over-ruled, since males are predicted to be cooperative even though females do not reciprocate.

The model of paternal care developed here suggests that even a temporary increase in female energetic costs (relative to male energetic costs) can seed the evolution of male care-giving. These are abstract models, and the pay-offs associated with different behaviours will vary in the real world. The point is that these models suggest that there are two stages in the evolution of paternal care. The first stage is concerned with the evolutionary origins of male care. In the first instance paternity certainty is not an issue. All that is required for male care giving to evolve is that female energetic costs should be considerably greater than male energetic costs. The second stage is concerned with the stability and maintenance of male care giving over many generations. Progression to the second stage will only occur if males attempt to increase paternity certainty. If this happens, paternal care and paternity certainty can co-evolve, raising the threshold value of MRC below which we would expect male care-giving. In this case, paternal care will become stable as long as there is a fair degree of paternity certainty and quite high female energetic costs in comparison to males.

This model of paternal care will be difficult to prove because the first stage is likely to be very short lived. Among primates, gibbons may prove to be a good test species. Gibbons are especially interesting because, although they are usually classified as monogamous, mate switching and copulations outside of the pair bond also occur. Palombit (1995), in a six year study of *Hylobates lar* and *Hylobates syndactylus*, found that only three out of seven adult females successfully reproduced. He reports that still births, abortions, premature births and early postpartum death are common for both species which indicates very high female costs. The small body size of the males indicates that male costs are somewhat lower than female costs. Palombit found that the most successful female, who had three offspring, also had the longest lasting pair bond and suggests that the stability of the

pair-bond is very important in determining a female's reproductive success. Furthermore, males may be described as non-reciprocal altruists as they are more active than females in maintaining proximity to their partner and in their aggressive interactions with neighbours. However, pair-bonding is not always associated with high levels of paternal care (strong non-reciprocal altruism), while some males do carry infants into their second year this is not a universal trait. Relatively high female reproductive costs and variability in the degree of male care suggests that gibbons may be good animals on which to test this model.

3.6.2 Polyandry, paternal care, and paternity uncertainty

In chapter 2, considerable space was devoted to a discussion of paternity certainty. It emerged that the correspondence between male care-giving and probability of paternity is not as straight-forward as usually assumed. This chapter has furthered this debate by showing that: (1) When male reproductive costs are relatively low, males can afford to help indiscriminatingly with infant care, without any loss of mating opportunities (section 3.4); (2) Once interactions and matings become linked, males will help females in offspring care even if they risk losing mating opportunities, if the probability of paternity is around 50% or more (section 3.5.4). This second prediction accords well with what we know about callitrichid mating systems. For instance, Terborgh and Goldizen (1985) found that out of six groups of *Saguinus fuscicollis*, five of them contained two adult males. Both males mated with the female to an equal extent (Goldizen 1987b) and hence they each had a 50% chance of paternity. Presumably unaware of actual paternity of the infants, both males donated equal proportions of time to helping the breeding female by carrying infants and sharing of large insects and fruits.

Polyandry has clear benefits for the female as more male helpers means that she can raise more young, but the benefits to males are unclear (Davies 1991). Ferrari (1992) suggests that male care in callitrichids may be a form of intra-sexual competition, where males attempt to impress the female with their care-giving skills. However, a recent study by Tardif and Bales (1997) found no evidence that captive common marmosets or cotton-top tamarins use infant-carrying as a courtship

strategy. Davies predicts that polyandry will only be beneficial to males in harsh environments, and that usually monogamy would be a better male strategy.

In callitrichids, not only are most groups polyandrous, but there is a distinct absence of competition between males, and each male tolerates the other's copulations with the breeding female. This combination of polyandry and male-male tolerance has also been observed in dusky moorhens (Garnett 1980), Galapagos hawks (Faaborg and Bednarz 1990), lammergeieers (Heredia and Donázer 1990), pukekos (Craig and Jamieson 1990; Jamieson *et al.* 1994), Tasmanian native hens (Maynard Smith and Ridpath 1972), and lions (Packer *et al.* 1988). In these cases, it seems that paternity *uncertainty* is the force that maintains male care. On the other hand, in the acorn woodpecker (Mumme *et al.* 1983; Koenig 1990), dunnocks (Davies 1992) and stripe-backed wrens (Rabenold *et al.* 1990) polyandry is associated with male competition.

Why male-male competition occurs in some polyandrous groups, and not others, is unclear. Sherman (1995) suggests that relatedness between males will favour mating tolerance, although there is absolutely no evidence of this. In tamarins adult males are assumed to be unrelated (Terborgh and Goldizen 1985) and in most other cases the genetic relatedness between male helpers is simply unknown. Vehrencamp (1983) predicts that when breeding sites are limited, and larger groups can maintain better sites, egalitarian groups should evolve where shared matings encourage males to stay with the group. Alternatively, male tolerance may be the least costly option if females specifically attempt to mask paternity. In the polyandrous white-winged trumpeter, Sherman (1995) reports that even subordinate males father some of the offspring. Sherman suggests that in order to equalise paternity probability for all of her helpers, the breeding female encourages mating attempts from subordinate males, and will occasionally discourage the dominant male. This strategy seems to work, since the subordinate males provide more food for the chicks than the dominant male. In callitrichids, the breeding female is normally dominant (Ferrari 1992) which gives her control of male mating, and this may explain the lack of competition between the males.

These discussions suggest that females may use paternity *uncertainty* to maintain the interest of two or more males. While it may seem surprising that males are willing participants in this arrangement, the models developed here suggest that a

probability of paternity of just 50% is enough to promote male care giving behaviours.

Paternal care is not restricted to mammals and birds. In many insect species, such as butterflies, costs of reproduction can be very asymmetric as females are solely responsible for egg production. It is quite common for males to donate nutrients, or 'nuptial gifts' to the females during mating (Boggs 1990; Karlsson 1995; Leimar *et al.* 1994). These male-derived nutrients are used by the female for egg production and somatic maintenance, and represent male investment in reproduction. Boggs (1990) suggests that male donations may be particularly important when female feeding is restricted. Leimar *et al.* (1994) also show that gift-giving buffers females against food shortages. In the language of this model, food shortages translate to high reproductive costs. In butterflies, male care is far more common in polyandrous species than monandrous species. In polyandrous species the females eggs are unlikely to be fertilised by a single male, and so the males have no way of judging how many of the female's offspring will be theirs. Like the tamarins described above, paternal care occurs with paternity uncertainty and Leimar *et al.* (1994) describe males *investing as a group* in females.

3.6.3 Non-reciprocal altruism in humans

Until now, discussion of cooperative and competitive strategies has been restricted to observations on non-human primates and other animals. However, perhaps the most intriguing evidence for non-reciprocal altruism is found in humans. If human inter-sexual relationships are based on non-reciprocal altruism then we would expect females to defect more often than males in Prisoner's Dilemma situations. Casti (1994) reports that in a large number of Prisoner Dilemma experiments females appear to defect more often than males. However, it is not clear which types of interactions provoke defection, or that female defection is accompanied by male cooperation. Furthermore, these types of laboratory experiments usually involve strangers and are not really indicative of the types of strategies individuals use in long-term relationships.

Murstein *et al.* (1977) compared cooperative relationships between friends and between marriage partners. They found that cooperative relationships between

friends tend to be highly 'exchange-orientated'. That is, they work on a reciprocal basis, in which favours of roughly equivalent value are exchanged. However, they found that marriages varied in the extent to which marriage partners are exchange orientated. They comment that an exchange orientated person (1977 p.543):

“may see love as a series of reciprocal exchanges and would feel badly if a person whom he loved did less for him than he believed he did for his beloved.”

On the other hand, a non-exchange orientated person (1977 p.543):

“is not at all concerned with keeping a mental balance sheet on just what he has done for others and what they have done for him. For a non-exchange orientated person, to love another is to forgive his transgressions and to accept him unconditionally.”

They found that both men and women in non-exchange orientated partnerships were happier, and found their marriage to be more satisfactory than those in exchange orientated marriages. Interestingly, the effect was strongest for men. It is not clear from this study that males are necessarily non-reciprocal altruists. On the other hand, Murstein *et al.*'s research appears to suggest that unconditional cooperation may be a recipe for a good marriage. This indicates that humans may be a good species in which to search for strategies such as non-reciprocal altruism.

3.6.4 Summary

In this chapter a new model for the evolution of paternal care has been developed. It is proposed that paternal care, in the absence of paternity certainty, is selected when the energetic cost of reproduction for the female is much greater than the same cost for the male ($MRC \leq 0.1 \times FRC$). If this selection pressure persists, then males will attempt to give care to their own offspring, and will thus establish closer relationships with females. Once this occurs, then paternal care will become an integral part of the mating system and should persist as long as $MRC \leq 0.6 \times FRC$. While infant care will raise the costs of reproduction for the males, it also allows for increased female investment which may further necessitate male aid. Even in this second stage of non-reciprocal altruism, probability of paternity need only be around 50%. It has been suggested that in some cases, in order to prevent male desertion, paternity *uncertainty* may play a key role. This certainly seems to be the case in many polyandrous species, such as the callitrichids. This chapter has also introduced the idea that in some instances it may pay males to invest as a group in the females. Finally, non-reciprocal altruism may be particularly important in understanding the cooperative strategies used in human inter-sex relationships. In the next chapter, this model of paternal care is tested using a comparison of male and female energy expenditure in primates. In addition, the applicability of this model to human evolution will be explored.

Chapter 4

Testing the Model: An Inter-specific Comparison of Sex Differences in the Energetic Cost of Reproduction

4.1: Introduction

In the previous two chapters theoretical models were used to show how sex differences in the energetic cost of reproduction affect patterns of cooperation within groups. It was shown that when females have high energetic costs they are likely to cooperate with each other, for instance in the care of each others offspring (allomaternal care). Furthermore, when male energetic costs are much less than female energetic costs, male investment in females and their offspring may evolve.

Generally, hypotheses regarding the evolution of male care focus only on female energetic costs, such as the costs of lactation (Dunbar 1988) or infant transport (Wright 1984, see also section 1.1.1). Wright (1990) points out that the energetic costs of infant transport are relatively higher in arboreal primates, especially those of small body size which tend to have proportionally bigger infants. But, the tarsier has the highest infant/maternal weight ratio of any primate that produces a single offspring, and yet its breeding system does not involve paternal care. Wright concludes that a combination of small body size, high litter weight, long lactation periods and over-lapping periods of gestation and lactation selects for paternal care, rather than any one factor on its own. Tardif (1994), in a cross-species analysis of the costs of lactation and infant transport in small bodied New World monkeys, found that the relationship between infant costs and care-giving was weak. Furthermore, Thompson *et al.* (1994) point out that callitrichids actually have low overall energy requirements for their body size (measured using standard metabolic rate).

The models developed here suggest that in order to understand the evolution of paternal care it is necessary to consider the balance between *both* male *and* female energetic costs. The advantage of theoretical models is that they allow the manipulation of variables such as energetic costs, and the observation of the origins of behaviour, in a manner which is impossible in the real world. None the less, the

application of such models to the real world is a necessary test of their validity. Because this is a model of the *origins* of male care this task is a difficult one. An animal may be so well adapted to its environment that it is impossible to observe the selective pressures that shaped its present behavioural repertoire. For instance, the absence of observations of predation does not mean that group living did not evolve as a predator-defence mechanism. To the contrary, it indicates that group living is a very effective means of predator defence. With this caveat in mind, the purpose of this chapter is to test the model of the evolution of paternal care developed in the previous chapter, using data from extant primates. This will require an investigation into male and female energetic costs and their relationship to social structure.

While several primate studies have attempted to measure energetic costs (see for example Altmann and Samuels 1992; Coehlo 1974, 1986 ; Coehlo *et al.* 1979; Dasilva 1992; Leonard and Robertson 1994, 1997; see also section 1.2.3), none have compared male and female energy expenditure. For female mammals, the energetic costs of reproduction are undoubtedly high since they must bear the costs of both pregnancy and lactation. Primate infants, with their large brain sizes and extended periods of development are likely to be an even heavier burden on the mother. As discussed in section 1.2.3, lactation in particular, imposes enormous energetic demands on the mother. In fact, the costs of reproduction are so great for females that Coehlo states (1986 p.153):

“It is a physiological fact that the actual costs of reproduction (pregnancy and lactation) are borne only by the female primate; there is nothing physiologically comparable in the male.”

But is Coehlo correct? Are male costs of reproduction negligible in comparison with female costs? Because males do not usually contribute directly to offspring care, male energetic costs of reproduction usually derive from the costs of male-male competition. In many species male-male competition is manifest in the much larger size of the males compared with females, which means that for males the costs of body maintenance will be relatively high. It is possible that in sexually dimorphic species, such as the gorilla, male energetic costs will be high, maybe even as high as female energetic costs. The question is, which sex requires the most energy to reproduce? The male gorilla who must maintain a body twice the size of the female, or the female gorilla who must invest in long periods of gestation,

lactation and infant care? Darwin (1871 p.581) suggests that male and female energetic costs are actually very similar:

“The expenditure of matter and force by the two sexes [in mating] is probably nearly equal, though effected in very different ways and at different rates.”

But, while Darwin’s prediction makes sense in sexually dimorphic species such as the gorilla, it is not so clearly applicable to those species in which sexual dimorphism is low. Under these circumstances males are free from both the costs of pregnancy and lactation, and the costs of maintaining a large body size which suggests that male energetic costs are low in comparison to the female. If this logic holds, then the balance of male and female energetic costs will vary with the degree of sexual dimorphism in body size. This means that the conditions under which male care is expected (relatively high female costs in comparison to males) will arise when sexual dimorphism is low.

Sexual dimorphism and mating systems have been theoretically inter-linked ever since Darwin (1871) suggested that sexual selection for large body size would occur in species in which male competition for mates is high. This means that sexual dimorphism is expected to be high in polygynous species in which breeding competition is great. In birds, for instance, increased body size dimorphism is associated with increased intra-sexual competition (Owens and Hartley 1998). Conversely, sexual dimorphism will be low in species where male mating competition is minimal, for instance in monogamous species. But, the sexual selection hypothesis does not address the question of why monogamy should have evolved in the first place. Furthermore, it is misleading in its view that sexual dimorphism results only from changes in male behaviour and physiology. Increases or decreases in female body size, which may profoundly affect reproductive success, also alter levels of sexual dimorphism (Martin *et al.* 1994; Wilner 1989). It is possible that the relationship between sexual dimorphism in body size and breeding system is more complex than the sexual selection hypothesis suggests. Changes in the level of sexual dimorphism may profoundly affect the balance of energetic costs between the sexes which will, in turn, feed back onto the structure of the mating system. This chapter tests the hypothesis that a decrease in body size dimorphism leads to an increase in relative energetic costs for the female in comparison to the

male, which in turn selects for the evolution of male care and allomaternal care. In order to do this, a cross-species examination of the relationship between male and female energetic costs will be conducted. This will be followed by an analysis of the benefits of care-giving behaviours.

4.2 Defining the Energetic Cost of Reproduction

The first stage in the analysis will be to estimate the energetic costs of reproduction. In order to develop a methodology for this, it is first necessary to arrive at a definition of the energetic cost of reproduction. As we have already seen (section 1.2.3) there is a considerable body of evidence suggesting that both males and females incur energetic costs due to reproduction. Female costs are associated with the production of gametes, gestation, lactation and child-care. Male costs arise primarily from the production of gametes, courtship, male-male competition and, in some instances, child-care. Additionally, behaviours such as grooming allies to stabilise coalitions, feeding to maintain a larger body size or to accumulate body fat, food sharing and predator defence may also affect reproductive success, whether directly or indirectly. In fact, it is difficult to isolate any single aspect of an individual's behavioural and physiological make-up that does not contribute to reproductive success (Morbeck 1997), and that should be excluded from an analysis of energetic costs of reproduction. Because of this, the following definition is proposed: **The energetic cost of reproduction is the sum of the energetic costs of every activity that contributes to the production of a single, surviving offspring.**

It is assumed that there is a minimum energetic cost of reproduction and that investments below this value will be unsuccessful. There is no theoretical maximum energetic investment, although there is likely to be an optimal value. What this optimal value is will depend not only on sex and species, but also habitat type and quality, age and rank. The analysis below examines species level data and so generates estimates of the average energetic cost of reproduction for males and females of each species.

The definition given above of the energetic cost of reproduction is an ideal, incorporating all behaviours which contribute to reproductive success. For practical purposes four main categories that contribute to energetic costs can be identified:

- a) Daily body maintenance,
- b) Activity expenditure on moving, social interactions, feeding, defence etc.,
- c) Intra-sex competition for mates,
- d) Parental care.

The costs of daily body maintenance are directly related to body size. Quite simply, larger animals require more energy for body maintenance, although energy requirements per unit of body weight decrease with increased body weight (Kleiber 1932, 1961). Thus, body weight data is required to estimate the cost of body maintenance.

The energetic costs of activities such as moving, grooming or feeding depend partly on body size, but will also vary with activity. The energy expended while walking, for instance, is greater than the cost of feeding per unit of body weight. Thus in order to estimate daily energy expenditure it is necessary to know how much time an animal spends on each activity. Time budgets provide such data, and can be translated into energetic costs using Coehlo's model (1974, 1986; Coehlo *et al.* 1979). Assuming that breeding competition involves increased moving and/or social time, then time budgets also provide a rough measure of the energetic costs of intra-sex competition.

The costs of parental care will be different for males and females. For females they will mainly derive from the costs of lactation and gestation and these will be important factors in calculating female energetic costs. The costs of male care could be measured in terms of the costs of infant transport. However, we are concerned here with using energetic data to predict those species in which male care giving has evolved. In order to do this, we require data on what the energetic costs of reproduction are for males and females in the absence of male care. If the energetic costs of male care giving are included in the model, then we automatically lose the ability to make any predictions. For this reason, male care giving will be explicitly excluded from calculations of male energetic costs.

Within species there will be individual variation in energetic costs due to variables such as age, rank and habitat quality. None the less, it should be possible to predict the average energy expenditure per birth. For females, inter-birth interval can be used to delineate the length of the time in which they are investing in each

offspring. However, male energy expenditure per offspring born is considerably more difficult to estimate with confidence, and is likely to be highly variable. Bercovitch and Nürnberg (1996) found that in rhesus macaques only a small number of males sire offspring in a single breeding season. Successful males have more body fat at the start of the breeding season than unsuccessful males, but this is gradually lost. By the end of the breeding season there is no difference in body fat between sires and non-sires. This research indicates very clearly the high overall energetic costs of mate following, guarding and male-male competition in rhesus macaques. But, what of the energetic costs per infant? Out of 21 adult males only 8 were successful, each siring an average of 3.25 offspring. This means that while overall energetic costs for sires were great, high reproductive output considerably reduced the energetic cost per infant born. In contrast, while non-sires may have expended less energy overall, their lack of success means that all of their energy expenditure was wasted.

Bercovitch, and Nürnberg's work on rhesus macaques is one of the only primate studies that uses genetic methods to test paternity. It highlights the considerable variation in male reproductive success and energetic costs, and the difficulties in estimating male energetic costs per offspring born. In theory, males who do not manage to reproduce should be excluded from the analysis entirely, since they have failed to meet the minimum requirements for reproductive success. This means that an accurate assessment of male energetic costs requires data of the type provided by Bercovitch and Nürnberg for rhesus macaques. In the absence of such data, it is only possible to estimate average male energetic costs. This will be done with reference to the amount of time and energy females invest in each reproductive event. For instance, if it takes a female one year to produce and rear offspring to maturity, how much energy does the average male expend in this time? In other words, how much energy does a male expend over the course of a female inter-birth interval? Measuring male energetic costs per female inter-birth interval is not ideal, but will provide comparable data for each sex.

In summary, the energetic cost of reproduction has been defined here as the sum of the energetic costs of all activities which contribute to the production of a single, surviving offspring. Using data on body mass, activity pattern, gestation length and lactation length it should be possible to calculate the average energetic cost of reproduction for each sex per offspring. Female inter-birth interval can be

used to delineate the amount of time individuals contribute to each offspring. Because we are concerned here with the origins of male care giving, the costs of paternal care will be excluded from the analysis. Some of the problems of estimating male energetic costs have been discussed here. Particularly problematic is accounting for individual variation in male reproductive success and energy expenditure. Since these data are unavailable, this analysis will be limited to consideration of average male energetic costs.

4.3 Data

The following data were collected, and are summarised in tables 4.1a, 4.1b and 4.2:

1) Body mass (male and female).

Body mass is an important variable in determining the cost of body maintenance, and for calculating daily energy expenditure. These data were taken from Smith and Jungers (1997), which represents the most up to date source of body mass estimates. These data were also used to calculate sexual dimorphism in body size (male body weight divided by female body weight) which was transformed into a categorical variable using the following categories: low (< 1.15), medium ($1.15 - 1.5$), and high (≥ 1.5).

2) Activity budget data.

These data were mostly gathered from the literature¹ (see table 4.1a for references). The average percentage of time spent moving, resting, feeding, sleeping and socialising per 24 hour period was recorded for each non-human primate species and for each sex. While many papers have been published on activity budgets very few of these present data by sex, limiting their usefulness for this study. Usually, only one set of data was available for each species, and where there was a choice of study sites (for example for the baboons), the population with the largest sample size was used. Data from wild populations were used for all species except for *Saguinus oedipus*, due to the practical difficulties of obtaining data for this species in the wild.

¹ I am very grateful to Mukesh Chalise, Robin Dunbar, Andreas Koenig and Volker Sommer who kindly donated their data for the purpose of this analysis.

	% TIME SPENT ON EACH ACTIVITY										REFERENCE
	MALES					FEMALES					
	feed	rest	move	social	sleep	feed	rest	move	social	sleep	
Callitrichidae											
<i>Saguinus oedipus</i>	7.58	37.85	2.68	1.90	50.00	9.85	34.65	2.93	2.58	50.00	Price 1992
Cebidae											
<i>Alouatta caraya</i>	4.50	37.50	10.50	2.50	50.00	6.50	36.00	6.50	1.00	50.00	Bicca-Marques & Calegario-Marques 199
<i>Alouatta palliata</i>	8.50	36.00	3.50	2.00	50.00	10.00	36.00	2.50	2.50	50.00	Milton 1980
<i>Aotus trivirgatus</i>	28.80	11.95	7.00	2.00	50.00	28.80	11.95	7.00	2.00	50.00	Wright 1978
<i>Ateles paniscus</i>	11.25	23.75	15.00	0.00	50.00	15.60	22.70	11.73	0.00	50.00	McFarland Symington 1988b
<i>Brachyteles arachnoides</i>	9.75	33.04	10.30	1.10	45.80	9.75	31.40	11.90	1.10	45.80	Strier 1987
<i>Callicebus torquatus</i>	11.50	16.00	6.21	12.20	54.00	12.04	23.60	6.04	4.20	54.00	Kinzey et al. 1977
<i>Lagothrix lagotricha</i>	13.00	9.50	26.00	3.00	50.00	9.70	9.10	30.00	1.10	50.00	Defler 1995
Cercopithecinae											
<i>Cercopithecus aethiops</i>	15.90	22.38	8.65	3.12	50.00	19.44	15.18	10.37	4.38	50.00	Baldellou & Adan 1997
<i>Cercopithecus mits</i>	12.45	23.40	11.45	2.60	50.00	18.15	16.05	11.20	4.55	50.00	Lawes & Piper 1992
<i>Erythrocebus patas</i>	15.00	25.50	9.00	0.50	50.00	15.00	21.50	11.50	2.00	50.00	Nakagawa 1989
<i>Macaca mulatta</i>	5.55	22.75	6.20	15.35	50.00	8.40	21.70	4.90	15.35	50.00	Post & Baulu 1978
<i>Macaca radiata</i>	15.00	21.50	3.00	10.50	50.00	25.50	7.50	5.00	12.00	50.00	Singh & Vinathe 1990
<i>Papio anubis</i>	24.50	9.50	8.00	8.00	50.00	29.25	3.75	7.75	9.25	50.00	Bercovitch 1983
<i>Papio cynocephalus</i>	21.05	12.95	13.20	2.80	50.00	20.50	11.25	13.00	5.25	50.00	Rasmussen 1985
Colobinae											
<i>Colobus badius</i>	11.00	34.00	2.00	3.00	50.00	15.50	28.00	2.00	4.50	50.00	Clutton-Brock 1974
<i>Presbytis entellus</i>	16.33	32.17	1.10	0.37	50.00	16.05	29.70	1.21	3.04	50.00	Mukesh Chalise (Pers. comm.)
Hylobatidae											
<i>Hylobates lar</i>	10.00	29.50	7.00	3.50	50.00	18.00	22.00	7.50	2.50	50.00	Nettlebeck 1993
Pongidae & Hominidae											
<i>Pongo pygmaeus</i>	26.80	15.30	4.40	0.50	53.00	18.90	21.00	5.70	1.40	53.00	Leonard & Robertson 1997
<i>Gorilla gorilla</i>	30.55	15.03	3.33	1.00	50.00	29.55	15.20	3.70	1.75	50.00	Watts 1988
<i>Pan troglodytes</i>	27.80	8.90	6.90	3.10	53.30	30.30	8.90	4.40	3.10	53.30	Leonard & Robertson 1997

Table 4.1a: Activity budget data.

	body mass (kg)		gestation	lactation	IBI	male care
	male	female	(days)	(days)	(years)	
Callitrichidae						
<i>Saguinus oedipus</i>	0.42	0.40	168	50	0.58	3
Cebidae						
<i>Alouatta caraya</i>	6.42	4.33	187	.	.	1
<i>Alouatta palliata</i>	7.15	5.35	186	630	1.88	1
<i>Aotus trivirgatus</i>	0.81	0.74	133	75	0.75	3
<i>Ateles paniscus</i>	9.11	8.44	.	824	2.88	.
<i>Brachyteles arachnoides</i>	9.61	8.07	.	390	2.82	1
<i>Callicebus torquatus</i>	1.28	1.21	.	120	.	3
<i>Lagothrix lagotricha</i>	7.28	7.02	223	315	1.50	1
Cercopithecinae						
<i>Cercopithecus aethiops</i>	4.26	2.98	163	365	1.33	1
<i>Cercopithecus mits</i>	7.93	4.25	140	60	0.83	1
<i>Erythrocebus patas</i>	12.40	6.50	168	213	1.00	1
<i>Macaca mulatta</i>	11.00	8.80	165	365	1.00	1
<i>Macaca radiata</i>	6.67	3.85	162	365	1.00	1
<i>Papio anubis</i>	25.10	13.30	180	420	1.12	2
<i>Papio cynocephalus</i>	21.80	12.30	173	365	1.75	2
Colobinae						
<i>Colobus badius</i>	8.56	7.42	150	790	2.12	1
<i>Presbytis entellus</i>	15.00	10.28	200	300	1.68	1
Hylobatidae						
<i>Hylobates lar</i>	5.90	5.34	213	730	2.69	1
Pongidae & Hominidae						
<i>Pongo pygmaeus</i>	77.90	35.60	250	408	6.50	1
<i>Gorilla gorilla</i>	170.40	71.50	260	1004	3.83	1
<i>Pan troglodytes</i>	59.70	45.80	235	1460	5.50	1

Table 4.1b: Life history variables for species used in activity budget analysis
See text for definitions and references. IBI is the inter-birth interval

Species	Body Mass (kg)		litter weight at:		gestation length (days)	lactation length (days)	inter-birth interval (years)	male care	allomaternal care
	male	female	birth (kg)	weaning (kg)					
Callitrichidae									
<i>Callimico goeldii</i>	0.50	0.47	0.05	0.21	155.00	70.00	0.47	3	3
<i>Callithrix jacchus</i>	0.36	0.38	0.06	0.13	148.00	90.00	0.52	2	3
<i>Cebuella pygmaea</i>	0.11	0.12	0.03	0.04	137.00	90.00	0.50	3	3
<i>Leontopithecus rosalia</i>	0.62	0.60	0.10	0.12	128.60	90.00	0.50	3	3
<i>Saguinus fuscicollis</i>	0.34	0.36	0.08	.	148.50	90.00	1.00	3	3
<i>Saguinus oedipus</i>	0.42	0.40	0.08	0.09	168.00	50.00	0.58	3	3
Cebidae									
<i>Alouatta palliata</i>	7.15	5.35	0.53	.	186.00	630.00	1.88	1	2
<i>Alouatta seniculus</i>	6.69	5.21	0.53	1.30	191.30	372.00	1.39	1	2
<i>Aotus trivigatus</i>	0.81	0.74	0.91	0.26	133.00	75.00	0.75	3	3
<i>Ateles fusciceps</i>	8.89	9.16	.	2.92	226.00	486.40	2.25	1	1
<i>Ateles geoffroyi</i>	7.78	7.29	0.45	2.01	225.00	820.80	2.66	1	1
<i>Callicebus moloch</i>	1.02	0.96	0.74	.	163.50	60.00	1.00	3	3
<i>Cebus apella</i>	3.65	2.52	0.21	.	155.00	519.00	1.79	1	2
<i>Lagothrix lagotricha</i>	7.28	7.02	0.47	.	223.00	315.00	1.50	1	1
<i>Pithecia pithecia</i>	1.94	1.58	.	0.70	163.50	122.00	1.58	2	2
<i>Saimiri sciureus</i>	0.78	0.66	0.11	0.30	170.50	168.00	1.17	1	3
Colobinae									
<i>Colobus badius</i>	8.56	7.42	.	.	150.00	790.40	2.12	1	1
<i>Colobus guereza</i>	13.50	9.20	0.57	.	170.00	390.00	1.00	1	3
<i>Colobus polykomos</i>	9.90	8.30	0.60	1.08	175.00	180.00	1.04	1	3
<i>Presbytis entellus</i>	15.00	10.28	0.50	.	200.10	300.00	1.68	1	3

Table 4.2: Data used for cross-species analysis

See text for definitions and references.

Species	Body Mass (kg)		litter weight at:		gestation length (days)	lactation length (days)	inter-birth interval (years)	male care	allomaternal care
	male	female	birth (kg)	weaning (kg)					
Cercopithecae									
<i>Cercocebus albigena</i>	8.52	6.21	0.43	1.83	174.90	365.00	2.12	2	2
<i>Cercopithecus aethiops</i>	4.26	2.98	0.34	1.28	163.30	365.00	1.33	1	2
<i>Cercopithecus ascanius</i>	3.70	2.92	0.37	.	171.60	180.00	4.33	1	1
<i>Cercopithecus mitis</i>	7.93	4.25	0.40	.	140.00	60.00	0.83	1	1
<i>Cercopithecus neglectus</i>	7.35	4.13	0.45	1.17	165.00	365.00	1.62	1	1
<i>Erythrocebus patas</i>	12.40	6.50	0.50	1.44	167.50	213.00	1.00	1	2
<i>Macaca arctoides</i>	12.20	8.40	0.50	1.93	178.20	300.00	1.48	1	1
<i>Macaca fascicularis</i>	5.36	3.59	0.34	1.35	160.30	420.00	1.07	1	1
<i>Macaca fuscata</i>	11.00	8.03	0.54	2.29	173.00	365.00	1.50	1	1
<i>Macaca mulatta</i>	11.00	8.80	0.48	1.60	165.20	365.00	1.00	1	1
<i>Macaca nemestrina</i>	11.20	6.50	0.46	0.95	167.00	365.00	1.11	1	1
<i>Macaca radiata</i>	6.67	3.85	0.40	1.60	162.00	365.00	1.00	1	1
<i>Macaca silenus</i>	8.90	6.10	0.48	.	180.00	365.00	1.38	1	1
<i>Miopithecus talapoin</i>	1.38	1.12	0.18	0.20	162.00	180.00	1.00	1	1
<i>Papio cynocephalus</i>	21.80	12.30	0.85	1.86	172.60	365.00	1.75	2	1
<i>Theropithecus gelada</i>	19.00	11.70	0.55	.	170.00	450.00	2.14	1	1
Hylobatidae									
<i>Hylobates lar</i>	5.90	5.34	0.40	2.28	213.00	730.00	2.69	1	1
Pongidae & Hominidae									
<i>Pongo pygmaeus</i>	77.90	35.60	1.81	6.13	249.50	408.37	6.50	1	1
<i>Gorilla gorilla</i>	170.40	71.50	2.12	15.39	260.00	1004.40	3.83	1	1
<i>Pan troglodytes</i>	59.70	45.80	1.85	20.56	234.50	1460.00	5.50	1	1

Table 4.2 (continued)

Population	Male mass (kg) ¹	Female mass (kg) ²	Male DEE (kcal) ³	Female DEE (kcal) ⁴	Lactation length (days) ⁵	Inter-birth interval (days) ⁶	References
Ache (Paraguay)	59.6	51.0	3186	2085	366	1095	1,2,3,4: Leonard and Robertson (1997); 5: United Nations (1987), avg. Paraguay; 6: Hill and Hurtado (1991)
Evenki (Siberia)	59.9	52.2	2849	2098	180	1967	All data: Leonard <i>et al.</i> (1996)
Kaul (New Guinea)	56.3	48.1	2347	1830	720	1231	1-5: Leslie <i>et al.</i> (1984); 6: estimate (see text)
!Kung	46.0	41.0	2319	1712	1095	1343	All data: Lee (1979)
Lufa (New Guinea)	57.8	50.5	2570	2245	720	1231	1-5: Leslie <i>et al.</i> (1984); 6: estimate (see text)
Machiguenga (Peru)	51.8	44.5	3205	1925	447	1231	1,2,3,4: Katzmarzyk <i>et al.</i> (1994); 5: United Nations (1987), avg. Peruvian; 6: estimate (see text)
Nunooa(Peru)	55.7	48.9	1632	1420	720	1231	1-5: Leslie <i>et al.</i> (1984); 6: estimate (see text)
Samoans (Ghana)	73.0	63.5	2909	2273	579	1231	1,2,3,4: Katzmarzyk <i>et al.</i> (1994); 5: United Nations (1987), avg. Ghana; 6: estimate (see text)
Scotland (students)	65.0	55.0	2933	2294	90	960	1,2,3,4: Katzmarzyk <i>et al.</i> (1994); 5,6: United Nations (1987)
Tamang (Nepal)	50.9	44.8	3110	2356	1050	1131	All data: Panter-Brick (1989, 1991, 1993, 1996)
Turkana (Kenya)	65.4	52.5	2162	1734	546	888	1,2,3,4: Katzmarzyk <i>et al.</i> (1994); 5,6: Gray (1994, 1996)
Tutyo (Amazon)	54.6	47.6	2802	2908	540	1231	1,2,3,4: Dufour 1983; 5: Dufour (pers. comm.); 6: estimate (see text)
Upper Volta (Africa)	58.5	50.6	2622	2248	561	1231	1,2,3,4: Katzmarzyk <i>et al.</i> (1994); 5: United Nations (1987), avg. Africa; 6: estimate (see text).

Table 4.3: Daily energy expenditure, lactation length and inter-birth interval for human populations.

Source references are given for all variables: male weight (1), female weight (2), male DEE (daily energy expenditure) (3), female DEE (4), length of lactation (5) and inter-birth interval (6). In some cases the average (avg.) value for a country or continent is used.

3) Gestation length and foetal growth rate.

Both of these variables provide measures of the energetic costs of pregnancy. Foetal growth rate is a measure of the energetic investment per day in gestation and is calculated by dividing litter mass at birth (in grams) by gestation length (in days). Data on gestation length were taken from a database compiled by A. MacLarnon, R.D. Martin, C.A. Ross and B.C.C. Rudder² (see Ross 1988). Data on neonatal mass were taken primarily from Smith and Leigh (1998) which is the most up-to-date source of neonatal body mass data. Rather than differentiate by sex, as Smith and Leigh do, the average neonatal mass for males and females was used. Neonatal masses for *Callicebus albigena*, *Papio cynocephalus*, *Theropithecus gelada*, *Leontopithecus rosalia* and *Saguinus oedipus* were taken from the MacLarnon *et al.* database (see Ross 1988).

4) Lactation length and post-natal growth rate.

As with the costs of gestation, the costs of lactation are determined not only by the length of time to weaning, but also the amount of energy transferred per day. Post-natal growth rate is a measure of the daily cost of lactation, and is calculated by dividing litter mass at weaning by age at weaning. These data were mostly taken from the MacLarnon *et al.* database (see Ross and Jones in press). The only exception was age at weaning for *Brachyteles arachnoides* which was taken from Strier (1991).

5) Inter-birth interval.

Inter-birth interval will be used to measure the time span of each reproductive event, for both females and males (see section 4.2 for a discussion of the limitations of this approach). If the inter-birth interval is long, it is also an indication of high energetic costs. Again, these data were taken from the MacLarnon *et al.* database (see Ross 1988), except for *Brachyteles arachnoides* which was taken from Strier (1991).

² I would like to thank MacLarnon *et al.* for allowing me to use these data.

6) Degree of male care, degree of allomaternal care.

The MacLarnon *et al.* database provided both male care and allomaternal care data (see Ross and MacLarnon submitted). Both care types are divided into three categories, based on the percentage of care-taking (usually infant carrying) that is performed by the male or allomother: low (<5%); medium (5-30%), high (> 30%). These categories are slightly less refined than those used by MacLarnon *et al.* who had an extra category for care giving above 50%. Using fewer categories helps to overcome the problem of small sample sizes.

In an ideal world, all of these data should be collected from the same population, but this is simply not possible. In each case, data from wild populations were used in preference to data from captive groups. All species for which a complete data set was available for male and female body weights, male care, allocare, gestation length, weaning age and inter-birth interval were included (table 4.2). Neonatal masses and mass at weaning (needed to calculate foetal growth rate and post-natal growth rate) were not always available, but were included wherever possible. Fortunately, these data cover a good cross-section of primate species: 6 callitrichidae, 10 cebidae, 16 cercopithecinae, 1 hylobatidae, 1 pongidae and 3 hominidae. Only the hylobatidae are noticeably under-represented. Seven of the total sample show high levels of male care, all of which are New World monkeys. Thus there are potentially problematic phylogenetic effects that need to be considered (Harvey and Pagel 1991). The comparative method is not an appropriate tool in this circumstance, because the number of phylogenetically independent incidences of male care are too few. None the less, when viewing the following results it must be remembered that close relatedness between the species of interest may magnify any positive relationships found.

Unfortunately activity budget data are available for only a small number of species (table 4.1a). The available data encompass all primate families: 1 callitrichid, 7 cebids, 7 cercopithecines, 2 colobines, 1 hylobatid, 1 pongid and 2 hominids. The callitrichids and hylobatids are under-represented in this sample, and unfortunately only 2 out of 21 species show high male care. There is, then, very little variation in male care between these species and the variation that exists is diminished because of phylogenetic factors (Harvey and Pagel 1991).

There have been numerous studies on humans that directly measure daily energy expenditure. Data on male and female daily energy expenditure, male and female body mass, gestation length, lactation length and inter-birth interval were collected from the literature for thirteen human populations as shown in table 4.3. Gestation length in humans is 267 days. In most cases lactation length data and energy budget data were drawn from the same study group. In some cases, estimates of lactation length were made on the basis of the average for that country or continent (depending upon availability). The data on inter-birth interval is less strong, as it was only available for six of the populations used here. The average inter-birth interval for these six populations (1231 days) was used as an estimate for those populations for which data were unavailable.

Activity budgets of individual animals will vary between members of the same group, and will vary quite significantly between different groups. For instance, the quality of the habitat and the distribution of resources will dramatically affect the time a group spends travelling. Because of the scarcity of data, there is very little that can be done here to correct for this ecological variation, and the assumption is made that males and females will be affected more or less equally by the quality and distribution of resources.

Since activity data were only available for a sub-set of the total number of species, the following analysis will proceed in two stages. In section 4.4 the energetic cost of reproduction will be calculated using only those species for which there are activity budget data (tables 4.1 a & b). It will be shown that intra-sex differences in activity budgets are minor compared with inter-species differences. In practice, the energetic costs of any activity are largely determined by body size and daily energetic costs can reasonably be estimated using body size. On this basis, a second set of analyses are performed in section 4.5 using the full data set (table 4.2) in order to overcome the small sample sizes that hamper the first analysis. The objective of both these analyses is to determine the relationship between male and female energetic costs of reproduction, and to determine the cause of variation in these costs. It will be shown that sex differences in energy expenditure are closely related to sexual dimorphism in body mass and that relative female energetic costs are greatest in monomorphic species. On this basis, section 4.6 will look at the impact of male care on energetic costs in species with low sexual dimorphism. Finally, in section 4.7, the models used here to look at extant species will be applied

to the hominids in order to ascertain how human patterns of energy expenditure may have evolved.

4.4 A Comparison of Energetic Costs using Activity

Budget Data

4.4.1 Method

For this first analysis, activity budget data (from table 4.1) will be translated into estimates of daily energy expenditure using Coehlo's energetic model (Coehlo 1974, 1986; Coehlo *et al.* 1979). Daily energy expenditure and various life history measures will then be combined to determine the energetic cost of reproduction for males and females of each species.

The larger an animal is in size, the more energy it requires simply to maintain basic bodily functions. The daily energetic costs of body maintenance are expressed as the basal metabolic rate (BMR) which is related to body mass by the following equation (Kleiber 1961):

$$B = 70 W^{0.75}$$

where B = basal metabolism (kcal/24/hr)

W = body mass (kg)

Kurland and Pearson (1986) have shown that the Kleiber equation is appropriate for estimating basal metabolic rate for the anthropoid primates. Activities such as sitting, feeding and moving elevate the body's energetic requirements. Thus, in order to estimate daily energy expenditure the following equation is used:

$$DEE = \sum_{i=1}^n A_i \quad (1)$$

where DEE = daily energy expenditure kcal/24/hr

A_i = energetic costs (kcal) for an individual activity "i", and:

$$A_i = \frac{D_i \times BMR \times T_i}{100} \quad (2)$$

where D_i = energy constant for each activity (see table 4.4)

T_i = proportion of time spent performing activity i .

Activity	Energy constant [D_i] (multiples of BMR)
Sleeping	1.00
Resting	1.25
Feeding	1.38
Socialising	5.00

Table 4.4: Energetic constants for various activities.

Adapted from Leonard and Robertson 1997 table 3.

The energy constants for sleeping, resting, feeding and socialising (table 4.4) have been taken from Leonard and Robertson's translation of Coehlo's energetic constants (Leonard and Robertson 1997). These constants represent estimates of the energetic costs of various activities, and are based upon studies on humans. Thus they may not be a true reflection of actual activity costs in other primate species. Furthermore, research on humans indicates that there can be considerable inter-individual and inter-population differences in the energetic costs of physical activities. Brun *et al.* (1988) found that the activity costs of different farming activities performed by Chinese females varied greatly between individuals. For example, the costs of bending and cutting rice ranged from 5.2 kJ/min to 17.9 kJ/min. Furthermore, Lawrence *et al.* (1988) found that the average Gambian woman expended almost half as much energy as the average Chinese woman when bending and cutting rice. Very little is known about the energetic costs of any activities in any non-human primate. At present the energy constants shown in table 4.4 are the best available estimates.

Because the energetic costs of movement depend upon method of locomotion, speed and distance travelled, there is no energy constant for locomotion. Leonard and Robertson (1997) use the following equation from Taylor *et al.* (1970) to calculate the energy cost of moving:

$$A_{loc} = (0.041 * W^{0.60})DR + (0.029 * W^{0.75})T_{loc}$$

where: A_{loc} = energetic cost of locomotion (kcal)

W = body mass (kg)

DR = day range (km)

T_{loc} = time spent moving

This equation can only be used if day range is known, which is rarely the case. Given that there is likely to be great intra-species variation in day-range and activity budgets, day ranges should be taken from the same populations as the activity budget data. Unfortunately, attempts to find appropriate day-ranges for species used in this analysis met with limited success. Rather than drastically reducing an already small data set, an alternative method was sought.

The energetic cost of locomotion increases with speed and body mass (Taylor *et al.* 1982) but is not greatly affected by the mode of locomotion (Taylor 1977). Taylor (1977) has shown that the transition speed between trotting and galloping is directly related to body size, and can be considered an equivalent speed for all animals, where:

$$V = 1.53 W^{0.24}$$

where V = cost of locomotion at the trot-gallop transition.

This means that as long as body mass is known, it is possible to calculate the energy constant for locomotion, D_{loc} , at the trot-gallop transition, using the following equation (adapted from equations 3 and 6 in Taylor 1977):

$$D_{loc} = \frac{\text{Energy cost of travelling at the trot-gallop transition}}{\text{resting metabolism}}$$

$$= \frac{(10.7 W^{0.4})V + 6W^{-0.25}}{3.5W^{-0.25}}$$

This formula gives the energy constants for locomotion (D_{loc}) shown in table 4.5. Taylor (1977) shows that for mammals in general the range in predicted values will be very small. Likewise, the range in predicted values for D_{loc} calculated here, from 6.03 for a female *Saguinus oedipus* to 9.11 for male *Gorilla gorilla*, is very small, considering the differences in body size between these species.

D_{loc} , was used as the energy constant of locomotion in equation 2. Of course, most animals do not spend their time travelling at the exact speed of the trot-gallop transition and hence these constants should be regarded as estimates. Coehlo (1986) estimates that the calorific costs of walking, running, swinging, jumping and many other forms of locomotion in the baboon are 8.8 times greater than the costs of sleeping, which is well within the range of values given in table 4.5, and very close the value of 7.97 calculated here for males of *Papio anubis*.

The energetic cost of each activity is summed to give the total daily energetic cost (equation 1). The energetic cost of each activity can also be compared in order to create an 'energy profile' for each sex and species. Energy profiles allow us to examine the ways in which energy is used by males and females of each species and to determine whether there are sex differences in energy use. Additionally, energy profiles are useful in determining which species minimise energy expended on costly activities such as locomotion.

Daily energetic costs are only part of the total energetic cost of reproduction. Most importantly, the costs of lactation and gestation need to be accounted for. Energy expenditure per reproductive event is calculated for males and females by modifying the equations for daily energy expenditure. A single reproductive event is measured by the length of the inter-birth interval. Coehlo (1974) suggests that the extra costs of gestation and lactation for females can be accounted for by assuming that they elevate energy requirements by 25% and 50% respectively (following Portman 1970). These values will be used in this model.

The average lactating human female produces around 750 ml of breast milk per day during the first few months of lactation. In order to support this output, the FAO/WHO/UNO (1985) calculate that a female requires an extra 2100 kJ/day. This equates to an additional energetic cost of around 25% above non-pregnant/non-lactating levels, i.e. less than the 50% estimate to be used here. Similarly, daily energy expenditure in pregnant women is not as high as assumed in this model (Ulijaszek 1995). Human females use a wide variety of mechanisms to meet the

Species	Male D_{loc}	Female D_{loc}
<i>S.oedipus</i>	6.04	6.03
<i>A.trivirgatus</i>	6.31	6.26
<i>C.torquatus</i>	6.50	6.47
<i>A.caraya</i>	7.24	7.05
<i>A.palliata</i>	7.30	7.15
<i>A.paniscus</i>	7.42	7.38
<i>L.lagotricha</i>	7.31	7.29
<i>B.arachnoides</i>	7.45	7.36
<i>C.aethiops</i>	7.04	6.87
<i>C.mitis</i>	7.35	7.04
<i>E.patas</i>	7.58	7.25
<i>M.mulatta</i>	7.52	7.40
<i>M.radiata</i>	7.26	7.00
<i>P.anubis</i>	7.97	7.62
<i>P.cyncocephalus</i>	7.89	7.58
<i>P.entellus</i>	7.68	7.48
<i>C.badius</i>	7.39	7.31
<i>H.lar</i>	7.20	7.15
<i>P.pygmaeus</i>	8.64	8.17
<i>G.gorilla</i>	9.11	8.78
<i>P.troglodytes</i>	8.27	8.13

Table 4.5: Estimated energy constants of locomotion (D).

Estimated energy constants of locomotion (D_{loc}) for the primate species used in these analyses.

energetic demands of lactation and gestation: increased energy intake; reduced physical activity; reduced BMR; and utilisation of body fat stores (Rogers *et al.* 1997; Ulijaszak). However, in comparison with other mammals, human females appear to be unusual in the extent to which they are able to compensate for the energetic burden of lactation (see section 4.7.3). In other mammals the costs of lactation appear to be met primarily through elevating energy intake, which increases by between 66 and 188% in lactating compared to non-lactating females (Clutton-Brock 1991; Gittleman and Thompson 1988). Dasilva (1992) argues that in the case of lactation a 50% increase in energy expenditure should be considered a minimum value, an observation supported by Muruthi *et al.*'s (1991) finding that energy intake of pregnant or lactating female baboons was, on average, 57% higher than that of cycling females. For most primate species, excluding humans, the assumption that pregnancy and lactation elevate energy demands by 25% and 50% respectively may provide a rather conservative estimate of actual energetic costs.

For females energetic costs per reproductive event are calculated using this equation:

$$F_{\text{energy}} = \text{DEE} ((T_{\text{gest}} \times 1.25) + (T_{\text{lact}} \times 1.5) + (T_{\text{ibi}} - T_{\text{gest}} - T_{\text{lact}})) \quad (3)$$

Where:

- F_{energy} : female energy expenditure per reproductive event (kcal)
- DEE: daily energy expenditure (kcal)
- T_{gest} : length of gestation (days)
- T_{lact} : length of lactation (days)
- T_{ibi} : inter-birth interval (days)

Gestation time and lactation time are multiplied by 1.25 and 1.50 respectively to account for the increased energy costs associated with these activities. The term $(T_{\text{ibi}} - T_{\text{gest}} - T_{\text{lact}})$ reflects the amount of time spent between births in which females are neither pregnant or lactating. In some species gestation and lactation phases of the reproductive cycle overlap, however, this equation remains appropriate if we assume that during this time the costs of gestation and lactation are cumulative.

Calculating male energy expenditure per reproductive event is impossible without knowing the reproductive success of individual males. As discussed earlier, these data are currently unavailable. Calculation of male energy expenditure per

female reproductive event will compromise the results in populations in which there is great variation in male reproductive success. At best this measure will give an indication of average male energy expenditure, at worst it will severely over-estimate energy expenditure for some males, and equally, severely under-estimate energy expenditure in others. None the less, this is the only measure of male energy expenditure that is possible with the given data. Male energy expenditure is simply calculated as:

$$\text{Menergy} = \text{DEE} \times T_{\text{ibi}} \quad (4)$$

Where: **Menergy** = male energy expenditure per female reproductive event.

Table 4.6 shows the total daily energy expenditure for each sex and species. The energetic costs of each activity provide an 'energy profile' which can be compared intra- and inter-specifically to examine sex and species differences in energy use which are independent from other life history parameters. Total energetic costs, which include the costs of gestation and lactation, provide insights into the relationship between male and female energetic costs of reproduction.

In summary: this section has shown how male and female daily energetic costs and total energetic costs of reproduction can be calculated using activity budget data in conjunction with data on gestation length, lactation length and inter-birth interval. It should be noted that there are many possible sources of error in these calculations, principally because of deficiencies in the data. It is assumed here that gestation and lactation elevate daily energy expenditure by 25% and 50% respectively. However these costs are likely to be variable and may often be considerably greater, except in humans in which they are almost certainly lower. Also, females may change their activity patterns during different parts of the reproductive cycle. For instance, Gambian women are less active during the later stages of pregnancy (Roberts *et al.* 1982) and pregnant gorilla females have been shown to spend less time travelling (Meder 1986). Male energetic costs are difficult to estimate because of variation in male reproductive success (see section 4.3). Finally, inter-specific differences in the energetic costs of different activities are simply unknown. It is assumed that all species use the same amount of energy, per unit body mass, when sleeping, grooming, feeding and so on. This assumption is

		Male DEE (kcal)	Female DEE (kcal)
Callitrichidae:	<i>S. oedipus</i>	46.73	46.33
Cebidae:	<i>A. palliata</i>	419.24	326.42
	<i>A. caraya</i>	522.36	319.70
	<i>C. torquatus</i>	133.84	120.39
	<i>A. trivirgatus</i>	92.01	85.23
	<i>L. lagotricha</i>	858.86	893.59
	<i>A. paniscus</i>	758.06	646.41
	<i>B. arachnoides</i>	687.17	632.31
Cercopithecinae:	<i>C. aethiops</i>	349.07	281.63
	<i>C. mitis</i>	617.58	382.65
	<i>E. patas</i>	795.51	529.03
	<i>M. mulatta</i>	713.63	576.05
	<i>M. radiata</i>	418.48	303.48
	<i>P. anubis</i>	1398.90	857.21
	<i>P. cyncephalus</i>	1454.27	934.18
Colobinae:	<i>C. badius</i>	455.28	413.30
	<i>P. entellus</i>	651.28	504.25
Hylobatidae	<i>H. lar</i>	422.17	398.01
Hominidae:	<i>P. pygmaeus</i>	2737.84	1589.85
	<i>G. gorilla</i>	4576.07	3179.08
	<i>P. troglodytes</i>	1954.45	1461.89

Table 4.6: Estimated daily energy expenditure (DEE) by sex.

particularly questionable when estimating energetic costs of locomotion. However Coehlo (1986) asserts that different modes of locomotion require similar amounts of energy, and an attempt has been made here to estimate an energetic constant for locomotion.

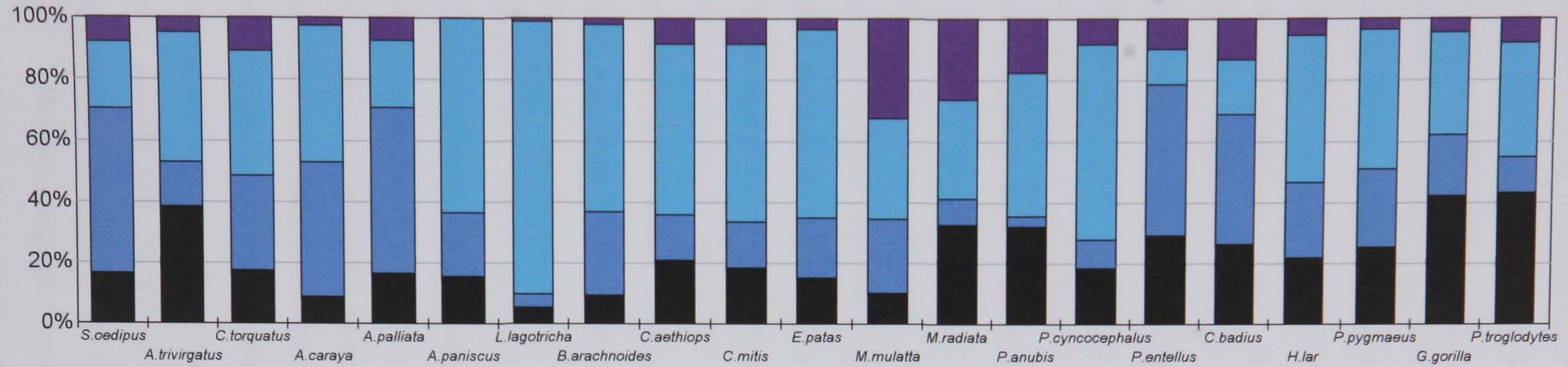
4.4.2 Results and discussion

Energy profiles for each species and sex were created, and are summarised in figure 4.1. This figure shows the percentage contribution of each activity to the daily energetic costs of males and females. Note that the time spent sleeping is fairly constant between species (see table 4.1a) and has thus been omitted from these figures.

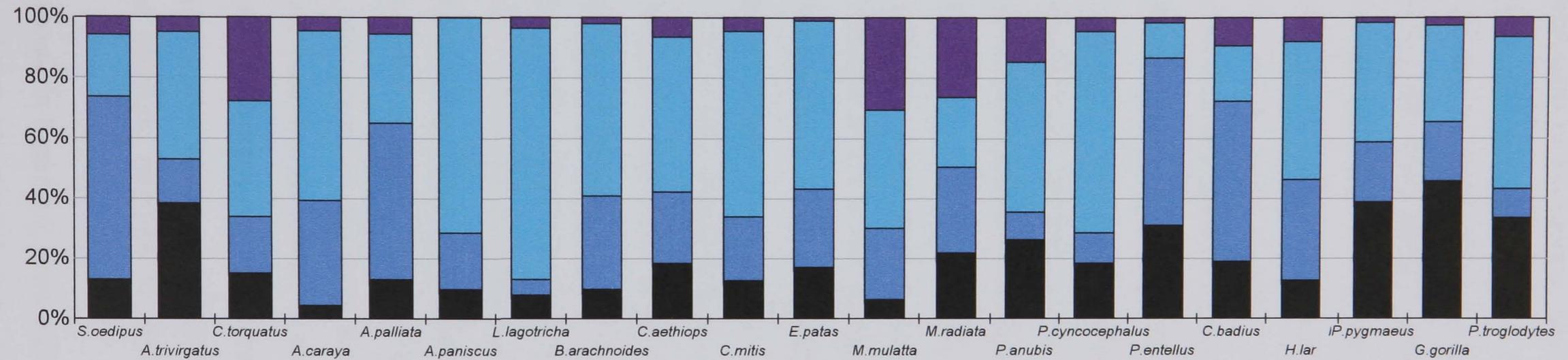
There is very little difference in the use of energy between males and females of the same species. No matter what the basic social structure, differences between male and female energy profiles are subtle. If the purpose of male caregiving is to relieve the energetic burdens on the female it might be expected that in monogamous species such as *Saguinus oedipus*, *Aotus trivirgatus* and *Callicebus torquatus*, the female would spend more time feeding and resting, and the male more time moving and socialising with the offspring. Some support for this hypothesis can be derived from the energy profile of *Callicebus torquatus*, in which males spend more time socialising and less time resting than females. Yet, there is no inter-gender difference in feeding time in any of the monogamous callitrichids or cebids and in *Saguinus oedipus* and *Aotus trivirgatus* male and female energy profiles are practically identical.

The greatest gender related difference in energy budgets occurs in *Macaca radiata*, where females spend more time feeding and moving, and less time resting than males. But, even in this case, differences are slight in comparison with the considerable inter-species variation. The atelines spend an enormous amount of their energy on locomotion, reflecting both the patchy distribution of the fruit upon which they generally feed, and their correspondingly large day range (Defler 1995). *Lagothrix lagothrica* expends around 80% of its daily energy budget on movement. In stark contrast, *Saguinus oedipus* spends the vast majority of both its time and energy budget resting. This supports Thompson *et al.*'s (1994) assertion that the callitrichids have low energy expenditure for their body size. The colobines *Colobus*

FEMALES



MALES



Feeding
 Resting
 Moving
 Socialising

Figure 4.1: Comparison of male and female energy profiles

badius and *Presbytis enetellus* also appear to maximise resting time and minimise energy expenditure. In these cases, the even distribution of their folivorous food supply is likely to minimise the energetic costs of locomotion. This is in agreement with Dasilva's observation that folivory and low activity are often associated (Dasilva 1992) and Leonard and Robertson's (1997) finding that daily energy expenditure and day range are positively correlated with dietary quality.

It is interesting that social behaviours contribute to a very small proportion of the total energy profile of most species, the macaques and *Papio anubis* being a notable exception. In most species, in energetic terms at least, social behaviour seems to be of little import. It may be that once social networks are established, the day-to-day maintenance costs of social relationships are low. Many social behaviours, such as feeding in close proximity, travelling together, carrying and food-sharing are unlikely to be recorded as social behaviours and hence energetic costs of social behaviours should be considered as minimum estimates.

The energy profiles of the great apes are noteworthy on two counts. Firstly, due to their large body sizes, the total energy requirements of these species are high, relative to other primates (table 4.6). Related to this is the considerable amount of time and energy the great apes expend on feeding. For instance gorillas of both sexes spend around 40% of their energy budget on feeding. Chimpanzee males and females spend respectively, just over 30% and 40% of their energy budgets on feeding. This indicates that feeding is likely to be a more severe constraint on the behaviour of the great apes than it is on other primates. It is interesting that the energetic costs of feeding in females are as great as, if not greater than, the feeding costs of the much larger males. This in itself is an indication of the high energetic burden on females. These observations support the idea that feeding efficiency is a major consideration in the evolution of hominoid behaviour. For example, Hunt (1994) contends that chimpanzees use bipedal posture as a mechanism for improving feeding efficiency, and that the australopithecines may have used bipedal posture in the same context. His hypothesis rests on the observation that chimpanzees assume a bipedal stance during feeding more often than during any other activity. Isbell and Young (1996) also suggest that bipedalism was an energetic response to decreased resource availability and increased day range.

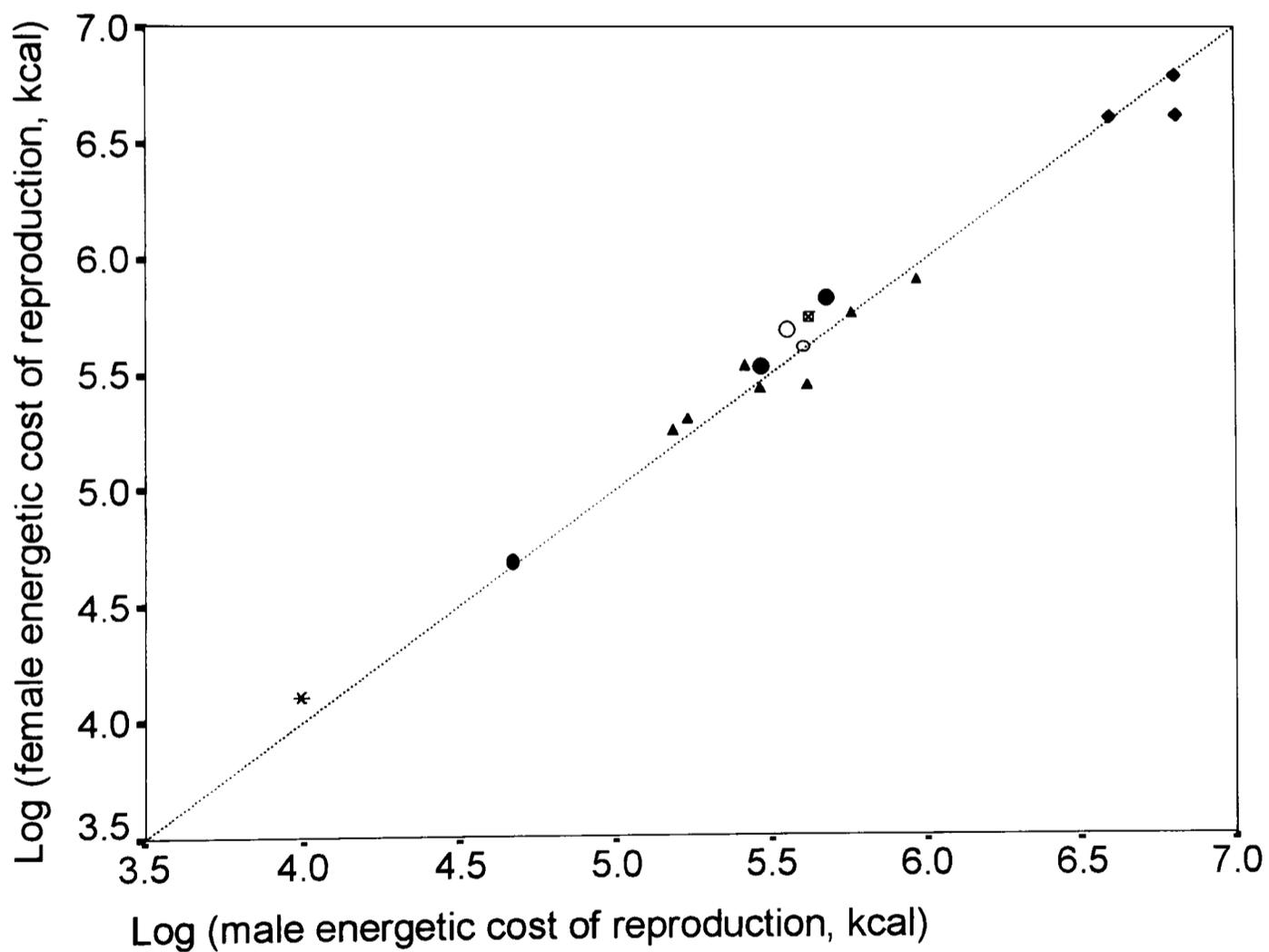
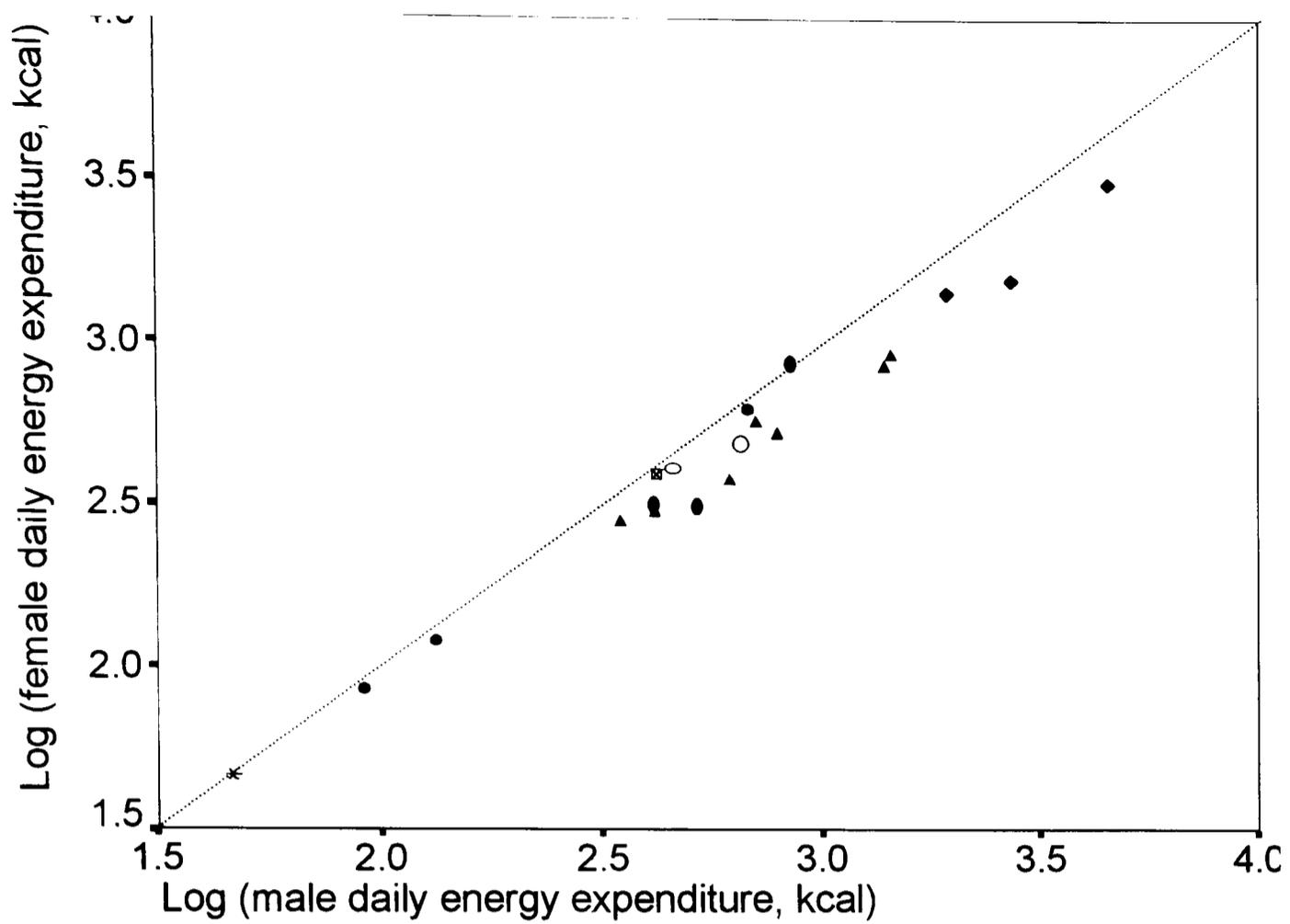
Human energy profiles are not shown in figure 4.1, since activity budgets are not available in the same format as those for non-human primates. According to data

given by Leonard and Robertson (1997), !Kung males and females spend around 70% of their daily energy budget on either walking or working. Ache males spend 92% of their energy budget on these activities, while Ache females spend 81%. Assuming that most of this “walking and working” energy is channelled into subsistence activities, it seems that humans concentrate their efforts on finding and processing food, rather than eating it. It is likely that this foraging strategy is only possible because the human diet usually includes food items of high energetic value, i.e. meat and/or other animal products.

Setting aside for the moment species differences in the patterns of energy use, figure 4.2 examines total energy expenditure in male and female non-human primates. Logarithmic plots of daily female energy expenditure versus daily male energy expenditure are shown in figure 4.2a. There is a close linear relationship between male and female daily energy expenditure ($r^2 = 0.98$) where male expenditure is, on the whole, greater than female expenditure. There is also a close linear correlation between male and female energy expenditure per reproductive event, as shown in figure 4.2b ($r^2 = 0.98$). However, in this case, female energy expenditure tends to be equal to, or greater than, male energy expenditure. These results appear to follow patterns of sexual dimorphism in body size, as shown in figures 4.2c and 4.2d. In sexually dimorphic species, males have a higher basal metabolic rate than females by virtue of their large size, which means that their basic energy requirements are also greater. Very large differences in activity budgets would be required to equalise daily energy expenditure patterns between the sexes in sexually dimorphic species. However, over the course of a reproductive cycle, high male energetic costs, associated with large body size, are counter-balanced by the energetic costs of pregnancy and lactation for the female. In species in which body size dimorphism is low or medium, female energetic costs of reproduction equal or exceed those of the male.

The distribution of male and female energy expenditure lends no support to the hypothesis that relatively high female energy expenditure is related to patterns of male care (figures 4.2e and f) but since only two closely related species are represented that display high levels of male care this result is inconclusive.

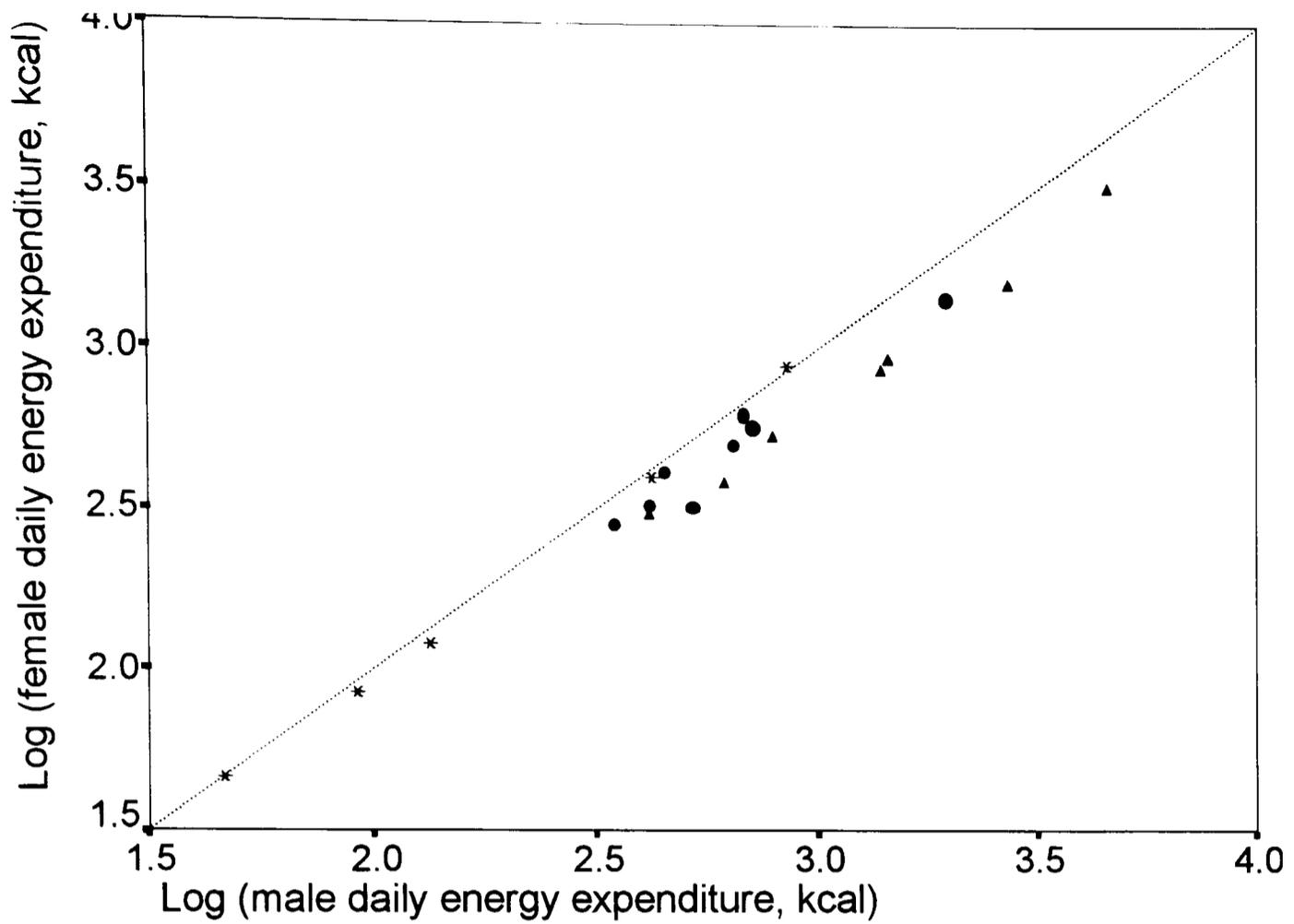
In humans, body size dimorphism is low. Therefore, on the basis of these results, we would expect that in humans: 1) Male daily energy expenditure will be similar to female daily energy expenditure; 2) The total energetic cost of



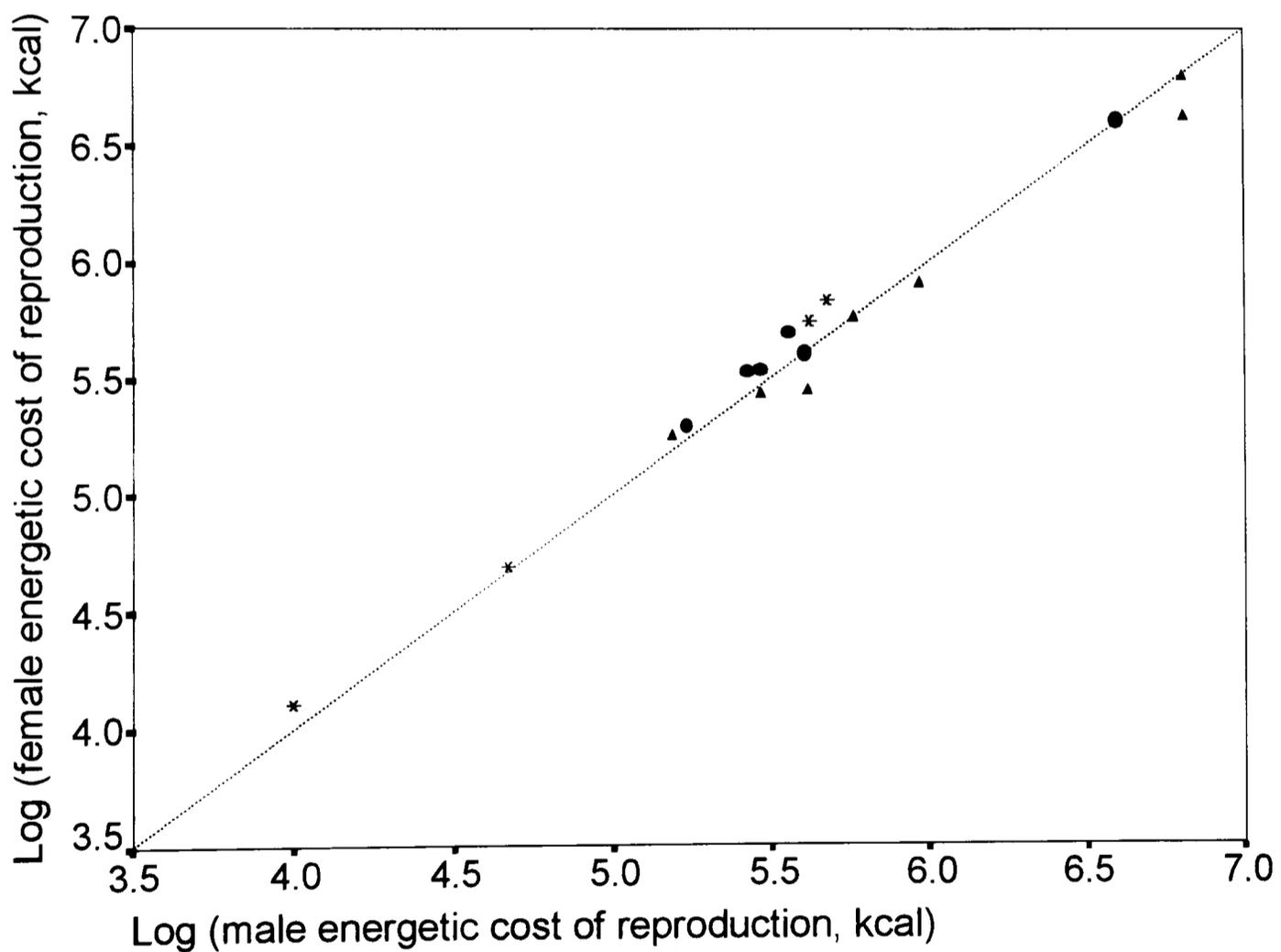
- Hylobatidae ○ Colobinae ● Cebidae
- ◆ Hominoidae ▲ Cercopithecinae * Callitrichidae

Figure 4.2: Comparisons of male and female energy expenditure

Comparison of: (a) male and female daily energy expenditure; and (b) male and female total energy expenditure over the course of a single reproductive event (i.e. the energetic cost of reproduction). Points below the isometric line (shown) indicate higher male costs compared with female costs.



(c)

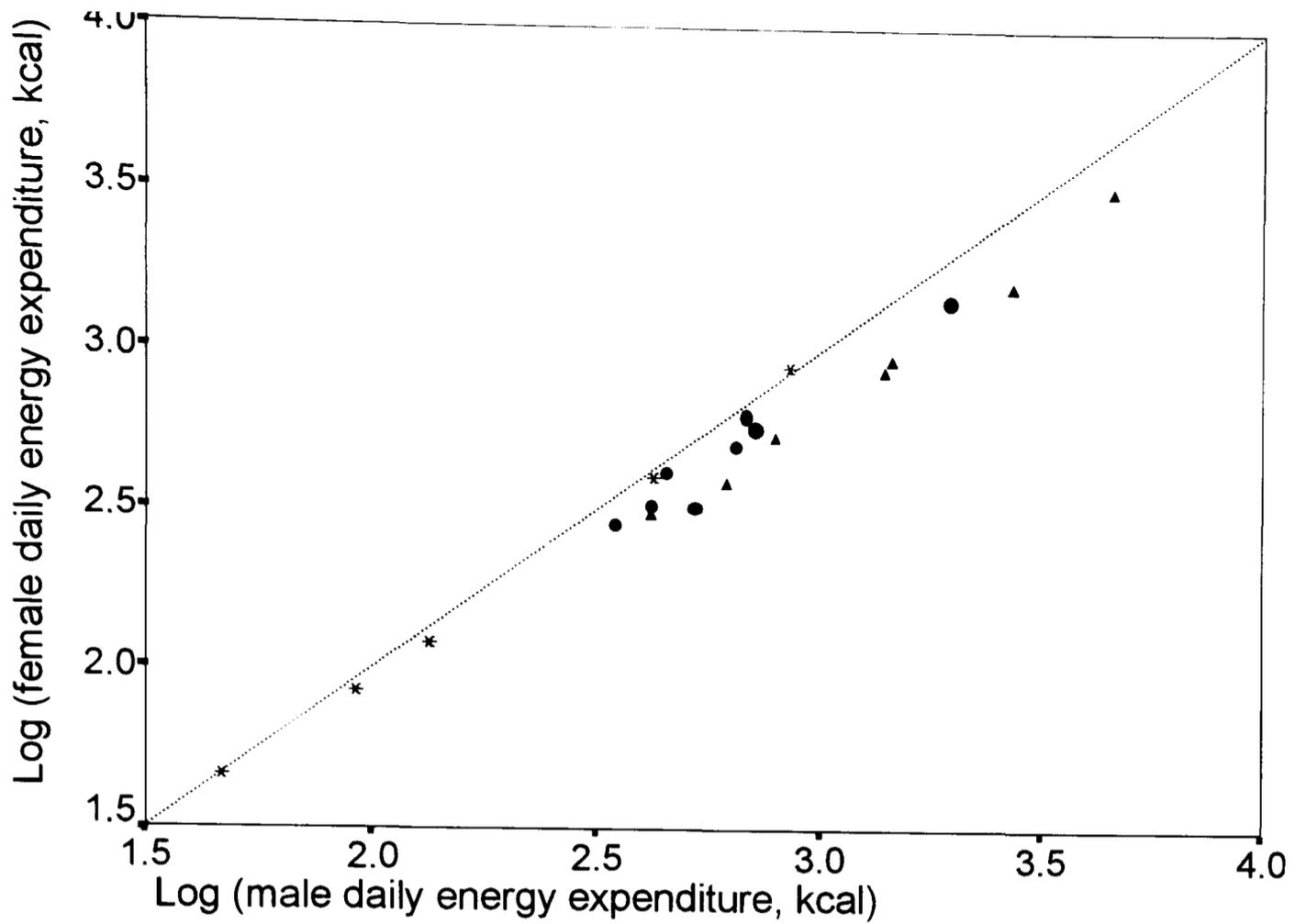


(d)

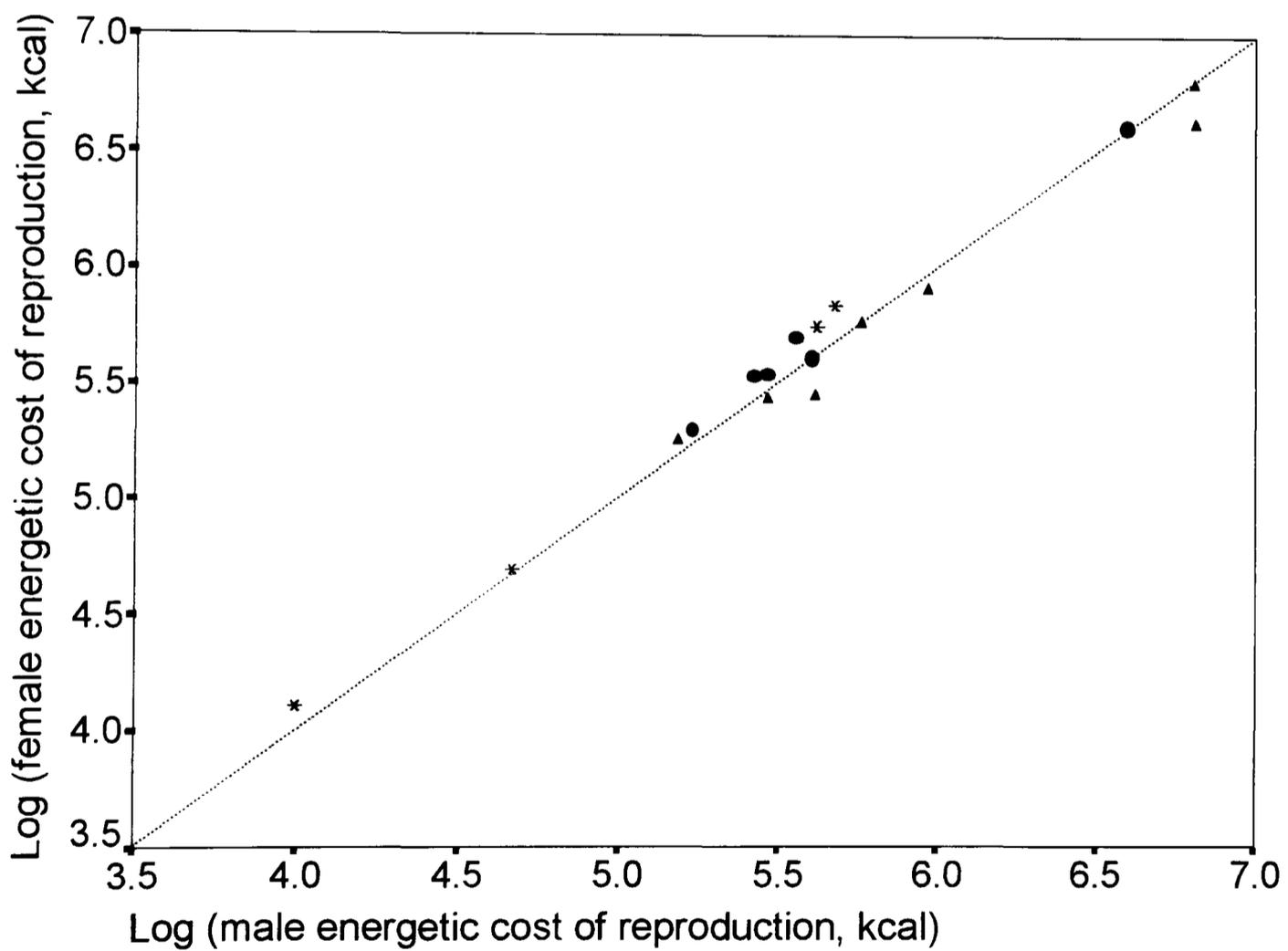
Body size dimorphism: \blacktriangle high \bullet medium $*$ low

Figure 4.2 (continued)

These figures are identical to figures 4.2 (a) and (b), except that individuals are scored by level of sexual dimorphism in body mass (for definitions see text, section 4.3). Figure (c) compares male and female daily energy expenditure, (d) compares male and female energetic costs of reproduction.



(e)

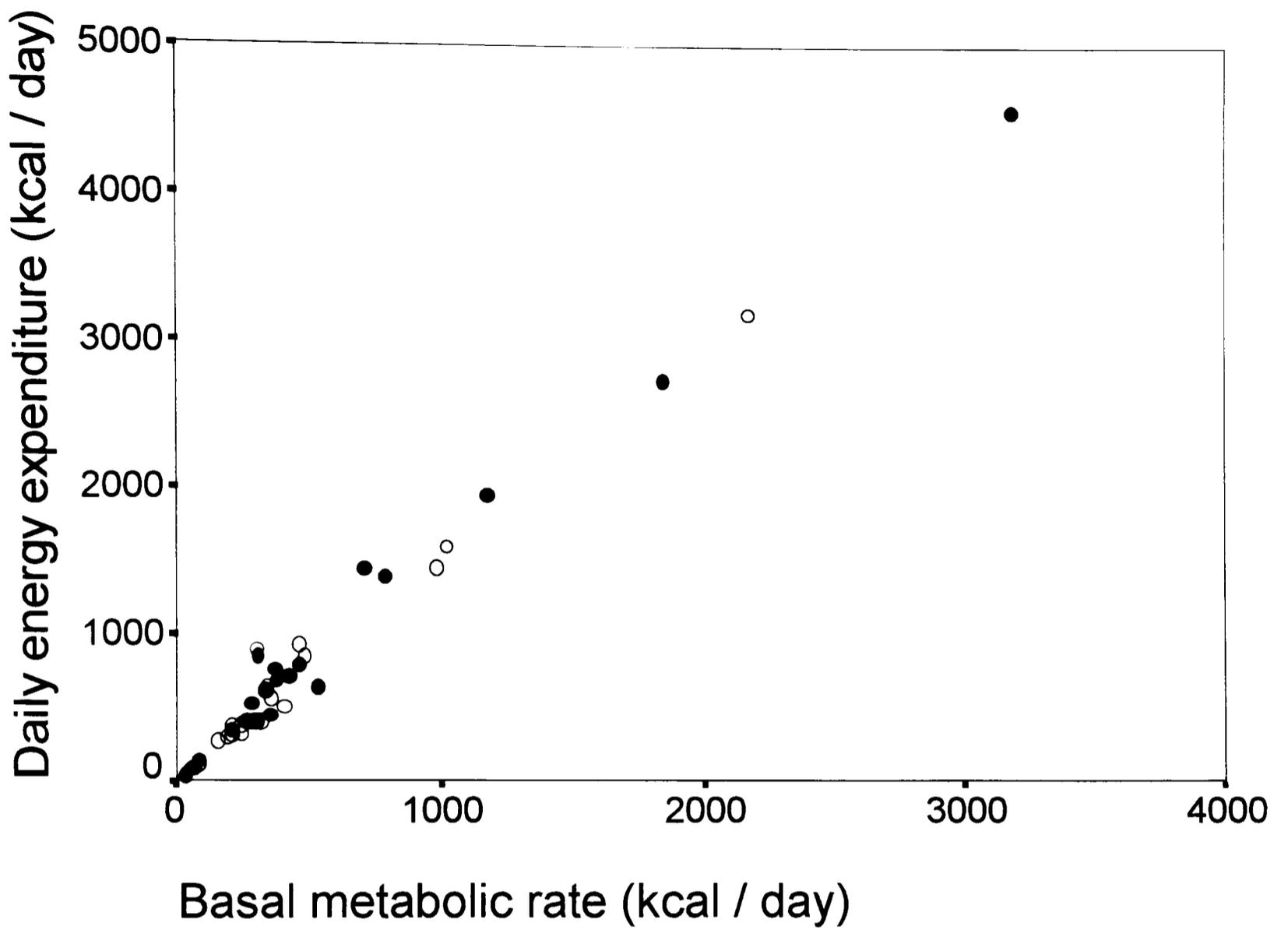


(f)

Male care : ^ high • medium * low

Figure 4.2 (continued)

These figures are again identical to figures 4.2 (a) and (b). This time, individuals are scored by level of male care (for definitions see text, section 4.3). Figure (e) compares male and female daily energy expenditure, (f) compares male and female energetic costs of reproduction.



SEX

- Male
- Female

Figure 4.3: The relationship between basal metabolic rate and daily energy expenditure

There is a very close relationship between daily energy expenditure and basal metabolic rate ($r^2 = 0.98$) regardless of sex.

reproduction will be greater for females than it is for males. These predictions were tested using the human sample (table 4.3). For the non-human primates already discussed, there is a strong correlation between BMR and daily energy expenditure (fig. 4.3, $r^2 = 0.98$). This relationship appears to be very similar for both males and females: an independent samples t-test performed on residual daily energy expenditure³ showed no significant difference between the sexes ($p < 0.05$). This means that expected daily energy expenditure can be calculated for humans from basal metabolic rate using the following equation:

$$\text{DEE} = 1.45 \times \text{BMR} + 88.03 \quad (5)$$

Expected daily energy expenditure for each sex was calculated for the human populations (using equation 5) listed in table 4.3, and compared with actual daily energy expenditure. The results, shown in figure 4.4a, deviate quite considerably from expectations. In all human populations male daily energy expenditure exceeds female daily energy expenditure by a greater degree than would be predicted on the basis of body size. This is contrary to the first prediction made above. Paired sample t-tests show that female daily energy expenditure does not differ from predicted values. Male daily energy expenditure, on the other hand, differs significantly from expectations (2-tailed, $p < 0.01$). Expected and actual daily energy expenditure were used to calculate expected and actual total energetic cost of reproduction for each sex, using equations 3 and 4. Once again the observed results, shown in figure 4.4b, differ quite considerably from expectations. It is expected that females will invest more heavily, over a reproductive cycle, than males. In actual fact there is considerable variation between human populations, and male energetic costs of reproduction often exceed the same costs for females. Once again male, but not female, costs differ markedly from expectations (paired sample t-test, 2-tailed, $p < 0.01$). Given that the energetic costs of gestation and lactation tend to be fairly low in human females (see discussion in 4.4.1 above) then female energetic costs may in fact be even lower than estimated here.

³ Residual DEE was calculated from a linear regression against basal metabolic rate.

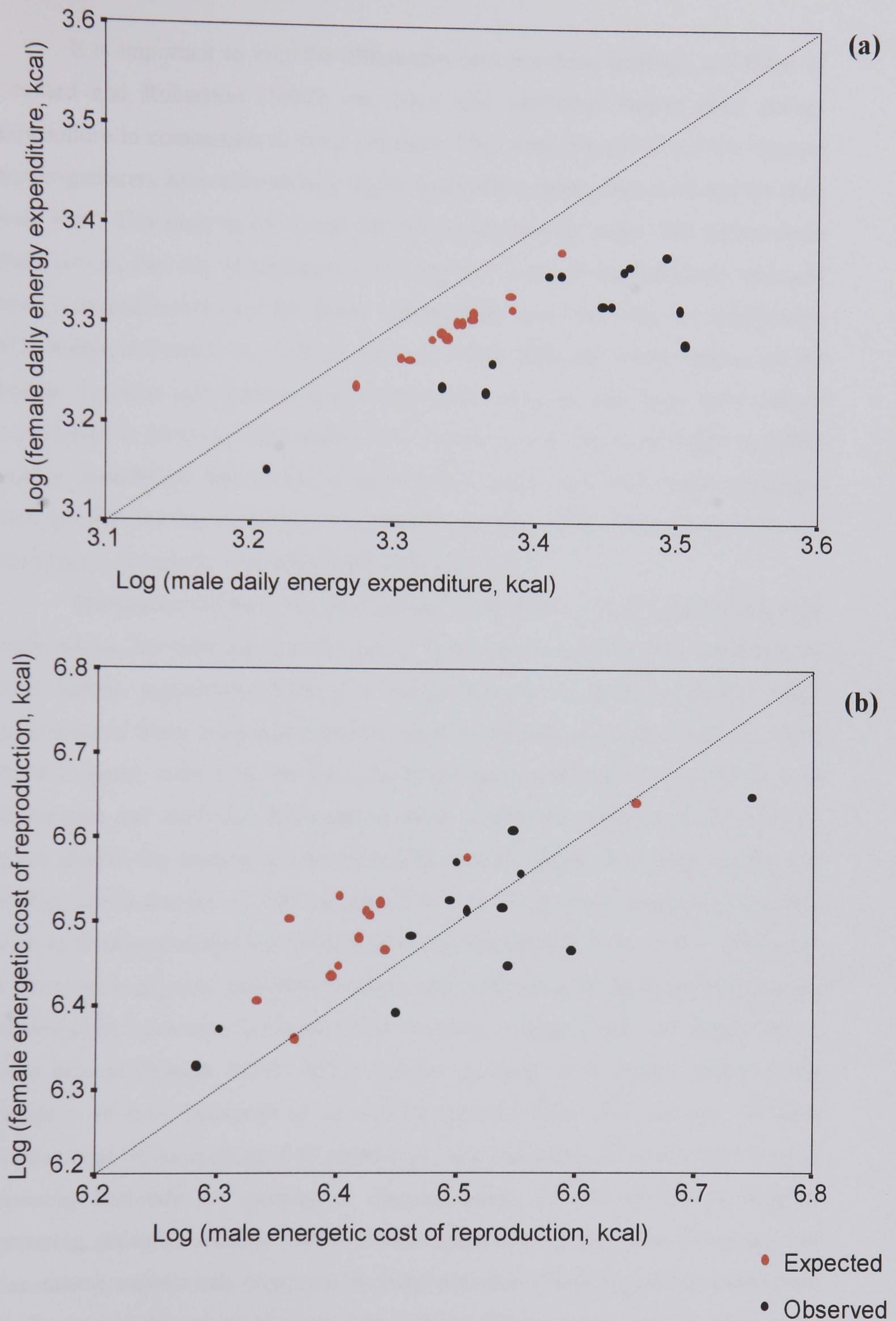


Figure 4.4: Comparisons of male and female energy expenditure in humans

Comparison of (a) daily energy expenditure, and (b) energetic cost of reproduction between males and females for a number of human populations. Each figure compares the expected distribution of values, based on the relationships shown in non-human primates, with observed values.

It is important to note the differences between these findings, and those of Leonard and Robertson (1997) who have also examined human daily energy expenditure in comparison to other primates. They state that (1997 p.271): “human hunter-gatherers have substantially higher expenditure levels than predicted for their body size.” This analysis has found that this is only true for males. The difference in these two studies can be attributed to the fact that Leonard and Robertson averaged energy expenditure values for males and females, thus obscuring sex differences. This subtle difference in analysis leads to rather different interpretations of the results. Leonard and Robertson’s interpretation suggests that high daily energy expenditure in humans, and probably their ancestors, was a result of a shift to a high quality, meat-based diet involving larger home range sizes. The results presented here indicate that this explanation can only be partially correct, since females do not have high daily energy expenditure for their body size.

The gender difference in daily energy expenditure, and the particularly high male values, are most likely to be due to gender differences in daily activities. In most human populations there is a sexual division of labour, whereby males participate in more strenuous activities, such as hunting and garden labour, while females spend more time on less physically demanding activities such as food preparation and child care (Katzmarzyk *et al.* 1994). For instance, in the Siberian group used in this analysis (the Evenki) male activities focus on fencing, herding and fishing, while females usually participate in less energetically expensive activities such as food preparation and household tasks (Katzmarzyk *et al.* 1994). These sex differences in physical activities translate into differences in the kinds of resources harvested by each sex. Cross-culturally, hunting is largely, but not exclusively, a male reserve (Hames 1989). When females do hunt, it is usually either in the company of their husbands or on an opportunistic basis. For instance, Achuara women hunt for an average of 83 minutes per day, but nearly all of this time is spent assisting husbands by spotting or carrying game, or alternatively in separate gathering activities (Hames 1989). Hames notes that amongst the Ye’kwana and Yanamamö, women only engage in ‘hunting’ activities if they happen to come across small game in the course of some other activity. Hames notes that one of the main problems faced by would-be female hunters is the difficulty of simultaneous child care. Similar sex differences exist in fishing activities, although fishing by women is more frequent than hunting. Hames suggests that this is because child care and

fishing are not mutually exclusive. None the less, women who do fish, such as the Ye'kwana, generally do so close to home. Furthermore, women do not appear to be efficient fishers: Ye'kwana women gain just 20% of the returns of male fishers over a given time period.

The sexual division of labour appears to have had a profound effect on human energy budgets. Male daily energy expenditure is considerably greater than expectations and this has a knock-on effect on total energetic costs of reproduction. The non-human primate data suggests that in humans the energetic cost of reproduction for females should be greater than that for males. In actual fact there is no significant difference between male and female total energetic costs of reproduction. That is, the high daily energetic costs for males match the high energetic costs of gestation and lactation for females.

Overall these results suggest that across primates the relationship between male and female daily energy expenditure follows patterns of sexual dimorphism in body size. When sexual dimorphism is high, male energetic costs are also high relative to female energetic costs. However, in the long term, male and female energetic costs are more similar. The energetic costs of lactation and gestation for the female counter-balance increased energy expenditure in the male. Again, the variation that exists seems to follow patterns of sexual dimorphism in body size. In species with low levels of sexual dimorphism female energetic costs of reproduction are greater than the same costs for the male. Humans appear to be exceptional in this respect due to the very high daily energy expenditure by males. Discussion of the sexual division of labour in humans, and how it may relate to female energetic costs and the evolution of paternal care, will continue in section 4.7.

These results may have been affected by errors in the energy calculations (see section 4.4.1). Overall female energetic costs should be considered to be conservative estimates, since the costs of gestation and lactation may be higher than assumed here (except in humans, in which these costs are probably lower). Also, daily energetic costs, as calculated here, do not take into account variation over the reproductive cycle. Male daily energy expenditure may be greater during consorting than at other times. Female daily energy expenditure may decrease during pregnancy and lactation (Panter-Brick 1989). Individual variation in male energy expenditure and reproductive success are further problems. However, it is difficult to ascertain whether male energy expenditure has been over or underestimated here. Finally, the

energetic costs of locomotion may have been overestimated for both males and females. The energetic cost of locomotion calculations were based upon the costs of travelling at the trot-gallop transition (see section 4.4.1), yet it is likely that both sexes spend much of their time travelling at slower speeds. A more confident assessment of energetic costs will only be possible with more field studies.

The small sample size adds a frustrating element to interpretation of these results. At this point very little can be said regarding the evolution of paternal care. A thorough exploration of energy expenditure, and its implications in terms of investment in offspring, requires a larger sample. The activity budget data have shown male and female energy profiles to be very similar within species (although quite different across species). Furthermore, since there is a close correlation between BMR and daily energy expenditure the latter can be reliably estimated on the basis of body mass alone. In the next section a comparison of energy expenditure will be performed using life history variables. This will double the sample size and permit a more thorough analysis.

4.5 The Relationship Between Male and Female Energetic Costs: A Wider Analysis

4.5.1. Method

In section 4.4 it was shown that basal metabolic rate strongly affects daily energy costs for both males and females, and can be used to estimate daily energy expenditure using equation 5. This means that total energy expended in reproduction can be calculated for males and females using body mass, gestation length, lactation length and inter-birth interval following exactly the same methodology described in section 4.4.1 (see equations 3 and 4). This was done using the larger data set in table 4.2. Humans appear to be exceptional in their patterns of energy expenditure (section 4.4) and are excluded from this stage of the analysis. In section 4.7 human populations are considered, and discussed in the context of human evolution.

4.5.2. Results

Daily energy expenditure for males and females is compared in figure 4.5a. Not surprisingly, the relationship between these variables is very similar to that shown in the previous section. There is a linear relationship between male and female daily energy expenditure ($r^2 = 0.93$) where male expenditure tends to be greater than female expenditure, presumably due to the costs of maintaining a larger body size. When total energetic costs of reproduction for males and females are compared (fig. 4.5b), the correlation between male and female costs remains ($r^2 = 0.92$), but in this case, male and female energetic costs are more similar. However, contrary to patterns of daily energy expenditure, in many cases total female energetic costs exceed total male energetic costs.

The energetic cost of reproduction for males (m_{energy}) was divided by the same cost for females (f_{energy}) to provide a ratio of male to female total energetic costs or *energy dimorphism*. This ratio is compared by level of sexual dimorphism in fig. 4.6 and table 4.7. An energy dimorphism score below 1.00 indicates that total female energetic costs exceed total male energetic costs. Conversely, energy dimorphism scores greater than 1.00 indicate relatively high total male energetic costs in comparison with females. Two-tailed Mann Whitney U-tests revealed

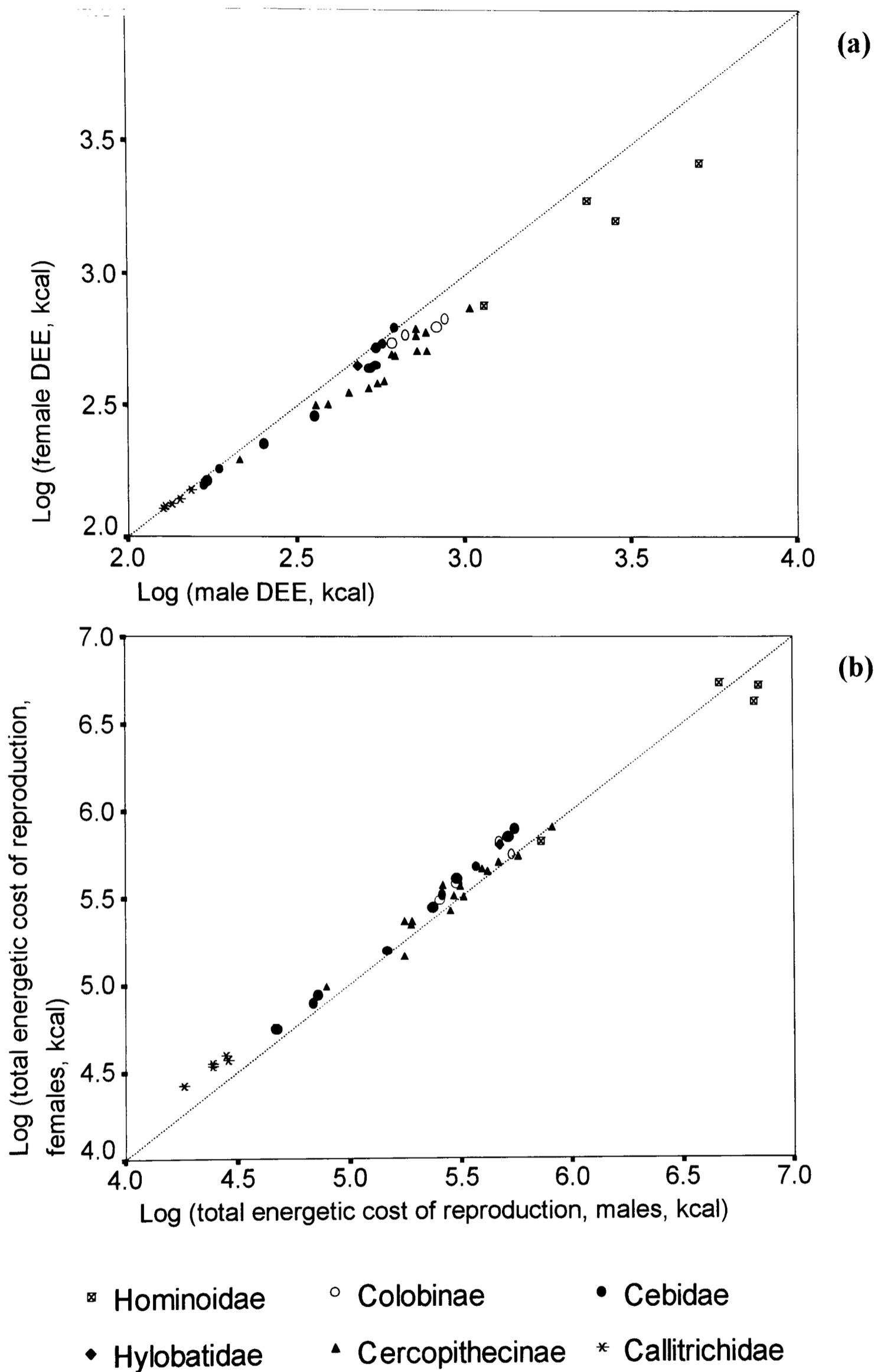


Figure 4.5: Comparison of male and female energy budgets using the whole data set.

Figure (a) shows the relationship between male and female daily energy expenditure (DEE); (b) shows the relationship between the total energetic cost of reproduction for male and females.

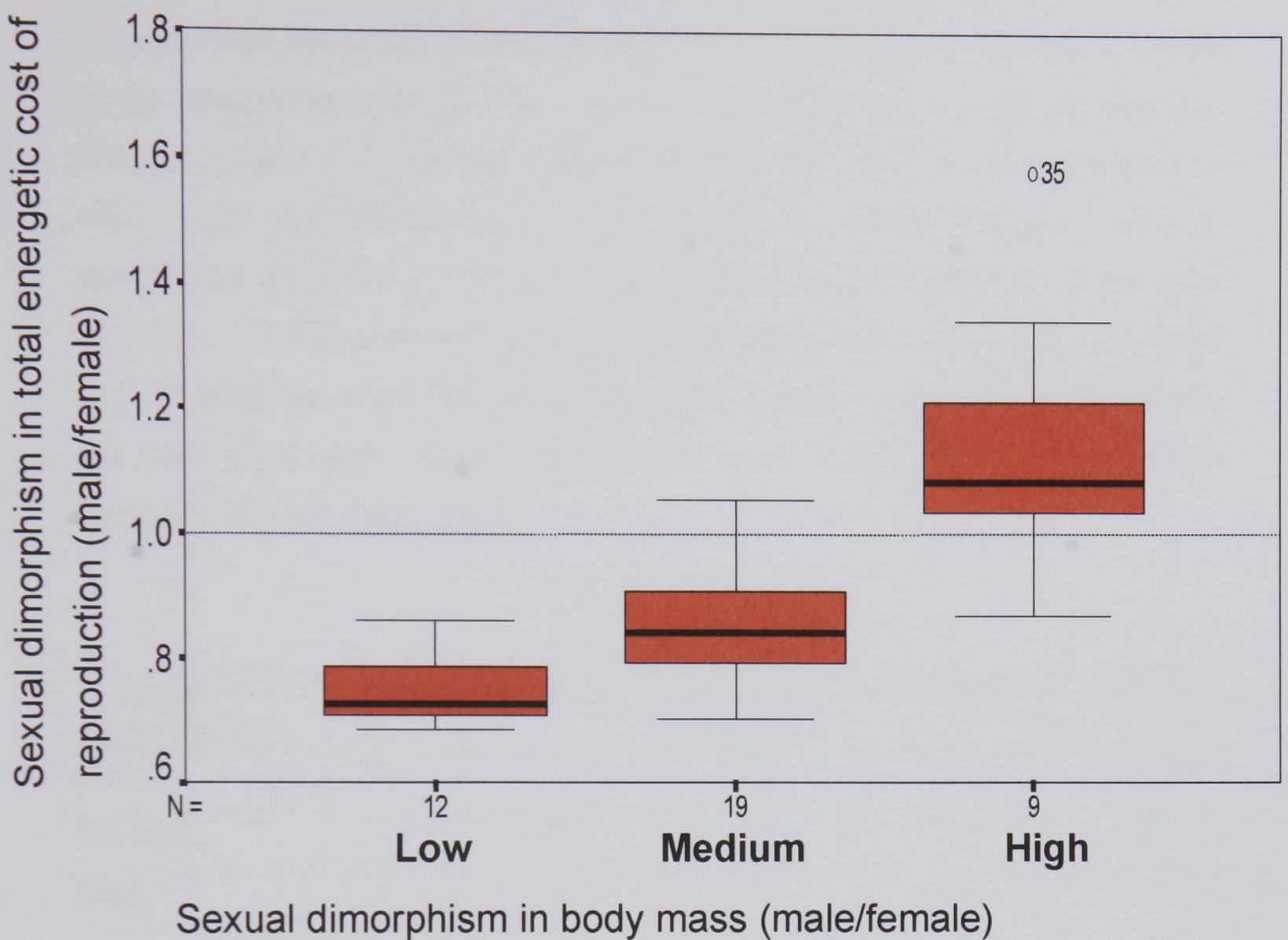


Figure 4.6: Comparison of sexual dimorphism in total energetic cost of reproduction with sexual dimorphism in body mass.

Sexual dimorphism in body mass is calculated by dividing male body mass by female body mass. Scores less than 1.15 are categorised as 'low', 1.15 to 1.5 as 'medium', and scores greater than 1.5 as 'high' (see section 4.3). Sexual dimorphism in the total energetic cost of reproduction is calculated by dividing the total male energetic cost of reproduction by total female energetic cost of reproduction. A score of 1.00 (indicated by the dashed line) indicates that male and female energetic costs are equal. A score of less than 1.00 indicates relatively high female energetic costs. Conversely, a score greater than 1.00 signals relatively high male energetic costs.

significant differences in energy dimorphism scores between all levels of sexual dimorphism in body size ($p < 0.01$). The lowest energy dimorphism scores are found in species with low levels of sexual dimorphism in body size, which have a median energy dimorphism score of 0.75. Species which have medium levels of body size dimorphism have a median energy dimorphism of 0.83. That is, in those species in which body size dimorphism is low or medium, female energetic costs of reproduction exceed those of the male. The highest energy dimorphism scores were recorded for species with high levels of sexual dimorphism, with a median value of 1.06. While energy dimorphism is most variable in highly sexually dimorphic species (see table 4.7), usually total male energetic costs equal or exceed total female energetic costs in these species.

sexual dimorphism	mean	median	standard deviation	minimum	maximum
Low	.74	.73	.06	.69	.86
Medium	.85	.84	.09	.70	1.05
High	1.13	1.08	.22	.87	1.58

Table 4.7: Descriptive statistics of energy dimorphism.

Descriptive statistics of the ratio between male and female energetic costs for different levels of sexual dimorphism in body size.

Earlier in this chapter it was proposed that the relationship between the male and female energetic cost of reproduction depends upon the degree of sexual dimorphism in body size. This hypothesis is strongly supported by these data. That is, female energetic costs are greatest, in comparison to males, when sexual dimorphism in body size is lowest. Using this result as a foundation, the next section explores the following questions: What is the relationship between male care giving and sexual dimorphism in body size? What is the relationship between allomaternal care and sexual dimorphism in body size? What are the benefits to females of male care-giving and allomaternal care?

4.6 The Energetic Benefits of Helpers

In the previous section it has been shown that the ratio of male to female energetic costs of reproduction is largely determined by the level of body size dimorphism. In species with high levels of body size dimorphism male energetic costs tend to be equal to, or greater than, female energetic costs over a single reproductive event. Over this time period, the excess energetic costs to the female of lactation and gestation are matched by the excess energetic costs to the male of maintaining a larger body size. In species in which male body size is less than 50% greater than female body size (i.e. medium or low levels of body size dimorphism) female energetic costs exceed those of the male. This is particularly true in species with low levels of body size dimorphism, in which total female energetic costs are around 25% greater than total male energetic costs (see table 4.7). According to the models being tested here, this implies that sexual dimorphism will have an effect on patterns of cooperation within groups, by virtue of its effect on the ratio of male to female energetic costs. In particular, in species in which body size dimorphism is low, and thus female energetic costs are relatively high, male care giving and allomaternal care are expected.

Table 4.8 shows the distribution of sexual dimorphism and male care amongst the 40 species of primate used in this analysis. Male care is strongly correlated with low sexual dimorphism ($X^2 = 20.02$, $p < 0.05$). In fact, high levels of male care never occur in intermediate or highly sexually dimorphic species. Patterns of allomaternal care appear to follow a similar trend to patterns of male care (table 4.9). For instance, allomaternal care does not occur in highly sexually dimorphic species. Furthermore, allomaternal care appears to occur particularly frequently in species which show medium levels of sexual dimorphism. However, the overall distribution of allomaternal care and sexual dimorphism in body size is not significantly different from expected values ($X^2 = 9.07$).

MALE CARE	BODY SIZE DIMORPHISM						TOTAL
	LOW		MEDIUM		HIGH		
	Obs.	Exp.	Obs.	Exp.	Obs.	Exp.	
LOW	4.00	8.70	17.00	13.78	8.00	6.53	29.00
MEDIUM	1.00	1.20	2.00	1.90	1.00	0.90	4.00
HIGH	7.00	2.10	0.00	3.33	0.00	1.58	7.00
TOTAL	12.00		19.00		9.00		40.00

Table 4.8: The relationship between body size dimorphism and male care giving. The Chi-squared test reveals significant differences between the observed (Obs.) and expected (Exp.) distribution of values ($X^2 = 20.02$, $p < 0.05$).

ALLO- MATERNAL CARE	BODY SIZE DIMORPHISM						TOTAL
	LOW		MEDIUM		HIGH		
	Obs.	Exp.	Obs.	Exp.	Obs.	Exp.	
LOW	8.00	7.50	9.00	11.88	8.00	5.63	25.00
MEDIUM	0.00	2.10	6.00	3.33	1.00	1.58	7
HIGH	4.00	2.40	4.00	3.80	0.00	1.80	8
TOTAL	12.00		19.00		9.00		40

Table 4.9: The relationship between body size dimorphism and allomaternal care. The Chi-squared test does not reveal a significant difference between the observed (Obs.) and expected (Exp.) distribution of values ($X^2 = 9.07$).

The correlation between male care and low sexual dimorphism in body size is well known and could be interpreted as supporting the sexual selection hypothesis (see section 4.1). However, this simple correlation actually tells us nothing about the factors which shape the relationship between body size dimorphism and breeding system. If body size dimorphism can, in itself, effect breeding systems by way of its influence on energetic costs, then the energetic benefits of male care giving in monomorphic species should also be apparent. The challenge then, is to discover

how male care may benefit females, and thus why this behaviour may have evolved. Here it will be shown that male care can substantially benefit females, in terms of shorter gestation lengths, lactation lengths and inter-birth intervals.

Gestation length, foetal growth rate, lactation length, post-natal growth rate and inter-birth interval provide measures of the energetic stress on females. As would be expected, each of these variables is closely correlated with body mass (table 4.10). Note that foetal growth rate and post-natal growth rate are calculated using neonatal mass and weaning mass data in conjunction with gestation length and lactation length respectively (see section 4.3 and table 4.1). Thus, even though they are rates, they are closely correlated with body mass by virtue of the variables from which they are derived.

Parameter	R ²
Gestation length	.57
Foetal growth rate	.94
Lactation length	.65
Post-natal growth rate	.77
Inter-birth interval	.67

Table 4.10: The correlation between body mass and various life history variables. Values of r^2 for various logarithmic measures of female energetic cost, against \log_{10} female body mass. See section 4.3 and table 4.2 for data sources.

In the case of foetal growth rate, body mass explains the observed variation so well that it will be excluded from any further discussion (see also Ross and MacLarnon 1995). For each of the remaining variables linear regression was used to remove the effects of body mass. In the following analysis residuals of gestation length, lactation length, post-natal growth rate and inter-birth interval are discussed.

The relationship between body size dimorphism and energy dimorphism implies that sex differences in energetic costs arise simply from sex differences in body mass. This is supported by the strong linear relationship between body mass dimorphism and the ratio of male and female energetic costs (energy dimorphism), as shown in figure 4.7 ($r^2 = 0.73$). However, at least 25% of the variation in energy dimorphism remains unexplained by body size dimorphism. Further analysis

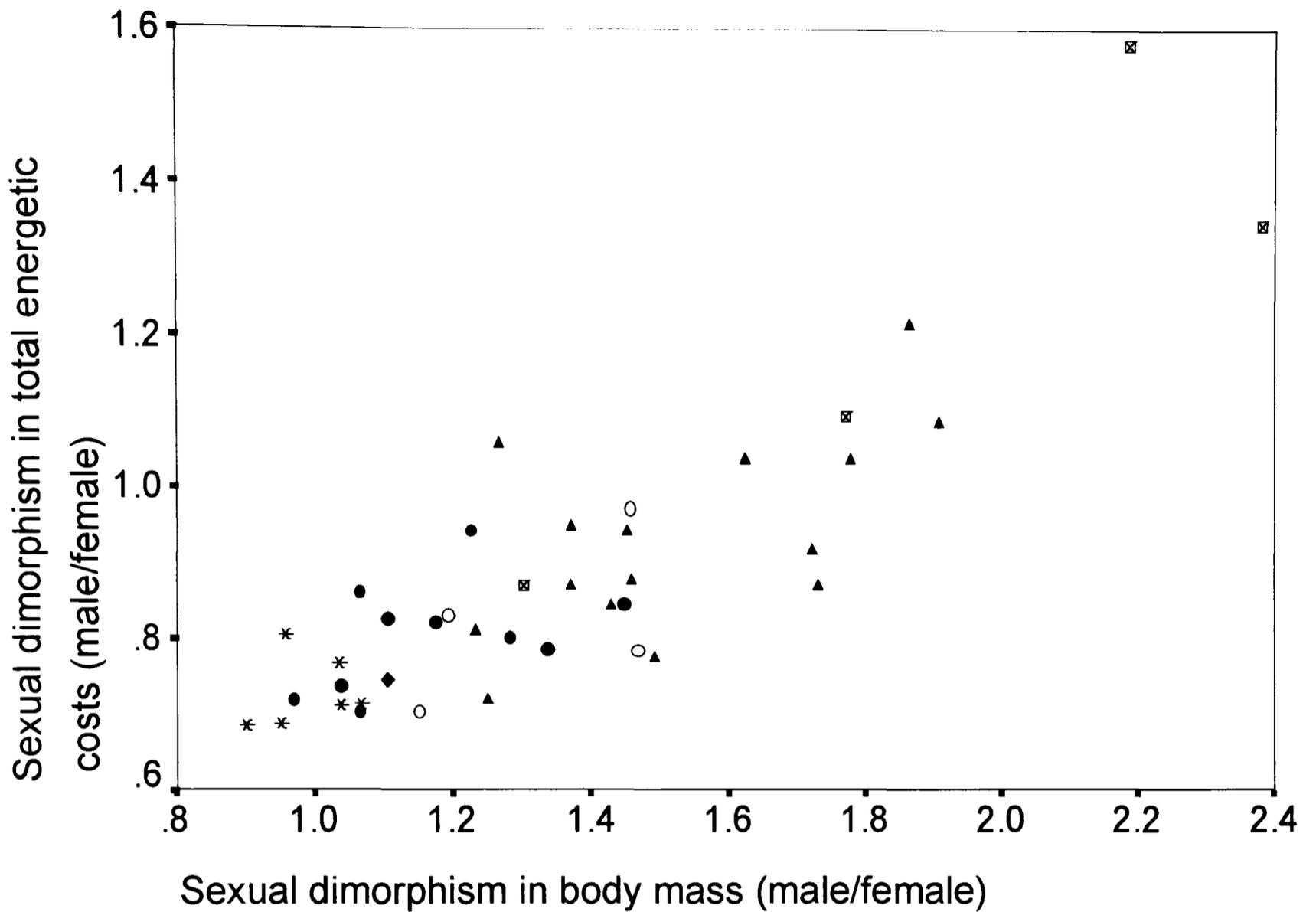
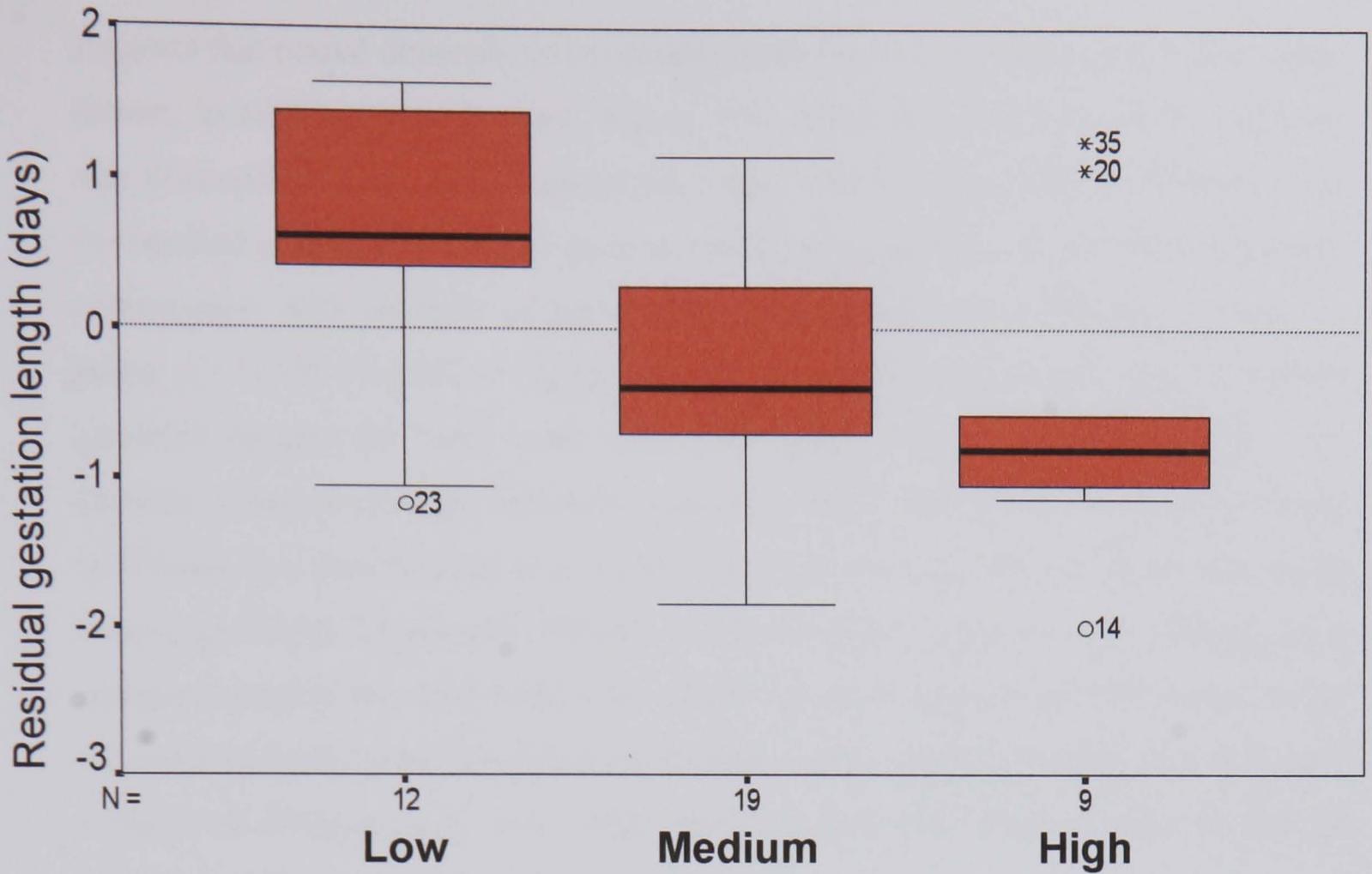


Figure 4.7: Energy dimorphism versus body size dimorphism

Sexual dimorphism in energy expenditure per reproductive event, compared with sexual dimorphism in body size.

(a)



(b)

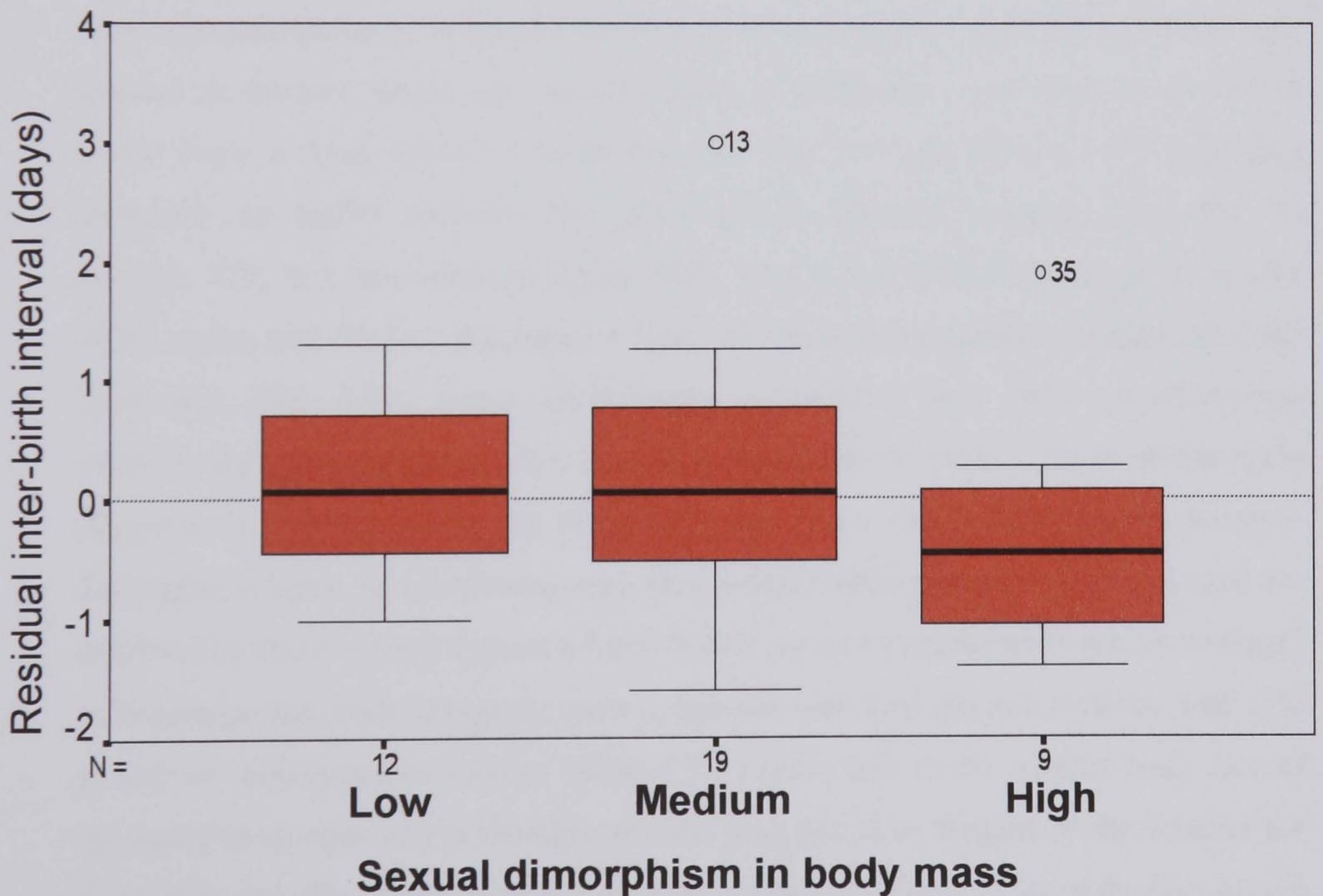


Figure 4.8: Boxplots of standardised residuals against sexual dimorphism in body mass

Boxplots show residual values of (a) length of lactation and (b) length of inter-birth interval. Figures below the dashed lines indicate gestation lengths/inter-birth intervals which are *lower* than would be expected for a given body mass.

suggests that sexual dimorphism in energy expenditure results from variation in other factors, in addition to body mass. Figure 4.8a shows the relationship between body size dimorphism and residual gestation length. There are significant differences in the residual gestation lengths of species with low sexual dimorphism when compared with species with medium or high sexual dimorphism (Mann Whitney U test, 2-tailed, $p < 0.05$). Females of highly sexually dimorphic species have relatively short gestation lengths for their body size. Accordingly, there is also a tendency for females of highly sexually dimorphic species to have shorter inter-birth intervals for their body size than females of less dimorphic species (fig 4.8b), although this result is not significant. Conversely, females of monomorphic species have relatively long gestation lengths for their body size. These results indicate that differences in the relationship between male and female energetic costs of reproduction are not simply a result of differences in male body size, but also arise from changes in female energetic costs associated with gestation.

To summarise the findings so far: the total energetic costs of reproduction have been compared in males and females. Female energetic costs are comparatively greatest in species which are monomorphic in body size, and least in species in which there is high sexual dimorphism (see fig. 4.6 and table 4.7 for summary statistics). In highly sexually dimorphic species female energetic costs are, on average, 10% less than male energetic costs. This is due to both the larger body size of the males, and the fact that females have relatively short gestation lengths for their body size (fig. 4.8a). Since intra-female cooperation and male non-reciprocal altruism are only expected when female energetic costs exceed those of the male (chapters 2 and 3), neither of these behaviours are expected in highly sexually dimorphic species. In accordance with this, neither allomaternal or paternal care are observed in these species (tables 4.8 and 4.9). Female energetic costs are, on average, 17% greater than male energetic costs in species with medium dimorphism, and 23% greater in monomorphic species (table 4.7). This is due to the smaller body size of the males in comparison to females, and the long gestation lengths of the females for their body size (fig. 4.8a). It was predicted in chapters 2 and 3 that male care giving and allomaternal care would arise in species in which female energetic costs are high in comparison to the male. Thus, we would expect male care giving and allomaternal care to arise in species with medium and low levels of sexual dimorphism in body mass. Expected and observed occurrences of male care and allomaternal care were

compared (tables 4.8 and 4.9). As predicted, paternal care giving is strongly associated with low body size dimorphism. But, none of the species with medium dimorphism show high levels of paternal care. This suggests that in these species, while female energetic costs are high relative to males, they are not high enough to stimulate the evolution of male care giving. Therefore, one might expect, that allomaternal care would be high in species with medium body size dimorphism. However, no significant trend could be discerned in the distribution of allomaternal care. Species that have low and medium levels of body size dimorphism will be looked at separately in the following analyses, in an attempt to uncover the advantages (if any) of allomaternal and paternal care.

Since allomaternal care only occurs in species with medium or low levels of sexual dimorphism the following analysis is restricted to just these species. In these cases female energetic costs are high, relative to male energetic costs, and it is possible that allomaternal care is a way in which females can offset these costs. If this is the case we would expect that females in species that practice allomaternal care would have an advantage over females in species that do not show allomaternal care. What sort of advantage would this be? Possibilities include: reduced energetic costs relative to the male; reduced absolute energetic costs; shortened inter-birth interval; shortened lactation length; shortened gestation length; or increased post-natal growth rate. All of these possibilities were investigated, and two significant relationships were uncovered (fig. 4.9). In general, in species in which there is no allomaternal care females have lactation lengths, gestation lengths etc. that conform to expectations based on body size. However, there are significant differences between species showing medium and high levels of allomaternal care with respect to length of lactation and length of the inter-birth interval (fig. 4.9a and b; 1-tailed Mann Whitney U-test $p < 0.05$). Species in which there are high levels of allomaternal care have *shorter* lactation lengths and inter-birth intervals than one would expect for their body size. On the other hand, species in which there are medium levels of sexual dimorphism tend to have *longer* lactation lengths and inter-birth intervals than would be expected on the basis of body size. Overall, there is a (non-significant) tendency for females that receive medium levels of allomaternal care to have higher total energetic costs, per reproductive event, than those that receive high levels of allomaternal care (fig. 4.9c). In short: while high levels of

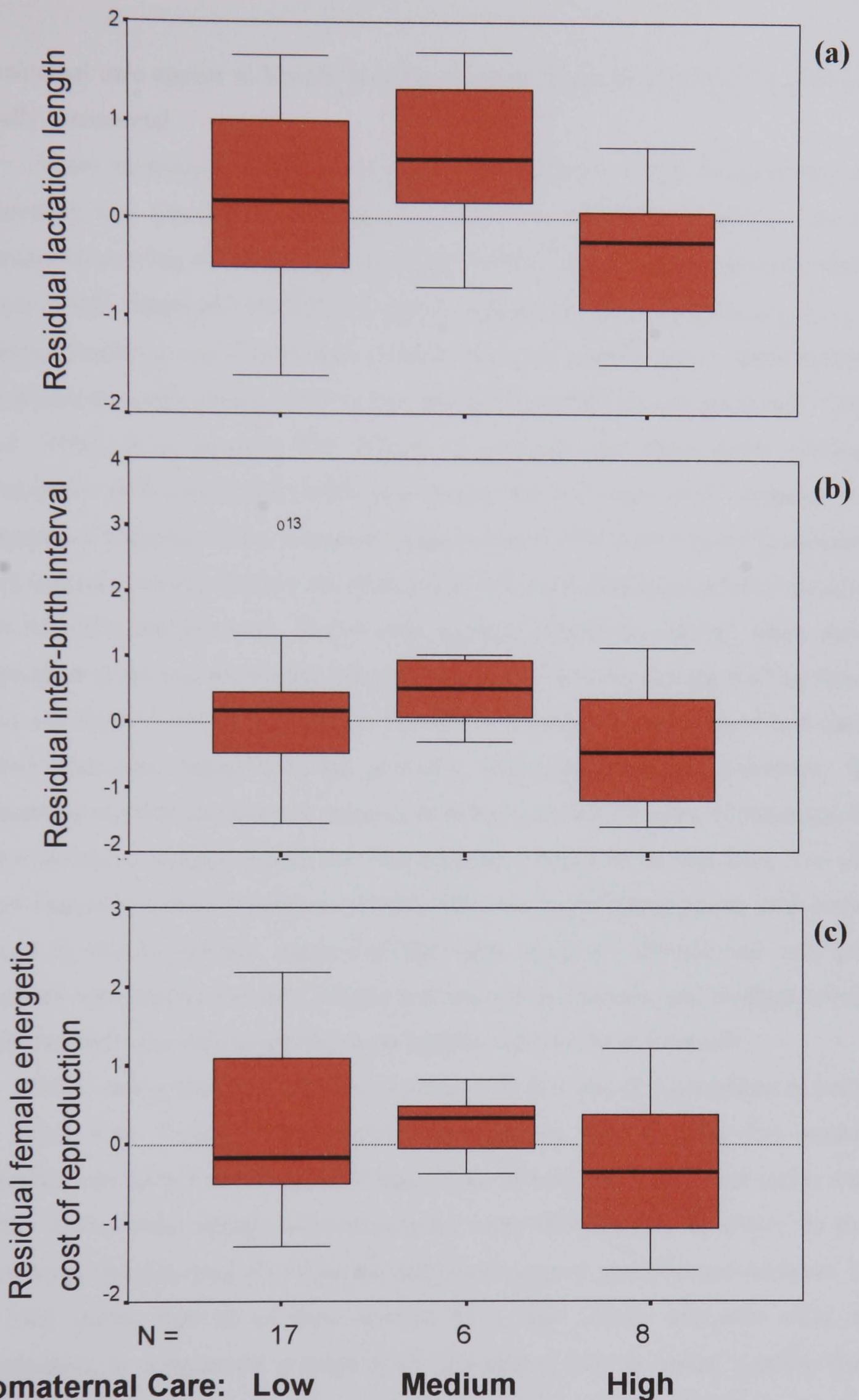


Figure 4.9: Boxplots of standardised residuals against degree of allomaternal care.

For all species which have medium or low levels of sexual dimorphism in body mass, the boxplots show residuals of (a) length of lactation, (b) length of inter-birth interval and (c) total female energetic cost of reproduction. Values that fall below the dashed lines are lower than expected on the basis of body mass. See section 4.3 for definitions of allomaternal care categories.

allomaternal care appear to benefit females, medium levels of allomaternal care are actually detrimental.

These seemingly contradictory results illustrate very neatly the problems in interpreting the function of allomaternal care. As discussed in section 2.6.1, allomaternal care has been described as both beneficial and detrimental to the mother (Khoda 1985). Stanford (1992) found that in capped langurs allomothering allows lactating females to spend more time feeding. Weaning usually occurs when infants have acquired a body weight which is four times greater than the weight at birth (Lee *et al.* 1991). It is possible that infants of mothers who have better feeding opportunities will acquire this body size sooner. On the other hand, research on chimpanzees (Nishida 1983), hanuman langurs (Hrdy 1977) and vervets (Lancaster 1971) suggests that allomothers are often young and inexperienced, and may actually harm the offspring involved. In this case mothers should be vigilant when their offspring is in the care of another female, which may actually disrupt feeding time. Mann and Smuts (1998) found that in bottlenose dolphins mothers spend less time feeding when their infant is in the care of a young, inexperienced allomother in comparison to when the infant is alone or is being cared for by older allomothers. If allomothering by inexperienced carers has a negative effect on feeding time, then we would expect lactation lengths to increase. The results presented above lend some support to this hypothesis, suggesting that high levels of allomaternal care are associated with shorter lactation lengths and inter-birth intervals, and medium levels of allomaternal care with longer lactation lengths and inter-birth intervals.

Male care giving only occurs in species with low sexual dimorphism in body size (table 4.8). Twelve of the species used in this analysis have low sexual dimorphism in body size. The similar body sizes of each sex means that males and females have similar energy requirements for body maintenance. However, in the longer term, females must also meet the additional costs of gestation and lactation. It has been shown that all of these species have high female energetic costs of reproduction, in comparison to male costs. Because of this the model predicts that male care giving should be high in monomorphic species. Indeed, 7 of these species show high levels of male care, and 1 shows medium levels. However, four species show little, if any, male care giving. The monomorphic species were separated into

two groups on the basis of presence or absence of male care⁴ to discover whether male care giving confers any energetic benefits to females. The two groups were tested for differences in lactation length, gestation length, inter-birth interval, overall female energetic costs and post-natal growth rates (fig. 4.10). Females from species which receive male care have significantly shorter lactation lengths and gestation lengths in comparison with those who do not receive male care (2-tailed Mann Whitney U test, $p < 0.05$). Furthermore, there is a (non-significant) tendency for shorter inter-birth intervals in species in which paternal care occurs.

Paternal care may reduce the energetic costs to the female of care-giving behaviours other than gestation and lactation, such as infant carrying. Furthermore, paternal care may allow the female to increase her energetic intake over the course of the reproductive cycle. In short, male care giving can reduce the energetic stresses of reproduction on females, allowing them to provide sufficient resources for the offspring in a shorter length of time. The results presented in figure 4.10 suggest that females can greatly benefit from male care in terms of shorter periods of lactation and gestation. Further, the tendency for shorter inter-birth intervals in species in which males contribute to offspring care indicates that these females are able to recover more quickly from the energetic stresses of reproduction.

In conclusion, male care giving has the potential to alleviate the energetic costs of gestation and lactation for females. Even so, when compared with male energetic costs, female energetic costs in monomorphic species remain high. It is important to be clear here. Male care giving only occurs in species with high female energetic costs *relative to male costs*. The principal benefit of male care giving is a reduction in female energetic costs *for her body size*. Without male care giving, the difference between male and female energetic costs per reproductive event would presumably be even greater.

⁴ Since only one species exhibited 'medium' levels of male care giving, the categories of 'medium' and 'high' male care giving were combined.

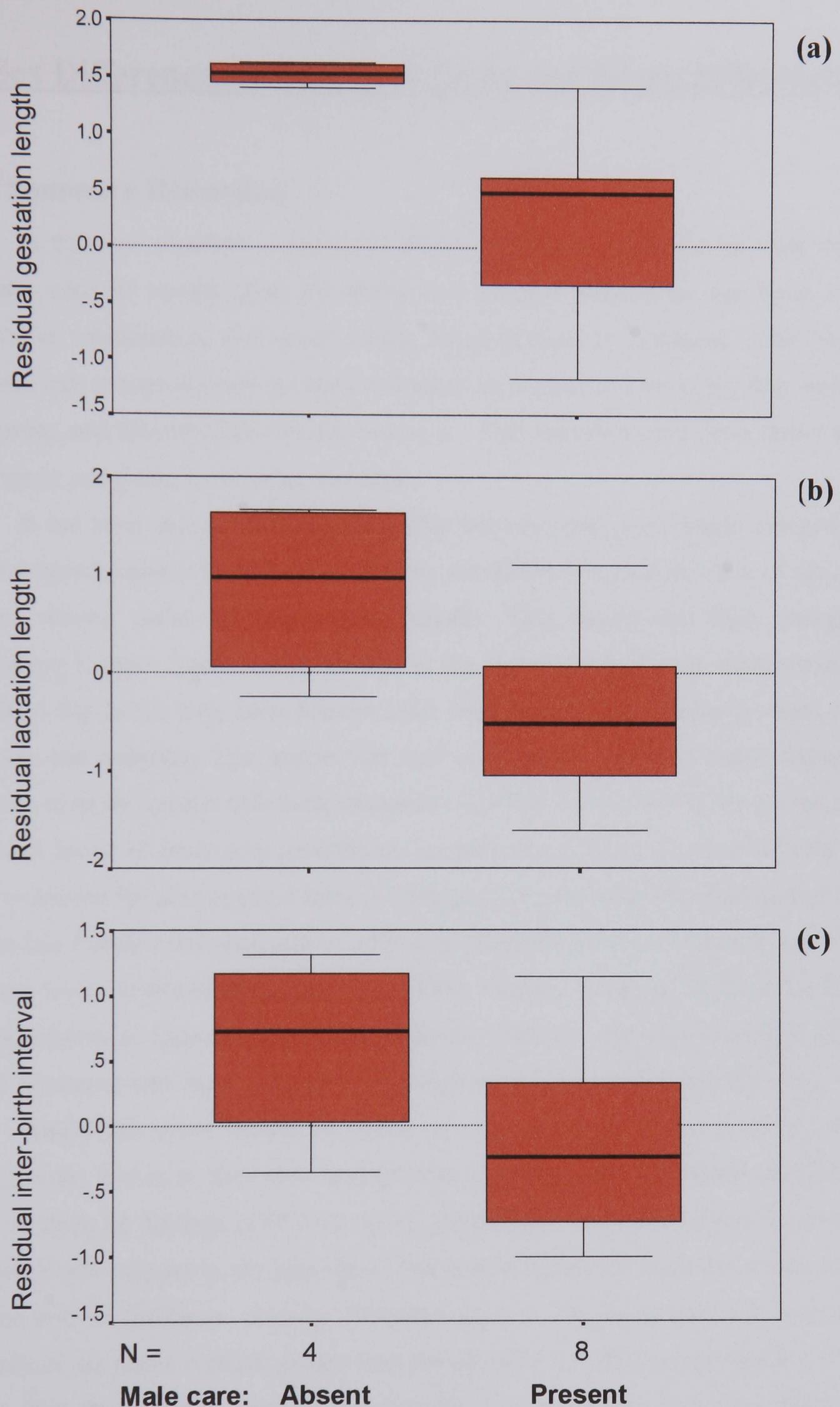


Figure 4.10: Boxplots of standardised residuals against presence of male care.

For all species which are monomorphic in body mass, the boxplots show residuals of (a) length of gestation, (b) length of lactation and (c) length of inter-birth interval. Values that fall below the dashed lines indicate shorter lactation lengths/ gestation lengths / inter-birth intervals than expected on the basis of body mass.

4.7 Sex Differences in Energetic Costs and Hominid Evolution

4.7.1 Summary Discussion

In previous chapters it has been argued that the relationship between the energetic cost of reproduction for males and females determines the types of cooperative relationships that occur within social groups. In particular, when the energetic cost of reproduction is high for females, in comparison to males, then male care giving and allomaternal care are expected. This hypothesis has been tested in this chapter using data from living primates.

It has been shown that the relationship between male and female energetic costs of reproduction is largely determined by sex differences in body size. In many primate species males are larger than females. This means that daily energy expenditure is often greater for males due to the higher costs of body maintenance (see fig. 4.5a). In the long term, females must meet the additional energetic costs of gestation and lactation. This means that over a single reproductive event, female energetic costs are greater than male energetic costs (fig. 4.5b). Only in those species with high levels of body size dimorphism do male energetic costs of reproduction equal or exceed female energetic costs of reproduction. Comparatively long gestation lengths (for female body size) add an additional energetic load on females in species with low levels of sexual dimorphism (fig. 4.8a). In short, female energetic costs are greatest relative to male energetic costs in species with low sexual dimorphism, and lowest compared with males in species with high sexual dimorphism (see fig. 4.6).

Ideally this model should be tested on individual populations, however, no other primate studies to date have attempted to compare male and female energetic costs. A study by Kenagy (1987) on energy expenditure in golden mantled ground squirrels lends support to the hypothesis that overall energetic costs for males and females will be similar in sexually dimorphic species. He found that daily energy expenditure for males is much greater than females (2.5 x BMR, as opposed to 2.0 x BMR). But, the energetic costs of lactation for the females are enormous. During peak lactation female energy expenditure is 82% greater than at the time of mating. Kenagy found that while males and females utilised their energy in different ways, when all factors were considered, male and female energy requirements over a breeding season were virtually identical.

Female energetic costs⁵ are greatest, relative to male costs, in species with low sexual dimorphism. Hence it was predicted that male care giving and allomaternal care would be found in species with low and/or medium levels of body size dimorphism. To support this it was shown that high levels of male care only occur in species that are monomorphic in body size (table 4.8). However, no relationship was found between allomaternal care and sexual dimorphism in body size. In view of these findings, section 4.6 explored the possible energetic benefits of allomaternal and paternal care. The energetic benefits of male care giving are clear (fig. 4.10): When males contribute to offspring care, females benefit in terms of significantly shorter gestation and lactation lengths for their body size. While female energetic costs are greater than male energetic costs in monomorphic species, male care giving helps to reduce this difference by reducing the energetic burdens of lactation and gestation. There is also a (non-significant) tendency for shorter inter-birth intervals when males contribute to offspring care. Palombit (1995) suggests that in siamangs male care giving may result in shorter inter-birth intervals and increased infant survivorship. This may be a particularly interesting test case since not all male siamangs practice paternal care.

While the benefits to the female of male care seem clear, the benefits to the male are less obvious. An important factor may be the relative stability of primate groups. For most primate species, age at first reproduction is high, and rates of migration are low (Dunbar 1988). This means that the number of reproductively mature females in a group will usually remain fairly stable over time and the availability of fertile females will severely limit a male's mating opportunities. The shorter the female inter-birth interval is, the better it is for the male. In harem social groups, new alpha males use infanticide as a mechanism to abruptly shorten inter-birth intervals (Hrdy 1977, 1979). Clearly with any degree of paternity certainty this is a maladaptive strategy. In monogamous or polyandrous species female reproductive output will severely affect male reproductive output, and any behaviour that will reduce the inter-birth interval, or alleviate energetic stress on the female, will also benefit the male.

⁵ For brevity, "energetic costs" refers here to the total energetic costs per reproductive event, unless otherwise stated.

The model has proved less fruitful in predicting female cooperation. Allomaternal care is more common than paternal care but does not occur in highly sexually dimorphic species where female energetic costs are low. There is some evidence that female cooperation may be important in reducing the energetic costs of lactation and shortening inter-birth intervals. However, when allomothering occurs at intermediate levels the energetic costs of lactation increases, as do inter-birth intervals (see discussion in section 4.6). Overall, these results confirm the complexity of motivations, costs and benefits associated with allomaternal care.

4.7.2 Energy budgets and the evolution of the australopithecines

The energetic profiles, discussed in section 4.4, offer an interesting insight into the whole problem of energy supply and demand. There is wide variation between primates in their methods of balancing energy intake and expenditure. *Lagothrix lagothricha* expends large amounts of energy on finding food, but little energy actually on feeding. This strategy is only possible because of the high energetic value of the food resource. Callitrichids, on the other hand, spend much of their time resting in order to minimise their energetic demands. Apes devote more time and energy to feeding than any other primate and are known to compromise their behaviour in order to meet their energy requirements. For instance, gorilla females alter their locomotor behaviour during pregnancy, by travelling less and at slower speed (Meder 1986) and have been shown to feed for slightly longer when pregnant or lactating (Watts 1988). Chimpanzee females have shorter day ranges than males at Mahale (Hasegawa 1990), in the Tai forest (Doran 1989) and at Gombe (Wrangham and Smuts 1980) although they do not necessarily spend less time travelling (Doran 1989). Furthermore, chimpanzee females with young or in the late stages of pregnancy have shorter day ranges than other females (Goodall 1986; Hasegawa 1990). The high energy requirements of the apes may also have cognitive implications: Byrne (1997) suggests apes have superior spatial-temporal skills, in comparison with monkeys, in order to improve foraging efficiency.

Apes, because of their large size, have the highest energy demands of all primates and compensate for this by minimising energy expenditure and maximising energy intake. While a chimpanzee female is able to dedicate 40% of her energetic

budget to foraging, in a patchy or poorer quality environment this would be impossible since the energetic costs of finding food would increase. Hunt (1994) suggests that bipedalism may have evolved in order to increase feeding efficiency. This hypothesis is based upon the observation that chimpanzees are more likely to adopt a bipedal stance during feeding than any other activity. It is likely that australopithecines lived in a patchy, woodland environment (Harris 1985; White *et al.* 1994), and that resources were scarcer and more highly dispersed than they are in modern chimpanzee habitats. Isbell and Young (1996) suggest that bipedalism provided an energetically efficient means of foraging over large distances. If australopithecines were following an ape-like pattern of energy utilisation, dedicating 40% of their energy budget to feeding, then it is likely that they had pushed it to its limit. They simply could not dedicate any more energy to feeding without sacrificing other important aspects of their energetic budget, such as movement and socialising. However, the evolutionary descendants of the australopithecines, members of the genus *Homo*, were considerably larger and occupied a rather more arid habitat (Reed 1997; Ruff 1991). It is likely that members of the genus *Homo* had to adopt a different energetic strategy compared with the australopithecines.

4.7.3 Energetic costs and the evolution of *Homo*

Humans appear to follow a rather different strategy of energy use compared with other primates. On the basis of body size dimorphism alone, which is low in humans, females should have a higher energetic cost of reproduction than males. However, in section 4.4 it was shown that human males have far higher daily energy expenditure than would be expected for their body size (see fig. 4.4). Female daily energy expenditure does not deviate from expected levels and it seems likely that high male daily energy expenditure arises from an increased work load associated with a sexual division of labour. Over the course of a reproductive cycle male and female energetic costs are approximately equal: that is, the high energetic costs of gestation and lactation for the female are balanced by increased daily energy expenditure in the male.

In one respect, the energetic costs of reproduction calculated for human females may have been over-estimated. As will be discussed shortly, the energetic costs of gestation and lactation appear to be rather low in humans in comparison with

other primates. In other respects, however, the energetic cost of reproduction for human females is likely to have been severely underestimated in the calculations. Over the course of human evolution there has been a considerable increase in encephalisation (see figure 1.1). Since brain tissue is metabolically expensive, consuming 22 times as much energy as skeletal tissue (Aiello and Wheeler 1995), an increase in brain size is likely to have considerable energetic implications. This is true for a number of reasons. Firstly, the costs of growing a large brained infant are borne primarily by the mother (Martin 1996). Brain growth is rapid both during pregnancy and over the first few years after birth, including the lactation period. This means that females are directly responsible for providing sufficient energy to their offspring for brain growth. Secondly, increased encephalisation has dietary implications. Aiello and Wheeler (1995) have shown that the increase in brain size in humans has occurred concomitantly with a decrease in the size of another metabolically expensive organ: the gut. Aiello and Wheeler argue that the only way that humans could meet the costs of encephalisation was by reducing gut size. This, in turn, was only possible with a change to a higher quality, more easily processed diet based on animal products. A reliance on animal products creates new behavioural challenges for females. Since immature and inexperienced offspring are unable to procure meat for themselves, this means that they are dependent upon their mothers for food for an extended period of time (we will return to this point in section 5.3.3). Human females must supply their offspring with food well beyond the weaning period. Bogin and Smith (1996 p705) note the extended period of childhood that follows weaning in humans:

“ Childhood is defined as the period following weaning, when the youngster still depends on older people for feeding and protection. Children require specially prepared foods due to the immaturity of their dentition and digestive tracts, and the rapid growth of their brain. These constraints necessitate a diet low in total volume but dense in energy, lipids and proteins. Children are also especially vulnerable to predation and disease and thus provide protection. There is no society in which children survive if deprived of this care provided by older individuals.”

Human childhood, and thus dependency, lasts until around 7 years of age (Bogin and Smith 1996). At this time brain growth is complete and the first permanent molars have usually erupted allowing the processing of an adult type diet.

Only at this age does the child gain a degree of self-sufficiency. Until this time, considerable investment is required from the child's mother, or other adults, to ensure survival.

Over the course of human evolution there has been a considerable increase in female energetic costs, compared with male costs, for three reasons: a) changes in body size dimorphism; b) increased encephalisation; c) an increased period of offspring dependency. As we have already seen, during hominid evolution there have also been considerable changes in male energetic costs due to the sexual division of labour. Males engage primarily in physically demanding activities, such as hunting, while females concentrate their efforts on less energetically expensive activities such as gathering and childcare. Food sharing, especially of meat, is common across hunter-gather societies (Musonda 1991).

There are three possible reasons why females do not participate in hunting activities themselves. Firstly, Hames (1989) suggests that the reason that females do not pursue animal resources is due to the incompatibility of simultaneous hunting and childcare. Without some kind of help from other individuals, females are simply unable to do both activities effectively. Second, hunting is an unpredictable foraging strategy (Hawkes 1993; Hawkes *et al.* 1997a). Studies of modern hunter-gatherers suggest that considerable day-to-day variation in hunting returns means that this is an unreliable means of obtaining a constant source of calories. Third, hunting and other activities carried out by males clearly have very high energetic costs: human males have significantly higher daily energy expenditure than would be expected for primates of their body size. Human females may be unable to increase their energy expenditure in a similar manner because it would suppress their fertility. A large number of studies on human females have shown that increased physical activity is associated with reduced fecundity (Bentley 1985). Problems included a late or delayed age of menarche, dysmenorrhea and secondary amenorrhea, abnormal oestrogen and progesterone levels and a short luteal phase. Low fertility associated with elevated activity levels is clearly a very large obstacle that could deter female's from hunting for themselves.

It seems likely that the sexual division of labour, food-sharing and increased energy expenditure by males, was a response to rapidly increasing energetic costs for females. But when during the course of hominid evolution did these changes occur? Put another way, when in hominid evolution did female energetic costs become

	Body Mass (kg)		Basal Metabolic Rate (kcal/ day)		Daily Energy Expenditure (kcal)		Energetic Cost of Reproduction (kcal)				Encephalisation Cost (kcal)	
	M	F	M	F	M	F	Chimpanzee data		Human data		Chimp. data	Human data
							M	F	M	F		
<i>A. afarensis</i>	44.6	29.3	1208.1	881.6	1904.0	1410.9	3822191	3944998	2444679	2335184	30898	12830
<i>A. africanus</i>	40.8	30.2	1130.0	901.8	1786.1	1441.4	3585597	4030455	2293353	2385768	31568	13108
<i>A. robustus</i>	40.2	31.9	1117.6	939.6	1767.2	1498.5	3547735	4190094	2269137	2480264	32818	13627
<i>A. boisei</i>	48.6	34.0	1288.5	985.6	2025.3	1568.0	4065849	4384355	2600523	2595254	34339	14259
<i>H. habilis sensu stricto</i>	51.6	31.5	1347.7	930.8	2114.7	1485.2	4245334	4152728	2715322	2458146	243940	101293
<i>H. habilis sensu lato</i>	37.0	31.5	1050.2	930.8	1665.5	1485.2	3343424	4152728	2138459	2458146	243940	101293
<i>H. rudolfensis</i>	59.6	50.8	1501.5	1332.0	2347.1	2091.0	4711703	5846738	3013613	3460891	343449	142614
<i>H. erectus (early African)</i>	62.7	52.3	1565.3	1361.4	2443.4	2135.4	4905072	5970827	3137291	3534343	701477	291281
<i>Neandertal</i>	60.1	51.8	1511.0	1351.6	2361.3	2120.6	4740289	5929577	3031896	3509926	812736	337480
<i>H. sapiens (early)</i>	70.0	56.8	1602.4	1394.4	2499.4	2185.3	5017594	6110412	3209261	3616968	837522	347772

Table 4.11 Estimates of energetic costs for selected extinct hominids

Body mass data were taken from McHenry (1992a). Basal metabolic rate and daily energy expenditure were calculated using the Kleiber equation (see section 4.4) and equation 5 (4.4.2) respectively. The energetic cost of reproduction was calculated using both chimpanzee and human values for lactation length, gestation length and inter-birth interval. The cost of encephalisation is an estimation of the additional costs of lactation that derive from having a larger brain size. These estimates are based on Foley and Lee's (1991) model. 'M' and 'F' stand for 'males' and 'females' respectively.

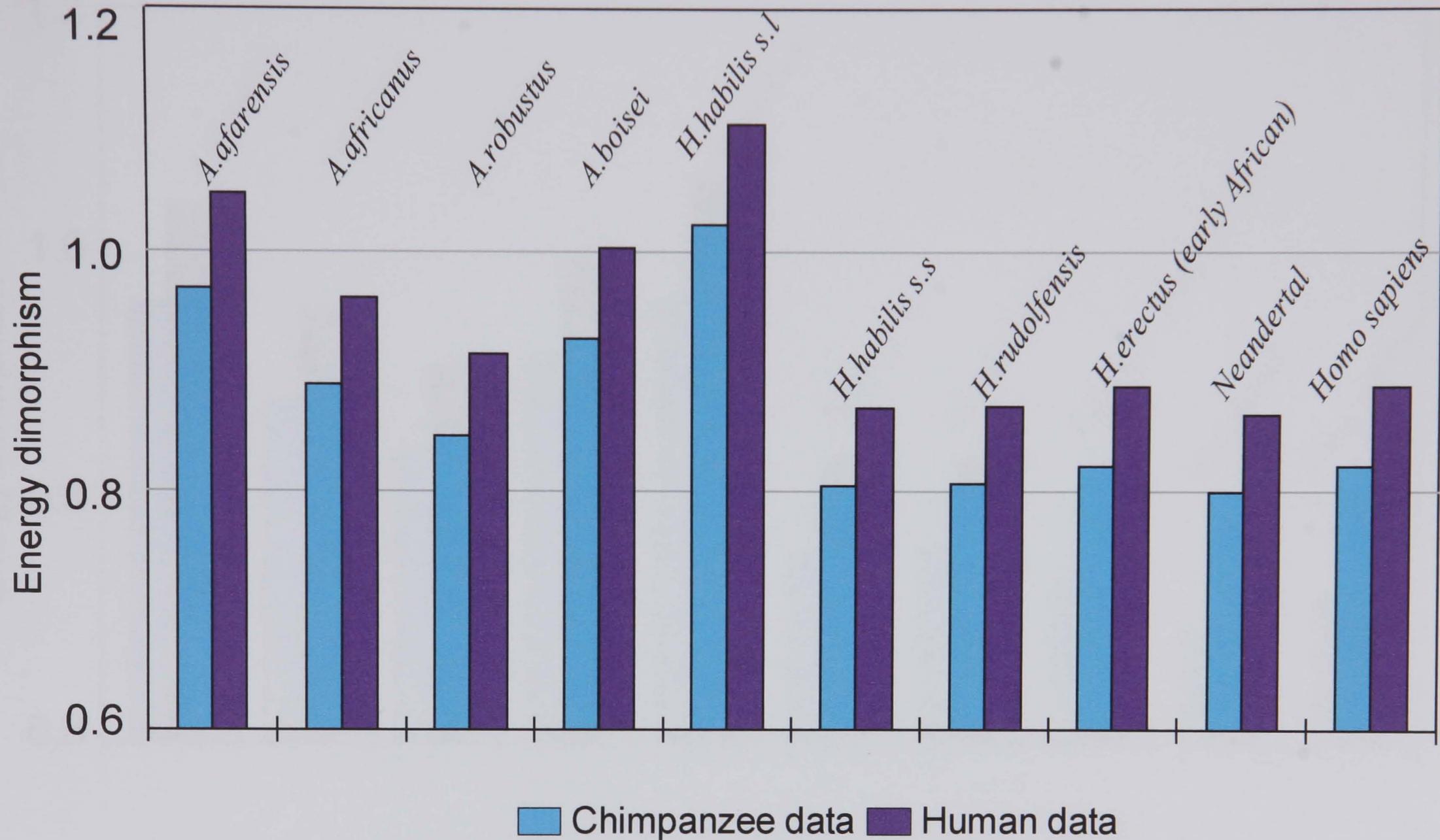


Figure 4.11: Estimated energy dimorphism in the hominids.

Energy dimorphism is calculated by dividing the energetic cost of reproduction for males by the energetic cost of reproduction for females. The values obtained depend on whether a chimpanzee or human model of gestation length, lactation length and inter-birth interval is used.

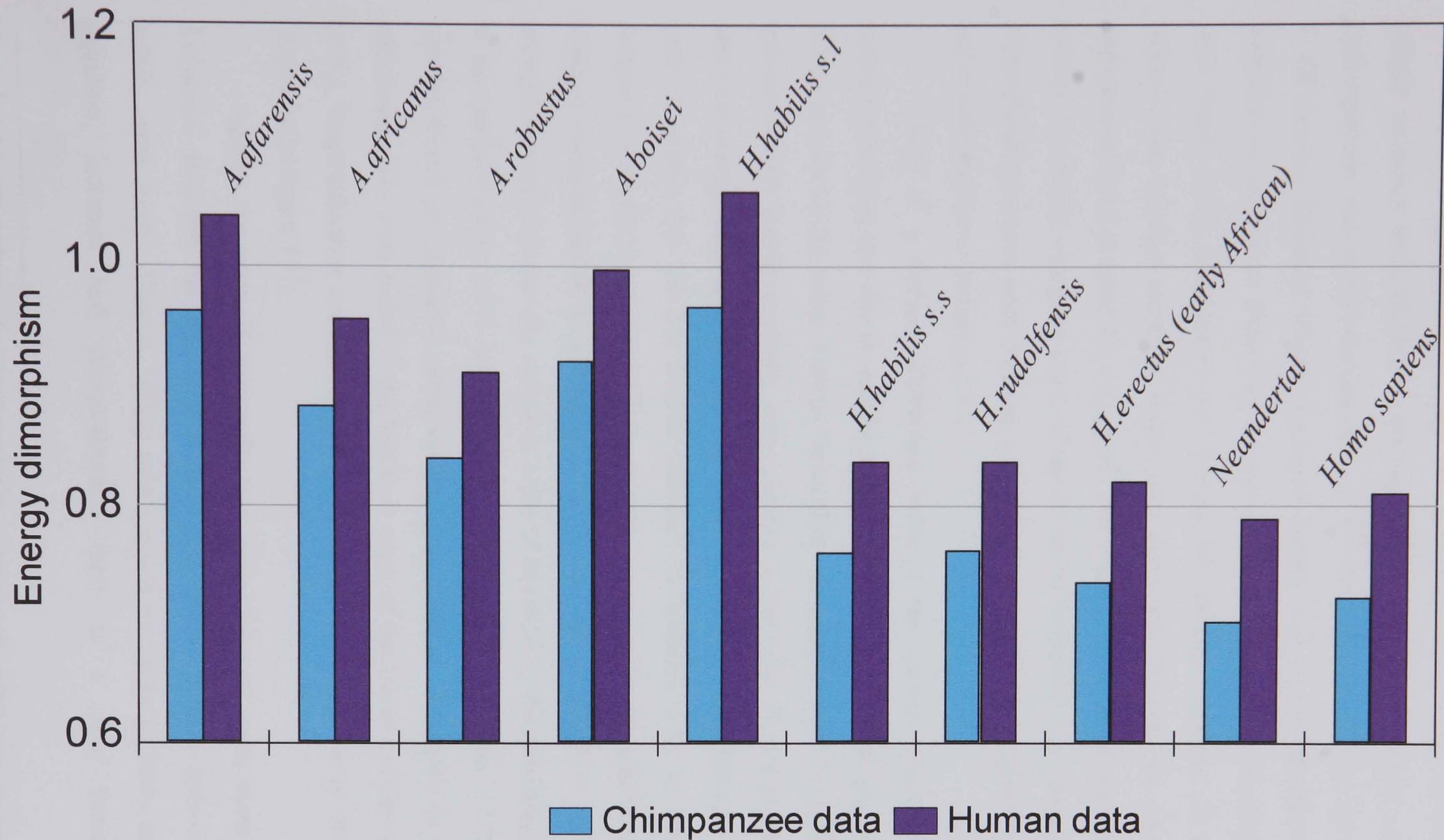


Figure 4.12: Estimated energy dimorphism in the hominids, including cost of encephalisation.

This figure is very similar to fig. 4.11. However, an estimate of the cost of encephalisation (see text) has been included in the calculation of female energetic costs of reproduction.

much greater than male energetic costs? In order to answer this question the energetic cost of reproduction for various hominid species was modelled using a similar methodology to that already applied in this chapter to extant species.

Daily energy expenditure was calculated for the hominids by applying body weight estimates from McHenry (1992a) to equation 5. Using these estimates, the total energetic cost of reproduction for each sex was calculated using equations 3 and 4. Of course, lactation length, gestation length and inter-birth interval for the hominids are unknown. Thus, two estimates of total energetic costs of reproduction were made, using chimpanzee and human life history variables. In the case of humans, the average lactation length and inter-birth interval for all the human populations listed in table 4.3 was used⁶. Male energetic costs of reproduction were divided by female energetic costs of reproduction to provide an estimate of energy dimorphism (compare with sections 4.5.2 and fig. 4.6). Data are given in table 4.11 and results are shown in figure 4.11.

There is a distinct difference between the energy dimorphism in the australopithecines and *Homo habilis sensu lato* on the one hand, and all the other *Homo* species on the other. Energy dimorphism is much greater in the latter group, indicating high female energetic costs relative to the male. It is interesting to note also that energy dimorphism is greatest when chimpanzee life history variables are used. It seems that the life history schedule in humans helps to reduce overall energetic costs for the female. These data do not consider the additional energetic costs of encephalisation to the female. Foley and Lee (1991) have calculated that encephalisation increases the energetic costs of lactation by the following values: 1% in australopithecines; 7.5% in early *Homo*; 15% in *Homo erectus*; 17.5% in *Homo sapiens* (based on estimated increased energetic costs at 12 months of age). These additional costs were added to the lactation stage of the model (values are included as the 'encephalisation cost' in table 4.11), and the effect on energy dimorphism is illustrated in figure 4.12.

Adding the costs of encephalisation serves to mark even more clearly the distinction between the australopithecines and *Homo* species (excluding *Homo habilis sensu lato*). That is, taking into account the costs of body maintenance, gestation, lactation and encephalisation there is a clear transition from

⁶ Excluding Scottish students, who are assumed to be a-typical with respect to our hominid ancestors.

australopithecines to *Homo*. In the australopithecines the energetic costs of reproduction are very similar for males and females. In *Homo* the energetic cost of reproduction for females is considerably greater than it is for males. This is particularly true of later hominid species, such as the Neandertals, in which female energetic costs are predicted to be between 20 and 30% greater than male energetic costs, depending on which model is used. Remember, these data do not include the additional energetic costs to the male that would occur with the sexual division of labour which is predicted to be a response to relatively high female energetic costs.

Figure 4.12 clearly illustrates the energetic implications of having a chimpanzee-like versus a human-like life history pattern. Using the chimpanzee model, hominid females are predicted to have higher overall energetic costs (and thus a lower energy dimorphism score) than when the human model is used. Why is this? Figure 4.13 illustrates the distribution across primates of residual gestation length, lactation length and inter-birth interval with respect to body size. Chimpanzee and human values are compared with these distributions. Chimpanzees have long gestation lengths, lactation lengths and long inter-birth intervals for their body size. Humans have long gestation lengths for their body size, and inter-birth interval conforms to expectations. However, lactation length in humans is noticeably shorter than would be expected on the basis of body size. Furthermore, during lactation energy demands increase by just 20-25%, considerably lower than in other mammals (Lunn 1994). Bogin and Smith (1996) have also shown that the typical human life cycle involves a shortened lactation (or infancy) period, followed by an extended childhood stage.

How were hominid females able to reduce the energetic costs of lactation to the levels seen in modern humans? One possibility, suggested by Hawkes *et al.* (1997a, b, c), is that menopause, long post-menopausal life spans and 'grandmothering' evolved to help ease the burdens of lactation on hominid females. Hawkes *et al.* found that senior post-menopausal Hadza women play an important role in provisioning their daughter's offspring. The benefits of this are clear for the child, the mother and the grandmother. With more provisioning the child would be expected to have higher a survival rate. The mother is relieved of some of the burden of providing food, reducing her energetic stress and shortening her inter-birth interval. Finally, the decreased mortality of the child and the increased fecundity of the mother equate to higher inclusive fitness for the grandmother. These

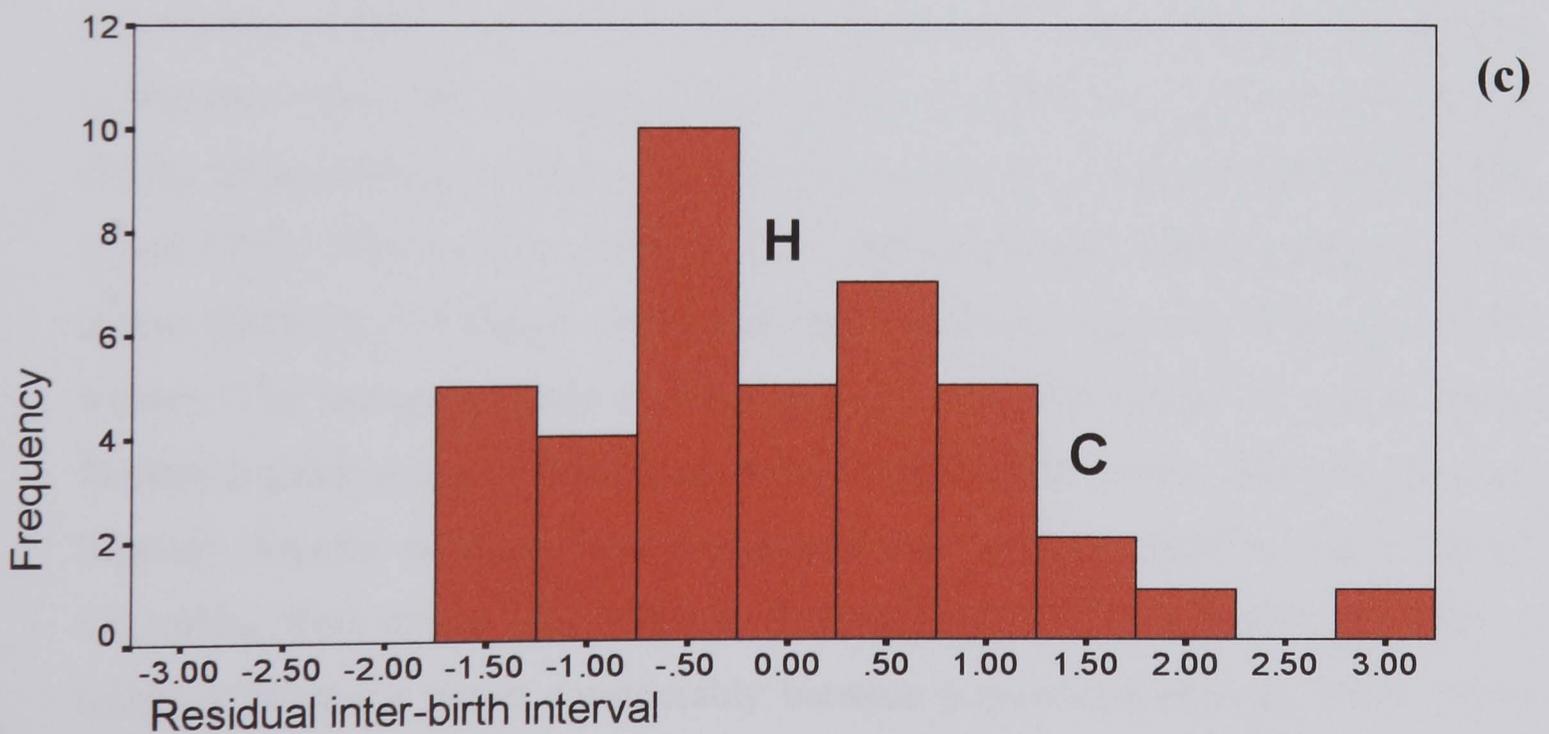
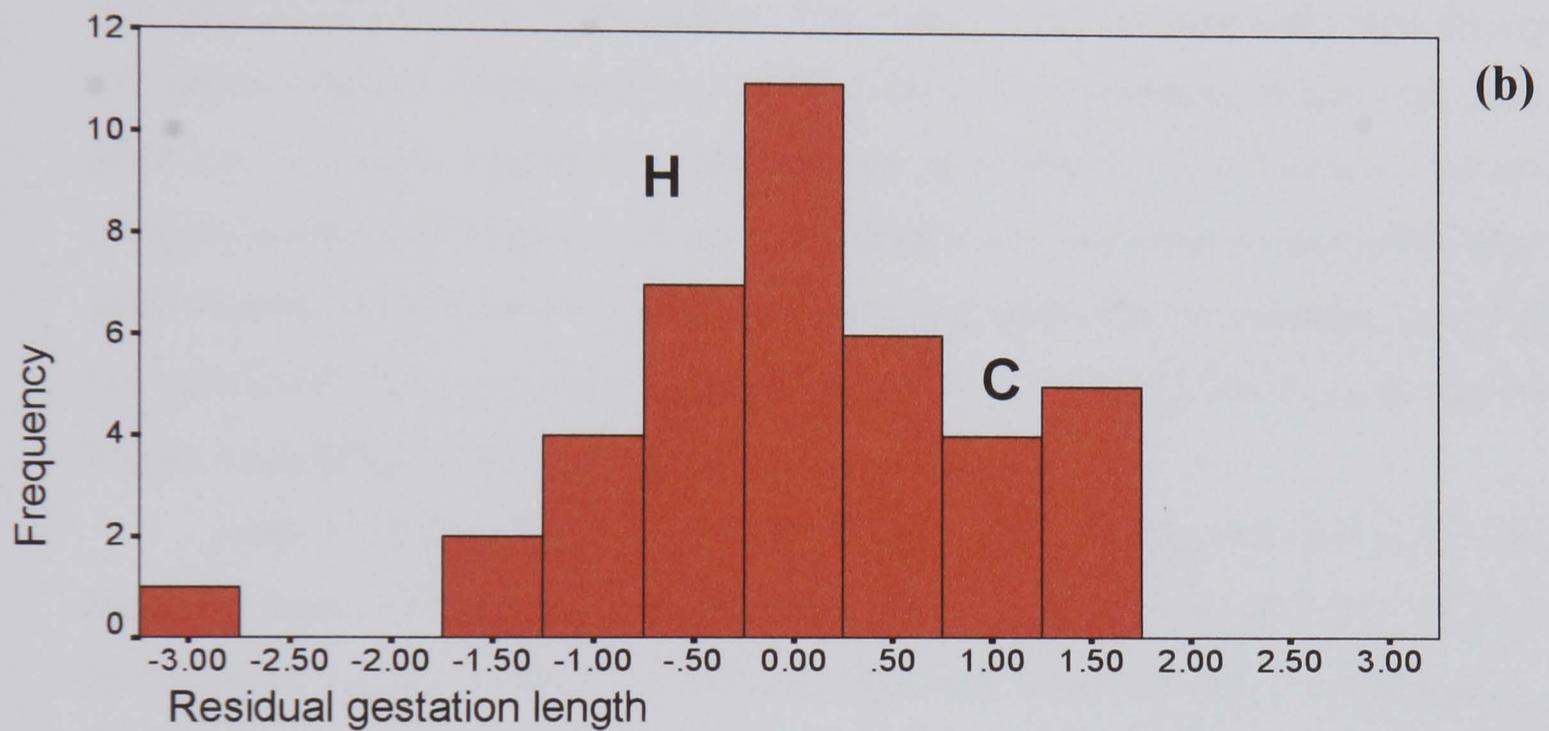
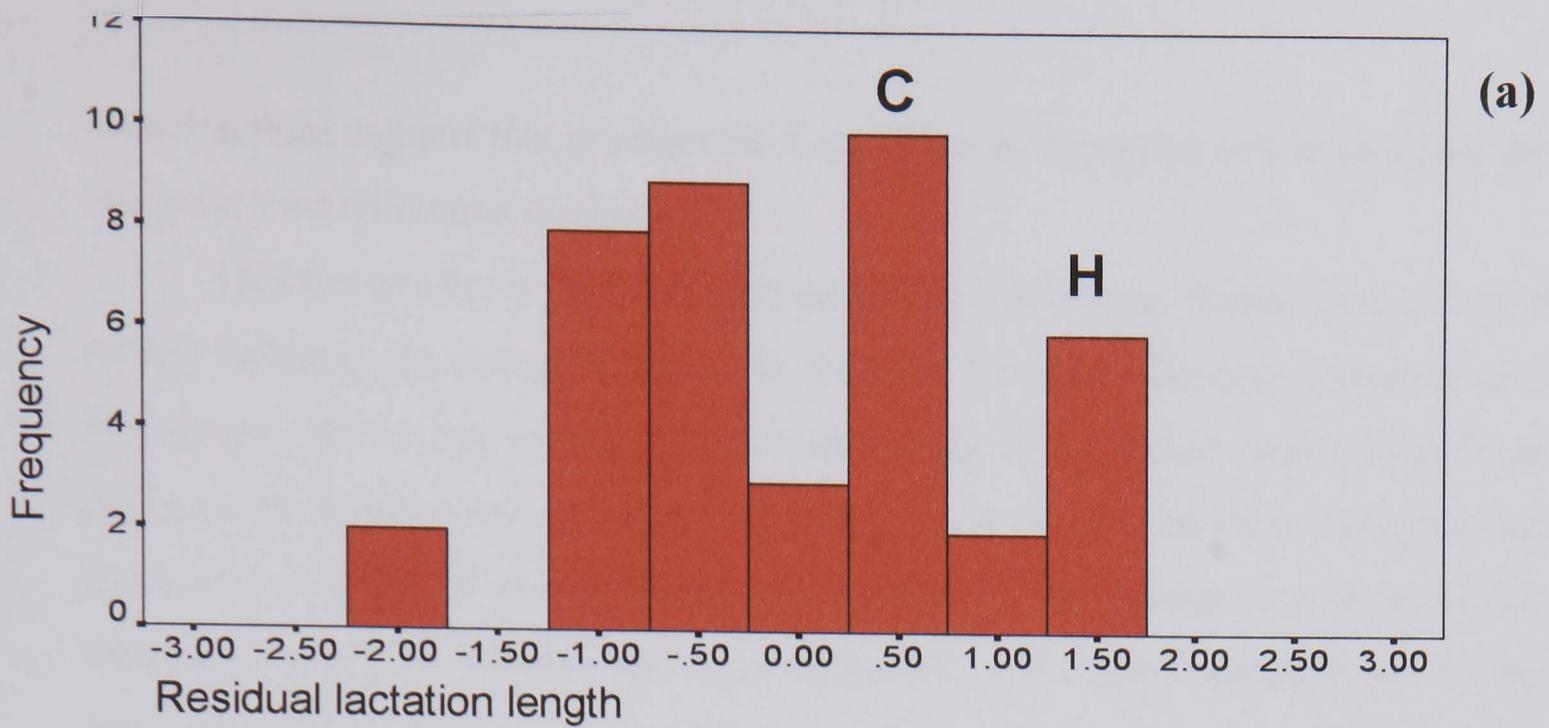


Figure 4.13: Distribution of residual values of selected life-history variables

The distributions of (a) residual gestation length, (b) lactation length and (c) inter-birth interval across primates. Negative figures indicate values that are lower than expected for body size, positive figures indicate values that are higher than expected for body size. Values for humans and chimpanzees are indicated by 'H' and 'C' respectively.

considerations suggest that grandmothers may play an important role in reducing the energetic load on human mothers.

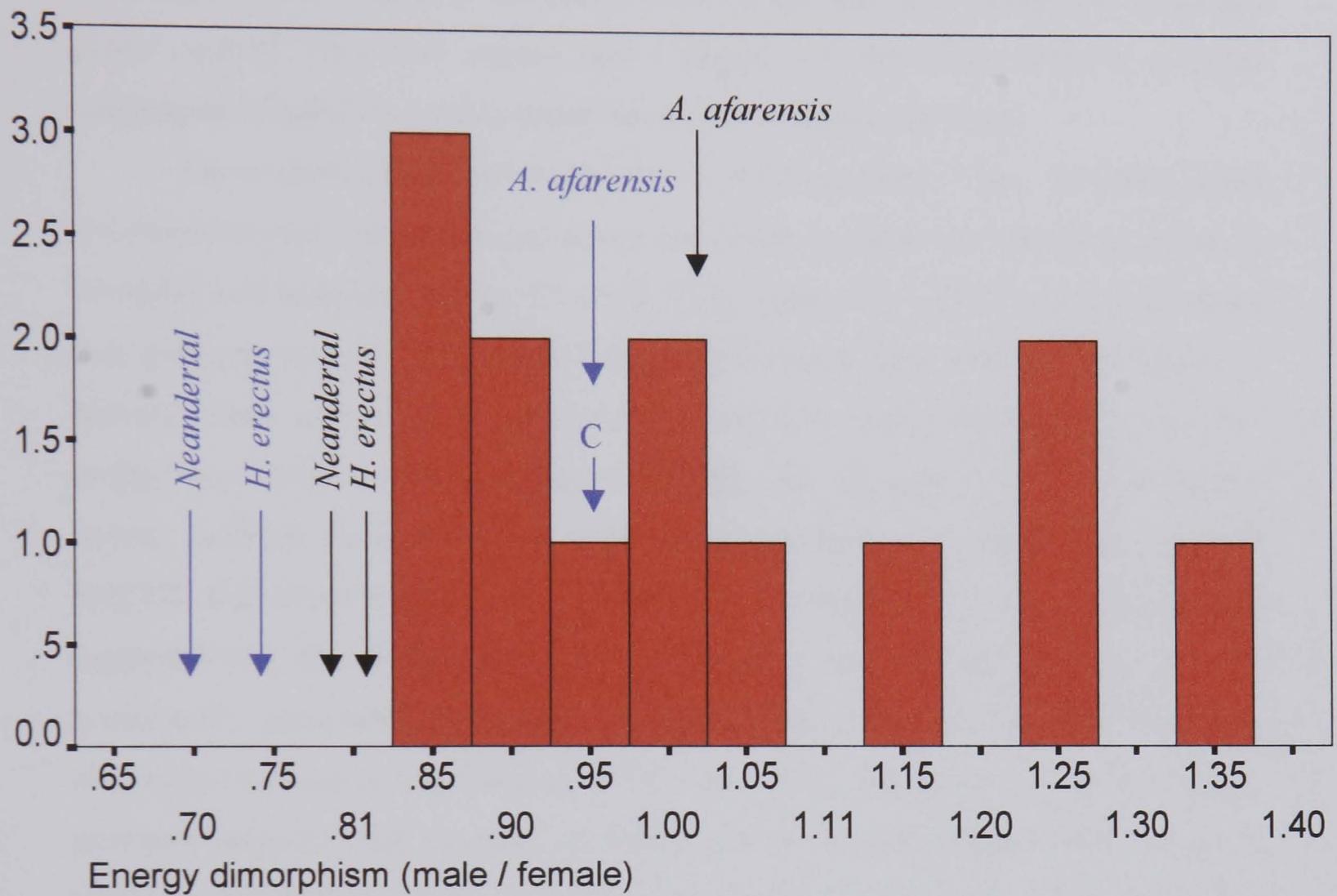
Hawkes and her co-workers play down the importance of male care giving in further reducing the energetic stress on females. However, the data presented here has shown that across primates, male care giving is correlated with a significant reduction in lactation and gestation length (section 4.6). On this basis I propose that the sexual division of labour in humans, involving male provisioning of resources, especially meat, to females and their offspring, contributed substantially to the reduction of the energetic costs of lactation in human females. This is particularly important since the costs to the mother of encephalisation are especially high during the lactation period (Foley and Lee 1991). Through provisioning, males may have helped to: a) reduce the costs to the females of finding food; b) increase female energetic intake both during and prior to lactation, in particular by providing high quality resources such as meat; c) allow females to wean offspring without incurring the additional costs of locating suitable foods for a weanling that would still be largely incapable of fending for itself.

Lunn (1994) isolates 5 mechanisms by which human females meet the energetic costs of lactation: 1) increased energy intake; 2) decreased activity; 3) decreased basal metabolic rate; 4) decreased diet-induced thermogenesis; 5) utilization of body fat. The importance of each mechanism varies between populations. Goldberg *et al.* (1991) found that the main source of energy for lactation in British women was increased energy intake (62%) followed by decreased activity (35%). In developing countries the principal mechanism is reduced physical activity (Lunn 1994). This has been shown to lower female energetic costs by around 15% in Indian (McNeill and Payne 1985) and Gambian (Lawrence and Whitehead 1988) women. The storage of body fat may also be a key mechanism by which human females are able to meet the costs of lactation (McFarland 1997). The Committee on Medical Aspects of Food Policy estimates that lactating females utilise around 12kcal/day from stored adipose tissue (Rogers *et al.* 1997), although the ability to build up fat stores varies considerably between populations (Durnin 1988; Hytten and Leitch 1971). Increased metabolic efficiency during lactation may also play a role in energy conservation, although again there is considerable inter-population variation (Rogers *et al.* 1997). Overall, human females clearly have at their disposal many different means of meeting the energy demands of lactation. The influence of

male provisioning on the effectiveness of these mechanisms is unknown. Conceivably males may play a very important role in allowing females to increase energy intake and reduce energy expenditure. Sustained provisioning of the females across the reproductive cycle may further enable the development of fat reserves.

I am suggesting that in humans male provisioning of females has greatly enabled their ability to meet the energetic costs of lactation. It is significant that in contemporary populations male provisioning nearly always involves animal products. As discussed earlier (section 4.4.2), females rarely participate in hunting or fishing, possibly due to the difficulties of simultaneous childcare. Yet, a meat component to the diet has been proposed to be of key significance in the evolution of the human brain (see above). The provisioning of meat by males to females, during pregnancy and lactation, and to newly weaned infants, may have been of primary importance. Hawkes (1990, 1991, 1993; see also Hawkes *et al.* 1991) argues against this view of hunting as a care-giving strategy. This is based on her finding in the Hadza that hunting provides unpredictable returns when compared to gathering (we will return to this argument in chapter 6). However, Hames (1989) argues that while hunting may not be the most efficient way of gaining calories, it is a considerably more effective way of gaining protein. In African and Amazonian societies low levels of animal protein intake (as opposed to overall caloric intake) have been shown to lead to high mortality and morbidity.

When, in hominid evolution, might male provisioning have arisen? In figure 4.14 the energy dimorphism of selected hominids is compared to the distribution of energy dimorphism in living human populations. It is assumed, in the first instance, that there is no sexual division of labour in the hominids, unlike humans, for whom the sexual division of labour significantly increases daily energy expenditure in males. Both *Homo erectus* and the Neandertals fall outside the range of human variation. This implies that if these two species had chimpanzee-like life histories and no provisioning by males, then females must have been under considerable energetic stress. It seems rather more likely that Neandertals (and by implication other archaic *Homo sapiens*) and possibly even *Homo erectus* conformed to a more human-like life history pattern. Arguably this was made possible by male provisioning and a sexual division of labour. Ruff (1987) asserts that sex differences in lower limb bone structure in Neandertals are indistinguishable from those of modern day hunter-gatherers. This suggests that Neandertals divided foraging



- Human data
- Chimpanzee data
- C Living chimpanzees

Figure 4.14: Energy dimorphism in selected extinct hominids compared with distribution of living human populations.

Energy dimorphism is calculated by dividing the energetic cost of reproduction for males by the energetic cost of reproduction for females. The values obtained for extinct hominids depend on whether a chimpanzee or human model of gestation length, lactation length and inter-birth interval is used. Note that the energy dimorphism of living chimpanzees (marked with a 'C') is 0.96.

activities by sex in the same way that hunter-gatherers do today. With respect to life histories, Bogin and Smith (1996) also point out the differences between human and chimpanzee life history patterns, the former including a shorter lactation period and a longer post-weaning, childhood period. They suggest that the transition to the human-like pattern began in late *Homo erectus*, and was well established in archaic *Homo sapiens*. They also suggest that a switch to a diet which included a higher component of animal-products would have been an important factor.

The evidence presented in this chapter indicates quite clearly that there was a transition between the australopithecines and *Homo* in patterns of energy expenditure by males and females (figures 4.11 and 4.12). More contentious is the proposition that male provisioning evolved *at least* 500,000 years ago, with the appearance of archaic *Homo sapiens*. It is interesting to note that this is the time that the first unequivocal evidence of large game hunting also appears in the archaeological record, with the earliest finds at Schöningen and Boxgrove dating from between 500,000 and 400,000 years ago (Thieme 1997). Aiello (1998, in press) has also suggested that during this period there would have been strong selection for male cooperation, particularly for providing animal food for females and their offspring. Yet, male care giving may have evolved even earlier. The fossil and archaeological evidence suggests that the diet of *Homo erectus* also included animal products (Shipman and Walker 1989). Leonard and Robertson (1994) and Aiello and Wheeler (1995) also argue, on the basis of brain size considerations, that the diet of *Homo erectus* must have had a meat component. If male care giving had not evolved at this point we must assume that either: a) males were the primary meat-eaters, an unlikely proposition if the connection made between brain size and diet is correct; or b) females were active providers of meat for their offspring, particularly during and after the weaning period and thus were able to meet the increased energetic demands of hunting and/or scavenging in addition to the costs of gestation and lactation. If this latter scenario is correct, then it is hard to imagine how hominid females could have met the costs of lactation by reducing activity levels and increasing energy intake, as human women do today. On balance, we cannot rule out the possibility that some degree of male provisioning may have occurred prior to the appearance of archaic *Homo sapiens*. Intra-female cooperation (i.e. allomothering and grandmothering) may also have played an important role. However, this analysis has found that it is

more difficult to make accurate predictions about female cooperation based on the kinds of data considered here. These issues will be explored further in chapter 6.

The alternative interpretation of these results is that changes in social structure, involving male provisioning, occurred before or in parallel with changes in sexual dimorphism in body size and encephalisation. For instance, Deacon (1997) suggests that pair bonding evolved in the transition from australopithecines to *Homo habilis* and thus the reduction in sexual dimorphism in body size, seen in *Homo*, was a result of reduced breeding competition. If decreased body size dimorphism occurred in response to changes in the breeding system, involving reduced male-male competition, then we would expect changes in male body size alone. However, the change in sexual dimorphism in *Homo erectus* was the result of changes in *both* male *and* female body size. Both sexes have increased in size, with the greatest increase occurring in females, possibly in response to thermoregulatory demands (Aiello 1996a, 1996b; Wheeler 1994). This indicates that, in this case, the relationship between body size dimorphism and breeding system is more complex than the sexual selection hypothesis suggests.

It has been argued throughout this thesis that it is important to consider *both* male *and* female energetic costs if we are to understand how different cooperative behaviours arise. This approach may prove to be particularly fruitful when considering the evolution of male provisioning in humans. Humans, because of the energetic demands of encephalisation, face unique energetic challenges compared with other primates. It has been argued here that this has led to two particularly important, mutually dependent, adaptations: a) the sexual division of labour involving male provisioning of females and their offspring with (primarily) animal-based resources; and b) a reduction in the energetic costs of lactation. The behavioural and cognitive ramifications of this will be discussed in chapter 6.

CHAPTER 5

The Effect of Habitat Quality and Seasonality on Cooperation

5.1 Introduction

In the first chapter the Prisoner's Dilemma was introduced using the story of two individuals, Romeo and Juliet, who had simultaneously happened upon some fruit which they would both like to eat. Each individual was given a choice between two behaviours: to share the fruit, or to threaten the other animal in the hope of gaining the whole lot. It has been shown, over the course of this work, that the decision to threaten (defect) or share the fruit (cooperate) will depend on a number of different factors: the energetic costs of reproduction for each individual, the history of past interactions, expectations as to how many times they are likely to interact in the future, and the relationship each individual has with other group members. However, no consideration at all has been given to the nature of the resource for which they are competing. For instance, would Romeo and Juliet be less or more cooperative if they had found unripe, less desirable fruit? Or, what if the dispute was not about fruit, but about meat? Perhaps the larger the prize, the higher the temptation to defect. On the other hand, if the resource is large, then even a shared meal may be enough to satisfy each individual's needs. The aim of this chapter is to further develop the Prisoner's Dilemma model, used throughout this thesis, by setting it within an ecological context.

Wrangham (1987a p.282) suggests that "ecological pressures bear the principal responsibility for species differences in social behaviour." Wrangham argues that it is particularly important for females to distribute themselves in the environment so that they maximise their ability to gain resources. Males, on the other hand, should distribute themselves so that they maximise their ability to gain access to females. According to this view, it is the dispersion of females that drives social organisation (Trivers 1972; Goss-Custard *et al.* 1972; Wrangham 1987a). Patterns of female dispersal are, in turn, dependent upon the distribution of resources. Groups of females are favoured when food is distributed in clumps which can support many individuals at once. If females can form groups they benefit in terms of lower

predation risk, and the ability to defend patches of resources (Dunbar 1988). When the food supply is more dispersed, group living may be untenable. For example, chimpanzees, spider monkeys and orangutans react to the dispersed nature of their food supply either by foraging in small groups (chimpanzees and spider monkeys) or alone (orangutans) (Wrangham 1987a).

The distribution of males depends on the opportunities for monopolising large numbers of females (Dunbar 1988). From a Darwinian perspective the ideal would be to have sole control of a group of females and so form a harem. However, if males are unable to monopolise matings with females, then a multi-male social structure will emerge. Male ability to monopolise mating opportunities is largely dependent upon the number of females there are in estrous at the same time (Dunbar 1988). This, in turn, largely depends upon whether the females are seasonal or non-seasonal breeders. In non-seasonal breeders females may come into estrous at any time of the year. Therefore, only one or two females are likely to be in estrous simultaneously and dominant males are easily able to prevent other males from gaining mating access. This means that in non-seasonal breeders males are able to establish quite large harem groups. In seasonal breeders many females will be fertile at the same time, leading to 'scramble competition' between the males for reproductive access. In this instance, multi-male groups are likely. Ridley (1986) has found this logic holds across primate species: multi-male social systems are associated with strong seasonality and short breeding seasons, while the opposite is true for harem systems.

Group size is another feature of social groups which is closely connected to ecological context. Group size appears to be a compromise between at least two environmentally determined selection factors: the necessities of predator defence (which selects for large groups) and the problem of obtaining sufficient resources for all individuals (which selects for smaller groups). The nature and quality of the food source is also important. Frugivores, for instance, require larger home ranges than folivores due to the more patchy distribution of fruit in comparison with leaves (Mace and Harvey 1983). Higher quality habitats are able to support greater population densities (Dunbar 1988). Also, the amount of time spent searching for food is related to habitat quality. In baboons (Dunbar 1988) and vervet monkeys (Struhsaker 1967) travelling time increases in poorer quality habitats.

In short, the quality, distribution and seasonality of the environment appears to play an important role in determining the size, distribution and structure of primate social groups. However, Wrangham admits that (1987 p.282):

“The problem, and this is true for most animal species, is that we do not know exactly what the relevant ecological pressures are, or which aspects of social life they most directly effect, or how.”

This chapter examines whether ecological factors effect cooperative and competitive strategies within groups. In particular, it examines the influence of habitat quality and seasonality, and how these factors might have differential effects on female-female, male-male and male-female interactions.

Habitat quality affects many different aspects of social life, and for this reason it is difficult to isolate its influence on cooperative behaviours alone. In poor quality environments individuals are forced to forage in smaller groups, thus lowering the potential for cooperative or competitive interactions. When resources are of higher quality larger group sizes are possible (Dunbar 1988), increasing the opportunities for both cooperation and competition. Folivores (e.g. colobine monkeys) tend to live in more egalitarian groups where competition and alliance formation occurs at a low frequency. Frugivores, on the other hand, live in groups where competition for resources is great (e.g. macaques, baboons). In response to this females in these groups tend to form strong kin bonds. Van Hooff and van Schaik (1992) suggest that the differences between frugivores and folivores result from either (a) differences in resource quality, or (b) differences in resource distribution. There is little available evidence to distinguish between these two possibilities. Van Hooff and van Schaik suggest that the second explanation is the most appropriate: that is, defendable patches of high quality resources, such as fruit, lead to high competition and thus strong female bonding. Leaves, because they are evenly distributed, are not easy to defend and thus they provoke very little competition or cooperation.

Intra-group competition has been related to the ‘patch size’ of available resources in chimpanzees (Isabirye-Basuta 1988) and black spider monkeys (McFarland Symington 1988a). In these cases feeding efficiency was found to decrease as patch size increased, indicating increased intra-individual competition. Since larger patches support greater numbers of individuals then competition would

be expected to increase with patch size. However, there is no clear way of determining the effect resource quality has on competitiveness. Larger patches may be considered to be higher quality patches, and this in itself may effect competitive versus cooperative tendencies. Computer simulations are a useful way of assessing the effect of resource quality as opposed to resource distribution.

Resource quality may be stable throughout the year, or may fluctuate on a seasonal basis. Animals respond to seasonal fluctuations in resource quality by shifting dietary strategies. During times of resource scarcity alternative and less nutritious food items are consumed (Foley 1987). In many animal populations living in seasonal environments reproduction follows a seasonal rhythm. Often births are timed to correspond to the period of greatest food availability (Lindburg 1987). For example, Butynski (1988) found that in African guenons, births tended to be coincident with wet seasons. In less seasonal environments birth seasons are either long or only weakly related to seasonal patterns (Butynski 1988). The strength of the association between seasonality and reproduction varies. Chimpanzees live in a seasonal environment but are not strictly seasonal breeders. Even so, Wallis (1995) observed seasonal patterns of anogenital swelling and conceptions in Gombe chimpanzees. Comparisons of captive versus wild populations support the importance of seasonal food availability in determining reproductive patterns. For instance, captive *Callimico* show no birth seasonality, unlike their wild counterparts. While Nishimura *et al.* (1990) report a distinct birth season in a wild woolly monkey group, Williams (1974) found no seasonality in a captive group. In some cases however, seasonal birth patterns continue even in the absence of environmental cues. Bernstein (1993) found that in captive rhesus macaques birth seasonality persisted even when the monkeys were housed indoors.

In vervet monkeys births occur most frequently during periods of high dietary quality (Lee 1987). Lee associates this with high energetic costs during the first few months of lactation (1987 pp. 413, 419):

“Nutrition of the mother is most important during the early phase of rapid infant growth, because at that time the energetic requirements of lactation are high.... For a seasonal breeder such as the vervet monkey, food supply – its quality, availability and distribution – plays a major role in the timing of reproductive events.”

It seems logical that females should time reproductive events so that the period of greatest energetic stress coincides with the period of greatest food availability. Given the high energetic costs of lactation, discussed at length in chapter 4, the post-natal period would appear to be the most energetically costly phase of the reproductive cycle. However, in some primates resource quality appears to restrict the ability to conceive. For example Koenig *et al.* (1997) found that in langurs, conceptions peaked at the time of greatest resource quality and that the majority of births actually occurred during periods of low resource quality. The fitness of the infants clearly suffers because of this. Koenig *et al.* report slow infant growth rates and average female age at first birth is 6.0 years, almost twice as old as in provisioned populations (3.1 years). Why do langur females follow this strategy rather than timing births to coincide with the time of greatest food abundance? Koenig *et al.* suggest that the nutritional state of the females restricts their ability to conceive (1997 p.230):

“At Ramnagar, conceptions occurred during, or immediately after, the months with the best dietary quality. Conceptions occurred only during the time of best physical condition, and females in good physical condition were more likely to conceive than females in poor condition.”

While the exact mechanisms that underlie the relationship between body weight and ovulation are unknown in this case, Koenig *et al.* point out that in rhesus macaques ovulatory frequency is directly related to body weight (Walker *et al.* 1983) and in humans ovulation may be disrupted following weight loss (Frisch 1984). This research suggests that for females there are two energetically critical periods: conception and birth. Females should time their reproductive cycle so that they can best meet the energetic demands of both conception and lactation.

In seasonal environments it is important for females to maximise their access to resources in times of plenty, especially if this is also an important reproductive period (whether conception or birth). Therefore, we might expect greater female-female competition during times of food abundance. The alternative hypothesis is that female-female competition decreases when food is plentiful, providing the opportunity for larger foraging parties which would be advantageous in terms of both defending resources from other groups and predator defence. Foraging group size in chimpanzees and spider monkeys is variable and appears to track seasonal variation

in food supply with the largest parties forming during the fruiting season (Wrangham 1977). In orangutans, occasional group foraging occurs during periods of food abundance (van Schaik and van Hooff 1983). If females time conceptions to coincide with food abundance, male-male competition would be expected to be greatest at this time. On the other hand, if births are timed to coincide with peak resource availability, male-male interactions may not be effected.

Interactions between males and females may also be effected by seasonal patterns of food distribution. Of particular interest is whether male care giving is more or less likely in a seasonal or non-seasonal environment. Busse (1985) argues that male-infant interactions are more likely to occur in non-seasonal breeders, such as baboons and mangabeys, than seasonal breeders such as macaques and vervet monkeys. This is because in seasonal breeders many females are in estrous simultaneously making it impossible to monopolise matings with a given female. Under these conditions low paternity certainty militates against male investment in infants. However, the models developed in chapters 2 and 3 suggest that paternity certainty is not necessarily the most crucial factor determining male care giving (see discussion in chapter 2). Furthermore, there is a central problem with Busse's hypothesis because it is based solely on observations of Old World monkeys. Male care giving is far more common in New World monkeys all of which are seasonal breeders.

All New World primates live in seasonal habitats, and all wild populations have distinct birth periods (Kinzey 1997). The most extreme of these is *Saimiri*, in which all births within a particular troop occur within a single week (Boinski 1987). Again, timing of reproduction appears to correlate with food availability. However, the timing of births varies across genera and there does appear to be two distinct strategies: either to maximise energy intake at conception, or at birth. For instance, in *Aotus*, *Callicebus*, *Pithecia*, *Lagothrix*, *Leontopithecus* and *Saguinus* birth peaks occur in the wet season, while in *Alouatta*, *Brachyles*, *Cacajao*, *Saimiri* and *Chiropotes* the birth peaks occur in the dry season (Kinzey 1997). In those genera which are capable of having two litters per year, such as *Cebuella* and *Callimico*, birth peaks are bimodal. There are interesting differences in male care giving between those New World monkeys which predominantly give birth in the wet season, compared with those that predominantly give birth in the dry season. All of the genera which give birth in the wet season also have high levels of male care

giving, the only exception being *Lagothrix*. None of the species which give birth in the dry season have male care. These observations suggest that the relationships between female fertility, seasonality and male care giving are far more complex than is currently recognised.

Social systems evolve within an ecological context. The quality or abundance of resources is likely to effect the types of cooperative or competitive strategies that individuals employ. Moreover, seasonal fluctuations in resource availability may cause individuals to alter their cooperative strategies over the course of the year. In this chapter the effects of habitat quality and seasonality on cooperative strategies are examined.

5.2 The Model

The concept behind this model is very similar to the earlier models (see chapter 2). The major difference is that resource quality and variability are incorporated into the model as features of the environment to which the agents must respond appropriately. Resource quality and variability are featured in the models by using multiples of the basic Prisoner's Dilemma pay-off matrix to represent 'poor', 'medium' and 'high' quality resources (fig. 5.1). The basic pay-off matrix, used in previous chapters, represents the situation where resource quality is poor. When resources are of medium quality and high quality, the pay-offs are multiplied by two and three respectively. In this way, although the magnitude of the pay-offs varies, the relationships between them is still a Prisoner's Dilemma. For instance, when resources are of high quality, mutual cooperation receives a pay-off of 9.00 points, which is higher than the pay-off if both players defect (3.00 points) but lower than the temptation to defect (15.00 points).

The model progresses in twelve-monthly cycles, where each month is coded as poor, medium or high quality. There are two types of experiment, seasonal and non-seasonal. In the non-seasonal models the environment remains constant, either at low, medium or high quality, so that each month the pay-off matrix remains the same. In the seasonal models the resource quality (as reflected in the pay-off matrix) cycles through the different types: poor, medium and high. The agents can detect resource quality and alter their behaviour accordingly. For instance, an individual could be a reciprocal altruist when pay-offs are low, and a defector when pay-offs are high.

Group size is small, there are only 50 agents (reasons for this will become apparent). The model proceeds on a monthly basis, where each month every agent interacts with every other agent for one game of the Prisoner's Dilemma. At the end of the month every individual that has enough points is given the chance to reproduce. Because agents play against each other every month, this is still an iterated game, even though only one bout of Prisoner's Dilemma is played between each pair in any given month. Each agent has a memory of its interactions with all the other agents for the last two months, and strategy choice is based on three factors: 1) the interactions between the players in the last two months, 2) the sexes of

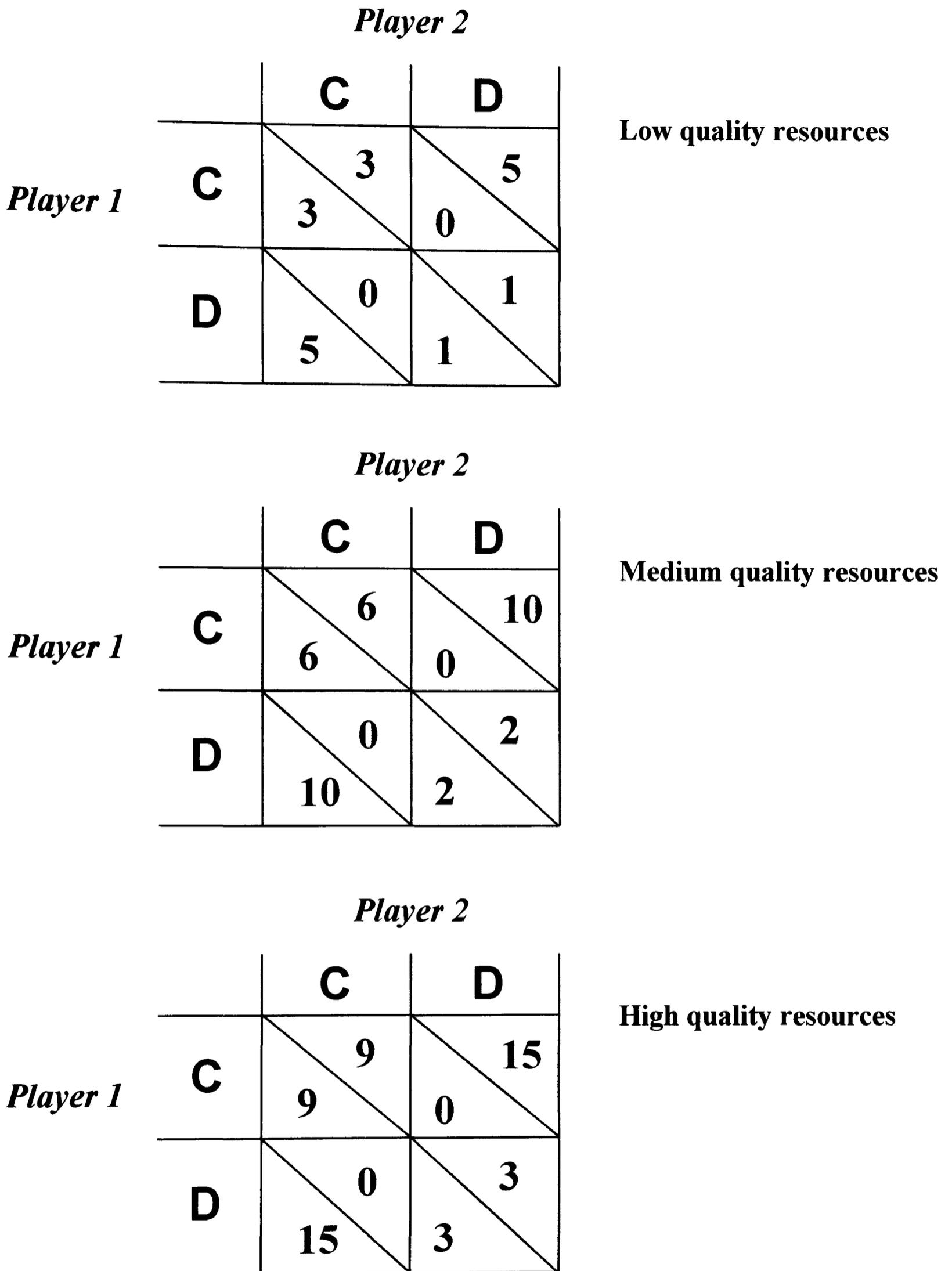


Figure 5.1: Pay-off matrices for resources of varying quality
 Pay-offs are multiples of the basic Prisoner's Dilemma matrix. 'C' and 'D' are cooperation and defection respectively.

the players, 3) the quality of the resource (poor, medium, high). In this way, strategies are highly individualised and very flexible. In order to be so flexible agents need 12 strategy strings, from the point of view of the agent these are:

- 1) I am male you are male, this is a poor quality resource
- 2) I am male you are female, this is a poor quality resource
- 3) I am female you are female, this is a poor quality resource
- 4) I am female you are male, this is a poor quality resource

- 5) I am male you are male, this is a medium quality resource
- 6) I am male you are female, this is a medium quality resource
- 7) I am female you are female, this is a medium quality resource
- 8) I am female you are male, this is a medium quality resource

- 9) I am male you are male, this is a high quality resource
- 10) I am male you are female, this is a high quality resource
- 11) I am female you are female, this is a high quality resource
- 12) I am female you are male, this is a high quality resource

The strategy strings themselves are identical to those used in model 1 (see chapter 2). They are 21-bit strings of 1's and 0's which code instructions to cooperate or defect respectively. Just as before, the strategy strings are a kind of look-up table, for example:

If: I am female and my opponent is female
and this is a high quality resource
and last month I defected and she cooperated
and the month before last she cooperated and I cooperated

Then: Refer to gene locus DCCC on strategy string 'female-female, high quality' which will give the instruction 0 (defect) or 1 (cooperate).

At the start of the experiment the strategy strings are randomly generated. These strategy strings are used to play the Prisoner's Dilemma through which agents acquire points. As before, reproduction is only possible once individuals have enough points to pay the cost of reproduction. During reproduction the strategy strings of the parents are crossed over, and may mutate (see chapter 2, fig. 2.1). This means that the strategies that are the most successful at acquiring points will have

the most offspring, and will be better represented in the next generation. The result is that over time the model evolves the best strategies for playing the Prisoner's Dilemma, within the parameters of the model.

This model is clearly more complicated than the original one. Agents have three times as many strategy strings, and must remember how they interacted with all the other agents for the last two months. Each agent has both a longer genetic code, and a memory that records all of its interactions with the other members of the population. The advantage of this is that each agent can respond in a flexible manner according to its current situation. The disadvantage of this set-up is that it restricts the population size. The larger the population, the larger an agent's memory must be to remember all of its interactions. Group sizes larger than 50, not only vastly increase experiment run-times, but also push the limits of the compiler in terms of the amount of memory it can handle.

The program code is outlined and given in full in appendix 4. The actual details of the model are slightly different to the first models, and proceed as follows:

- 1) At the start of the experiment the user sets the cost of reproduction for males and females (MRC and FRC respectively) and programs the resource quality for each month in the 12 month cycle. In a non-seasonal experiment each month would be coded to be the same. 50 agents are created. They are assigned a sex, a score (score = 0), and they are given 12 strategy strings which are coded randomly with 1's and 0's. These represent instructions to cooperate or defect and operate identically to the strategy strings in the earlier models (see section 2.2 and above).
- 2) The program progresses on a monthly basis. Each month the pay-off matrix is updated so that it reflects the quality of the environment (poor, medium or high quality: see figure 5.1). Every agent then plays a single game of the Prisoner's Dilemma with every other agent in the population. As described above, agents remember their interactions with every other player for the last two months and base their behaviour (cooperation or defection) on the history of interactions, the sexes of the players and the current resource quality. Each player's score increases in accordance with the relevant pay-off matrix.

- 3) At the end of each month all the individuals that have scored enough points are given the chance to reproduce. All the females with enough points are put into a 'fertile female' array, while all the males with enough points are put into a 'fertile male' array. Pairs are then selected randomly from each array to reproduce, until one of the arrays is empty. After reproduction the appropriate reproductive cost (MRC or FRC) is subtracted from an individual's score, and if they still have enough points to pay the reproductive cost they are returned to the fertile male or fertile female array. In this way, it is possible for an agent to reproduce more than once in any given month. Reproduction occurs through cross-over and mutation of each of the strategy strings (see fig. 2.1), so that two new offspring are created during each reproductive event. The offspring are randomly assigned a sex, given a score of 0, and then held in an offspring array.
- 4) The program continues to cycle through stages 2 and 3 until 50 new offspring have been created, i.e. the generation is complete. Generation time depends upon the costs of reproduction and the strategies of the players. In some experiments generation time was less than 12 months, in others it was greater than 12 months and so the yearly cycle was repeated. The offspring become the new parent generation and the cycle begins again, always starting from month 1. This continues for 20,000 generations.

This is an evolving model, designed to explore the relationship between resource quality, seasonality, reproductive cost and the evolution of cooperation. For each set of variables the experiments were repeated 30 times. These 30 runs are collectively described in the following text as a 'set'. For each experiment, the average score per player per game is recorded for each interaction type (male-male, male-female, female-female and female-male) for each month. Because different pay-off matrices are used it is no longer appropriate to summarise the results simply using the average score. To make the results from each experiment comparable, the average score is translated into one of the following 'strategy-types': suckers, defectors, weak defectors, weak cooperators, cooperators and exploiters. The index for translating average scores into strategy types is shown in table 5.1.

Strategy Type	Environment Quality		
	Poor	Medium	High
Suckers	< 1.00	< 2.00	< 3.00
Defectors	1.00 - 1.49	2.00 - 2.99	3.00 - 4.49
Weak defectors	1.50 - 1.99	3.00 - 3.99	4.50 - 5.99
Weak cooperators	2.00 - 2.49	4.00 - 4.99	6.00 - 7.49
Cooperators	2.50 - 3.00	5.00 - 6.00	7.50 - 9.00
Exploiters	> 3.00	> 6.00	> 9.00

Table 5.1: Strategy types.

The range of average scores that qualify for each strategy type in different environments.

The programs were run on 486 PCs. Extensive testing was done prior to running the simulations in order to check for programming errors. This included setting the strategy strings to known values and tracking the model's development over several generations.

Four main types of experiments were performed:

- 1) Non-seasonal environment of uniformly low, medium or high quality; male reproductive costs equal to female reproductive costs (section 5.3.1).
- 2) Non-seasonal environment of uniformly low, medium or high quality; male reproductive costs less than female reproductive costs (section 5.3.2).
- 3) Seasonal environment with cycling resource quality; male reproductive costs equal to female reproductive costs (section 5.4.1).
- 4) Seasonal environment with cycling resource quality; male reproductive costs less than female reproductive costs (section 5.4.2).

5.3 The Effect of Resource Quality in a Non-Seasonal Habitat

5.3.1 Equal male and female reproductive costs

In all of these experiments resource quality remains constant throughout the simulation. Resource quality was selected to be either low, medium or high and the appropriate pay-off matrix was used (see figure 5.1). Male reproductive cost was equal to female reproductive cost in each experiment. For each resource quality the experiment was run using each of the following reproductive costs: $MRC = FRC = 100, 200, 400, 600, 1000, 2000$ and 3000 . This was done separately for each resource type: poor, medium and high quality. In total, 21 sets of experiments were performed (3 different quality types x 7 different reproductive costs). Each of these sets involved 30 simulations. For each set of experiments the percentage of runs where agents evolved to be cooperators was calculated (see above and table 5.1 for definitions of 'set' and strategy type 'cooperator').

Because males and females have equal costs of reproduction, there is absolutely no difference between them. This was borne out by the results which were very similar for each interaction type (male-male, female-female, male-female and female-male). For clarity, results will be presented only for male-male interactions.

The results show that as resource quality decreases, the percentage of cooperators increases (fig. 5.2). For any given reproductive cost (RC), cooperation is always most likely when resource quality is poor, and least likely when resource quality is high. For example, when $RC = 3000$ and resource quality is low, cooperation evolves in around 65% of experiments. However, when $RC = 3000$ and resource quality is medium or high, cooperation evolves in only 50% and 25% of experiments respectively.

The relationship between resource quality and probability of cooperation parallels that between reproductive cost and percentage of cooperation. In fig. 5.2 the points at which the dashed line meets the curves indicate at which reproductive costs cooperation is expected in 25% of experiments. This point is reached at $RC = 1000$ with poor quality resources (pay-off matrix x 1), $RC = 2000$ with medium quality resources (pay-off matrix x 2), and $RC = 3000$ with high quality resources (pay-off matrix x 3). There is an inverse relationship between resource quality and

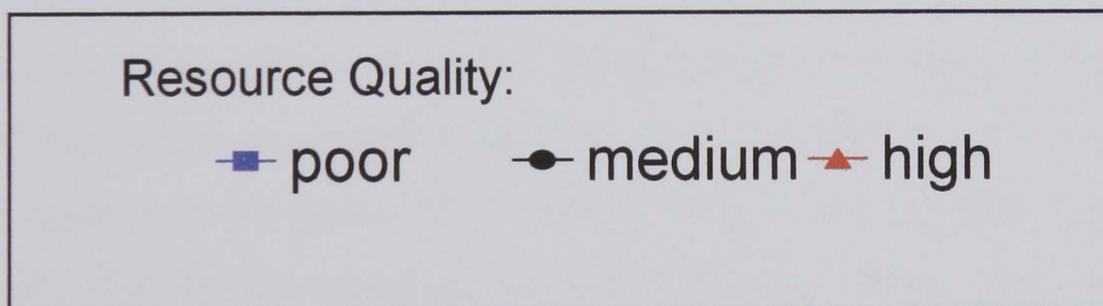
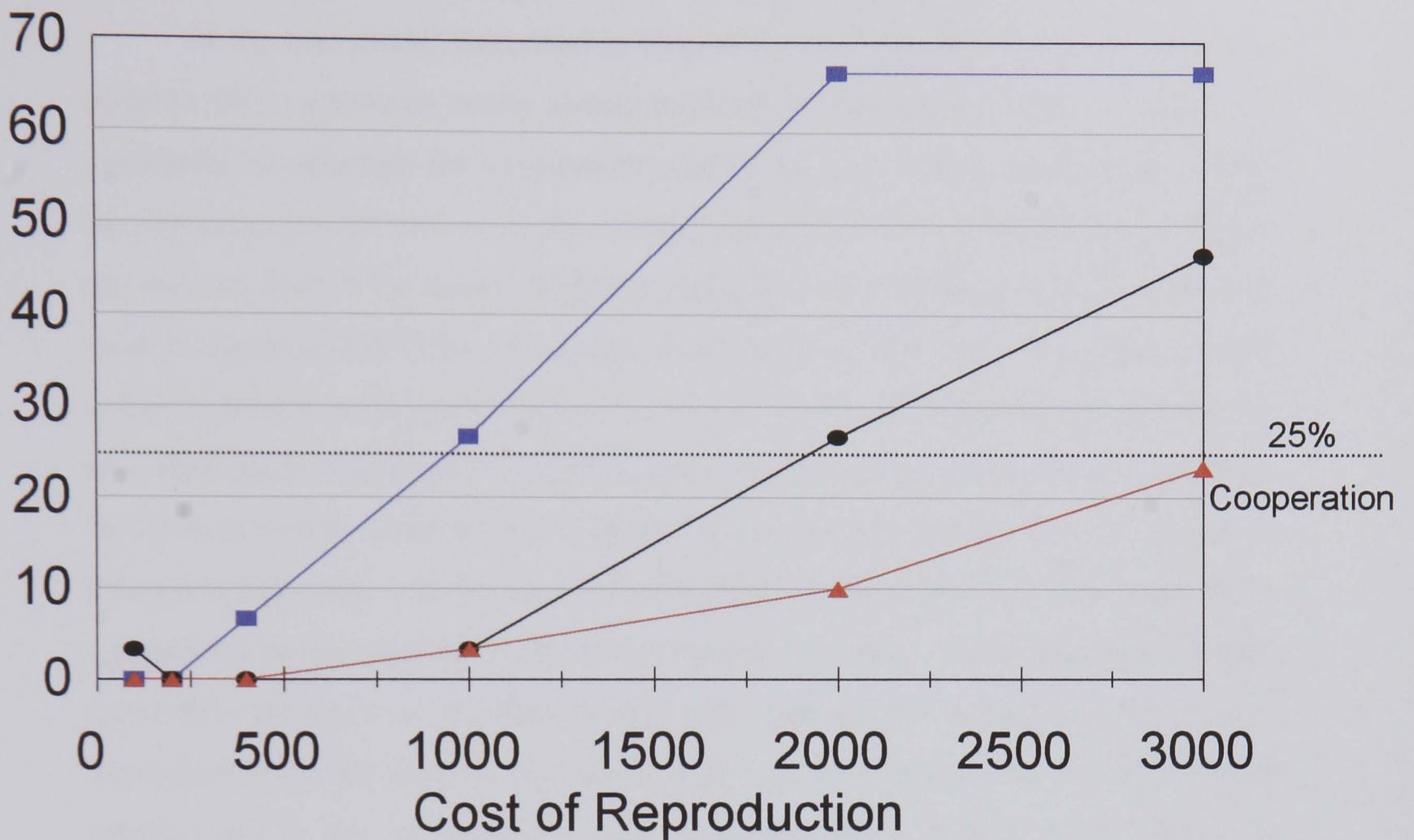


Figure 5.2: Percentage of simulations in which cooperation evolves in the control model.

The cost of reproduction is equal for males and females. For each reproductive cost the model was run 30 times, and each point on the graph represents the percentage of those runs in which cooperation evolved.

reproductive cost. The results for low resource quality at $RC = 1000$ are almost identical to those for high resource quality at $RC = 3000$. In effect, as resource quality decreases the cost of reproduction becomes relatively higher.

In the first model, described in chapter 2, at all reproductive costs greater or equal to 200 cooperation nearly always evolved. In this model, at $RC = 200$ there is practically no selection for cooperation even in the poor quality environment which has the same pay-off matrix as the original experiment. This difference in results is not due to a fault in the model. Rather, it exposes a basic difference between the two models. Axelrod (1984) has shown that cooperation is most likely to emerge when w is high, where w is the probability of future interactions with the same player. If w is low, then the best strategy is to defect since punishment in future games is unlikely. In the first model, when a pair of agents is chosen they interact for 100 games of Prisoner's Dilemma, which means that for most of the game w is very high. Since agents only have a memory of the last two games, and they cannot keep track of what game they are on, w is in effect always very high. In this model the size of w is dependent upon the cost of reproduction and environment quality. If the cost of reproduction is low or resource quality is high it does not take many months to produce a new generation of offspring. This means that w is low.

Consider, for instance, an experiment where resource quality is poor, and where every individual defects. Every month every individual interacts with 49 other individuals scoring $49 \times 1 = 49$ points. If the reproductive cost is 100, all agents will have enough points to reproduce in only 3 months, and hence the population will replace itself in a maximum of 3 months. This is not enough time to develop a cooperative relationship based on reciprocal altruism¹. What happens if the cost of reproduction is increased to 1000? Using the same reasoning it will take defectors 21 months to gain enough points to reproduce, a fairly long time compared with cooperators who could reproduce in just 7 months. However, even with this huge time advantage, cooperation is unlikely because 7 months is not enough time to foster cooperation. In this model, only at very high reproductive costs are individuals likely to interact often enough to make cooperation possible.

¹ Note that the small population size is irrelevant to this result, in fact the process speeds up in larger populations: a population of 1000 defectors at $RC = 100$ could replace itself ten times over in just one month.

In summary, this model shows that cooperation is most likely when the cost of reproduction is high and/or the environment quality is low.

5.3.2 Male reproductive costs lower than female reproductive costs

In the previous experiment males and females had equal reproductive costs. In chapters 2 and 3 it was shown that differences in male and female reproductive costs can have quite profound effects on the evolution of cooperative strategies and there is every reason to expect that the same will apply to these models. Therefore, the experiments were re-run with female cost kept stable at $FRC = 1000$, while male cost was varied. Again, the purpose of this experiment is to look at how resource quality effects strategy choice in a non-seasonal environment. For each set of reproductive costs, the experiments were run separately with resources kept constant, at either low, medium or high quality, as reflected in the Prisoner's Dilemma pay-off matrix (fig. 5.1). For each experiment the average score per agent per game was recorded for each interaction type, and then translated into a strategy type (see section 5.2 and table 5.1). For each set of experiments, the percentage of runs in which agents evolved to be suckers, defectors, weak defectors, weak cooperators, cooperators and exploiters was recorded (see table 5.1). These results were then compared with the results that would be expected on the basis of the previous experiment, in which male and female reproductive costs are equal (section 5.3.1). Female-female, male-male and male-female interactions will be discussed separately.

Female-female interactions

Figure 5.3 shows, for each set of experiments, the percentage of runs in which each strategy type evolved, comparing both the expected and observed results. Female reproductive cost was kept constant, at $FRC = 1000$, and so expected results are drawn from the experiment where $MRC = FRC = 1000$. Female-female interactions are predicted to be unaffected by the value of MRC , and to vary only with resource quality. This means that we would expect females to be most cooperative when resource quality is poor, and least cooperative when resource quality is high.

Cooperative strategies in female-female interactions do not differ markedly from expectations. Resource quality clearly has the expected effect: cooperation is

highest when resource quality is lowest and visa versa. When resource quality is high most females evolve to be weak defectors, in contrast to the low resource quality condition in which most females evolve to be cooperators or weak cooperators. The value of MRC has a slight effect on female-female strategies. Referring only to the observed results in fig. 5.3, and comparing the results when MRC = 400 or 600 with MRC = 100 or 200, at higher values of MRC females are slightly more cooperative. However, this is a very minor effect and resource quality clearly has the most marked influence on strategy choice.

Male-male interactions

The results for male-male interactions are illustrated in the same manner as those for female-female interactions (fig. 5.4). Male-male strategies are expected to vary with both the value of MRC and resource quality. Cooperation is predicted to increase as MRC increases and resource quality decreases. Taken as a whole, the observed results differ from expectations. In nearly every case, males were more cooperative than predicted (the only exception is MRC = 600 when resource quality is poor). Comparing the observed results for poor, medium and high quality resources shows that resource quality has a fairly weak effect. The trend is as expected: male cooperation decreases as resource quality increases. But, even when resource quality is high, levels of cooperation are considerably greater than expected.

In the poor quality resource condition the value of MRC has no effect on the outcome. Males evolve to be weak cooperators in approximately 60% of runs, and weak defectors in 40% of runs, regardless of the value of MRC. The results for medium and high resource quality indicate that the value of MRC has quite a strong effect: cooperation decreases as the value of MRC increases. An alternative way of viewing this result is that male-male interactions become more similar to expectations as MRC increases.

These experiments indicate that male-male strategies are affected by the presence of females with higher reproductive costs. Most strikingly, males are more cooperative than would be expected. None the less, full cooperation (as opposed to weak-cooperation) is rare and there still seems to be considerable competition between males for points. This competition increases as the value of MRC increases.

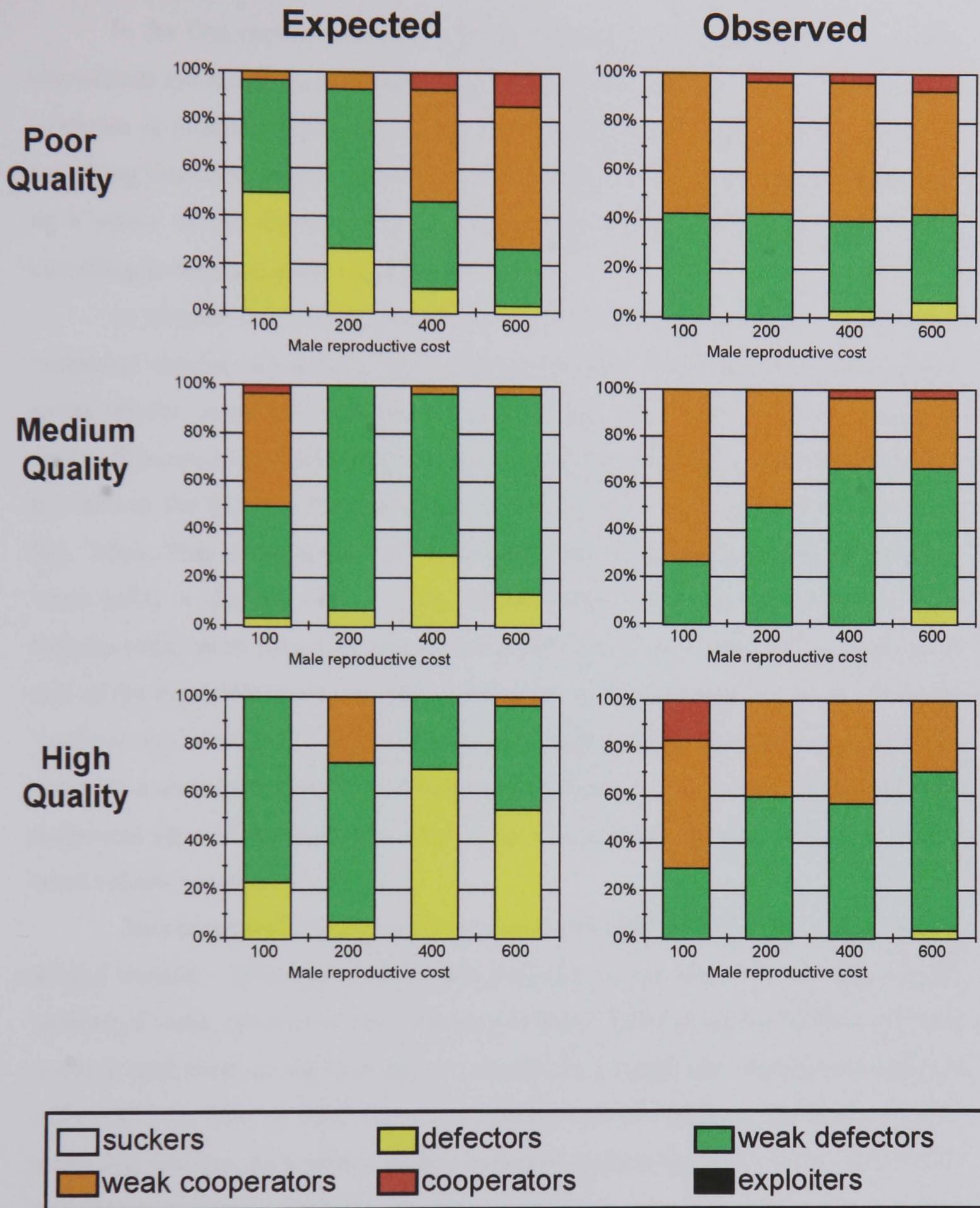


Figure 5.4: Male-male interactions

Female reproductive cost is held constant $FRC = 1000$ and male reproductive cost (MRC) is varied. Expected values are derived from experiments where male and female reproductive costs are equal. The results are shown for the three different resource types: poor, medium and high quality.

Mixed-Sex interactions

In the first experiments, described in chapter 2, it was found that mixed-sex interactions are rather more complex than single sex interactions and that a range of strategies is possible depending on the cost of reproduction for each sex. It is not surprising therefore, that the same is true here (figure 5.5). The results are illustrated as a series of pie charts which summarise the range of strategies that evolve according to resource quality and gender.

In chapter 2 it was shown that when $FRC = 1000$ and $MRC = 100$ non-reciprocal altruism can evolve. Non-reciprocal altruism describes situations in which males always cooperate with females but females only occasionally cooperate in return. The outcome of non-reciprocal altruism is low pay-offs to the males and high pay-offs to the females. Exactly the same results were observed in this experiment (fig. 5.5a). That is, regardless of resource quality, non-reciprocal altruism evolves when $MRC = 100$ and $FRC = 1000$. For instance, when resource quality is poor females score more than 3.00 points, and are classified as ‘exploiters’ in more than half of the runs. Males, on the other hand, gain very low scores, i.e. in the range of ‘suckers’ and ‘defectors’². This pattern of very high female scores and very low male scores is a clear indication of non-reciprocal altruism by the males. Although non-reciprocal altruism evolves no matter what the resource quality, it is most likely when resource quality is low.

Non-reciprocal altruism also evolves when $MRC = 200$ (fig. 5.5b), albeit a diluted version. Although females gain pay-offs greater than 3.00 in only a small number of cases, the overall pay-offs are markedly biased in favour of females. This result is surprising, as the basic model (chapter 2) predicts male-female competition when MRC is 20% of FRC . Resource quality has an effect on pay-offs for both males and females. As resource quality increases females suffer lower pay-offs while male scores increase. This is most clearly the case when the results for the high quality experiments are compared with those for either the low or medium quality experiments. None the less, even when resource quality is high females still gain more points than males.

² In this instance, the term ‘defector’ is misleading, since the low scores are a result of cooperation rather than defection.

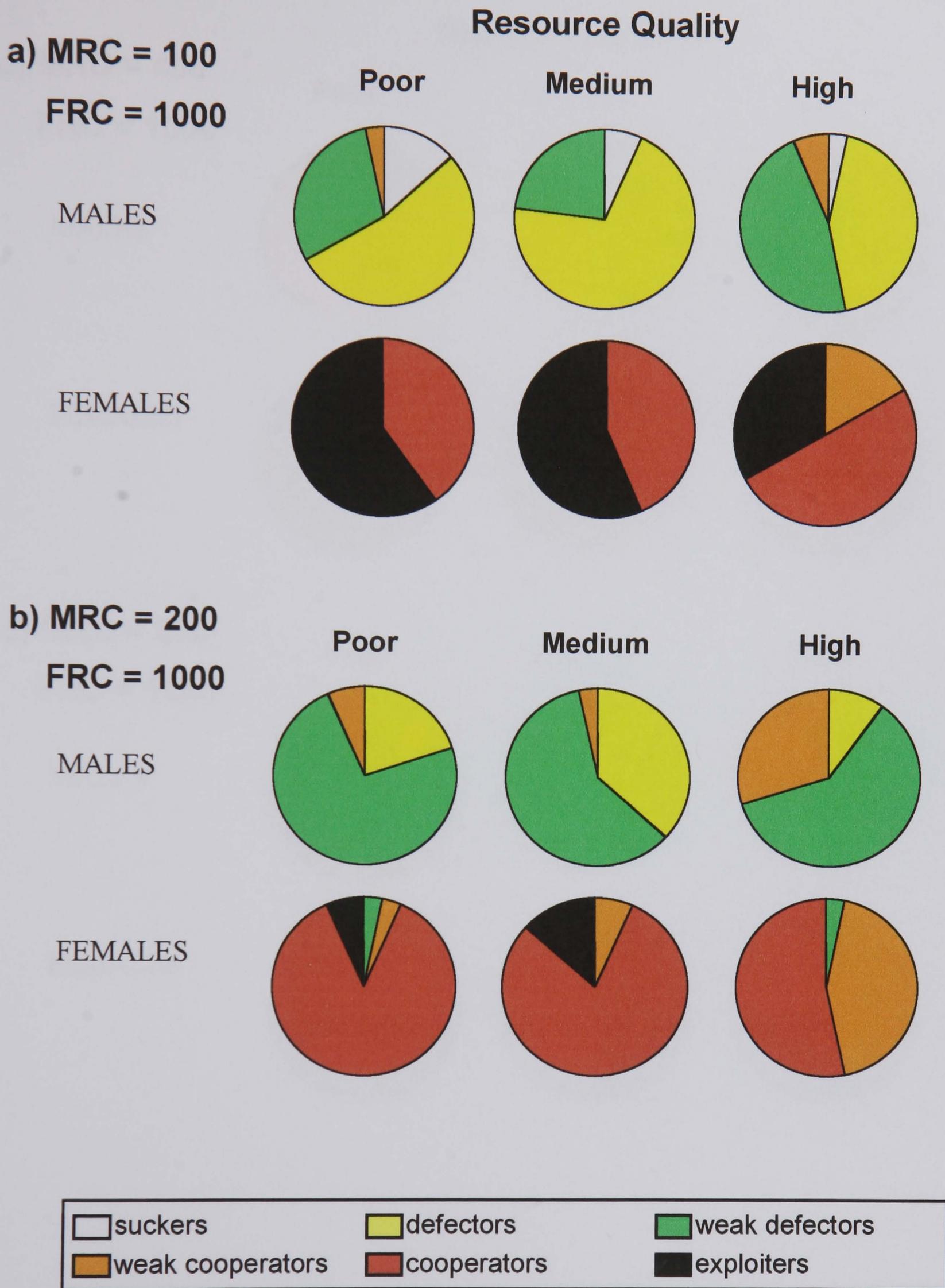


Figure 5.5: Mixed sex interactions, FRC = 1000

Each pie chart summarises the strategies that evolve in each set of 30 experiments.

Resource Quality

c) MRC = 400
FRC = 1000

MALES

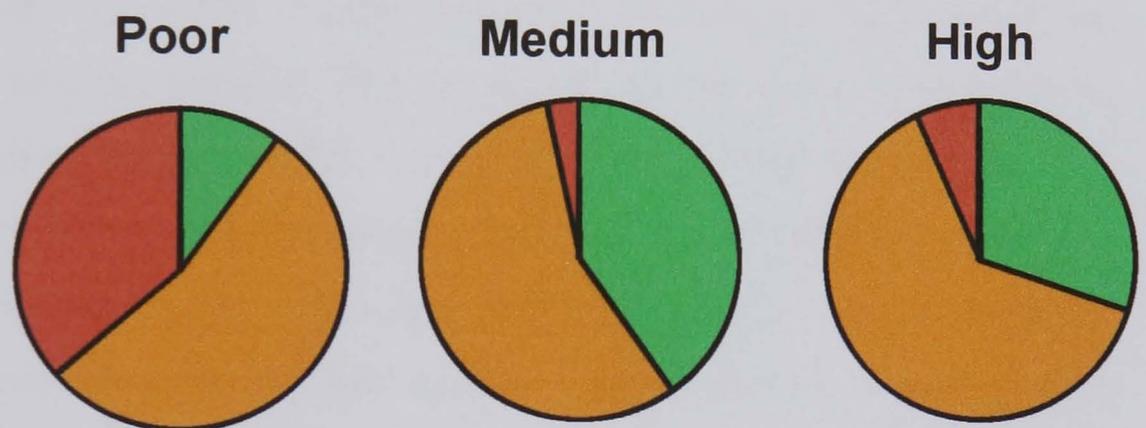


FEMALES



d) MRC = 600
FRC = 1000

MALES



FEMALES

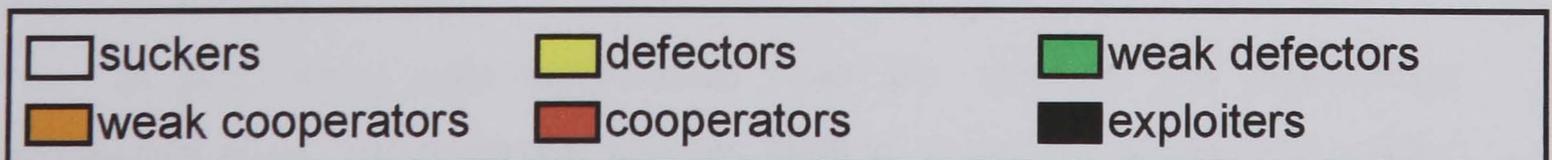
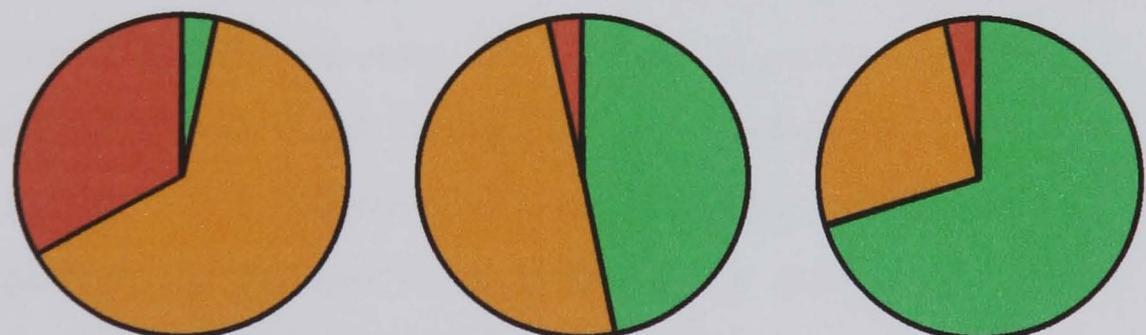


Figure 5.5: Mixed sex interactions, FRC = 1000 (continued)

When $MRC = 400$ (fig. 5.5c) and $MRC = 600$ (fig. 5.5d) there is a distinct shift in strategies. There is absolutely no evidence of non-reciprocal altruism: male scores are, on average, very similar to female scores. Overall, interactions are more competitive than at low values of MRC. Resource quality also has a strong effect on strategy, which is most clearly demonstrated when $MRC = 600$ (fig. 5.5d). When resource quality is poor, cooperation or weak cooperation usually evolves. However, when resource quality is medium or high, weak cooperation and weak defection are the most common strategies.

In order to double-check these results the experiments were repeated at $FRC = 2000$. The results, shown in figure 5.6 parallel those for $FRC = 1000$. When $MRC = 100$ (fig 5.6a), there is extremely strong selection for non-reciprocal altruism no matter what the resource quality. Equally, when $MRC = 200$ (fig. 5.6 b), there is selection for non-reciprocal altruism in all the experiments. Here selection for non-reciprocal altruism is particularly strong when resource quality is low, and evolves in more than 75% of runs. When $FRC = 2000$ and $MRC = 400$ (fig 5.6 c) the scores are skewed favourably towards females. This is similar to the dilute form of non-reciprocal altruism observed when $FRC = 1000$ and $MRC = 200$ (fig. 5.5 b). Fig. 5.6d shows that when $MRC = 800$, the advantage to females has vanished. Males and females score an equal number of points, and interactions are notably competitive, particularly when resources are of high quality. The similarities between these results, and those when $FRC = 1000$, indicate once more that it is the *relative* energetic costs of reproduction between males and females, rather than the *absolute* values for either, that determines which strategies evolve. When male costs are relatively high (in comparison to females), and when resource quality is high, interactions are competitive. On the other hand, relatively low male costs and low resource quality serve to increase the amount of cooperation between the sexes. When male energetic costs are very low relative to female energetic costs, non-reciprocal altruism evolves.

In sum: when male reproductive costs are 20% or less than female reproductive costs, non-reciprocal altruism evolves, regardless of resource quality. When male reproductive costs are greater than 20% of female reproductive costs, mixed-sex interactions are considerably more competitive. When this is the case, resource quality has quite a strong effect on strategy choice: strategies become less cooperative as resource quality increases.

Resource Quality

a) MRC = 100

FRC = 2000

MALES



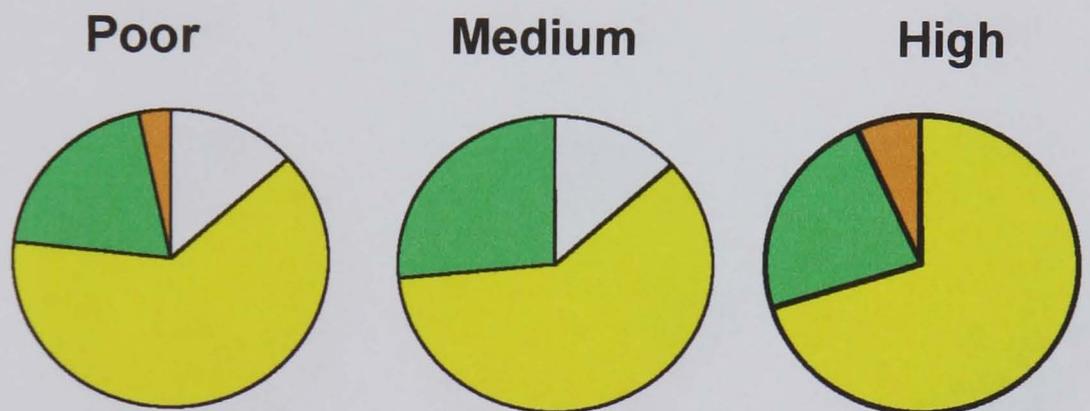
FEMALES



b) MRC = 200

FRC = 2000

MALES



FEMALES

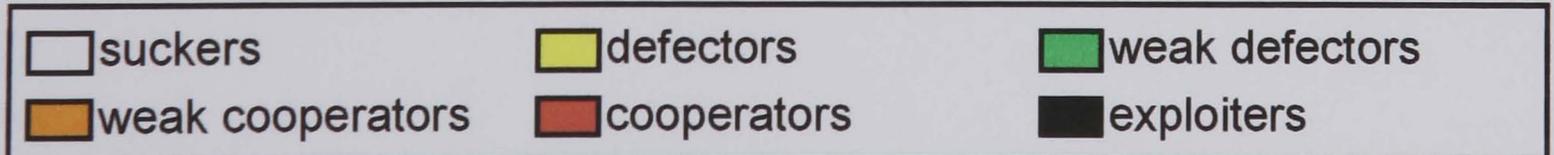
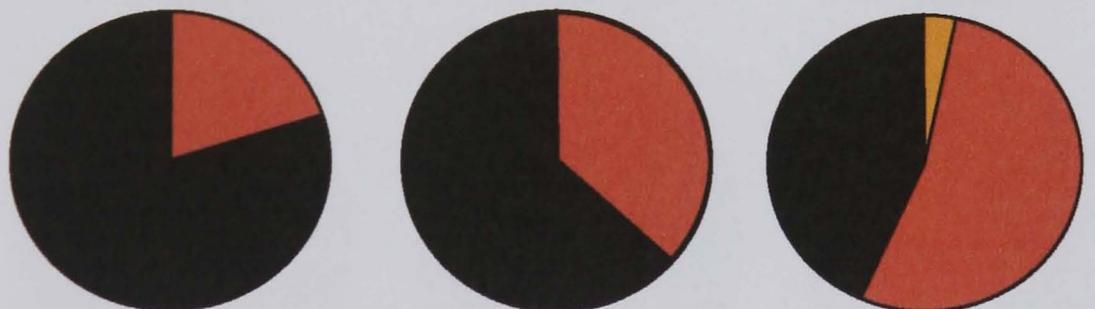


Figure 5.6: Mixed sex interactions, FRC = 2000

Resource Quality

c) MRC = 400
FRC = 2000



d) MRC = 800
FRC = 2000

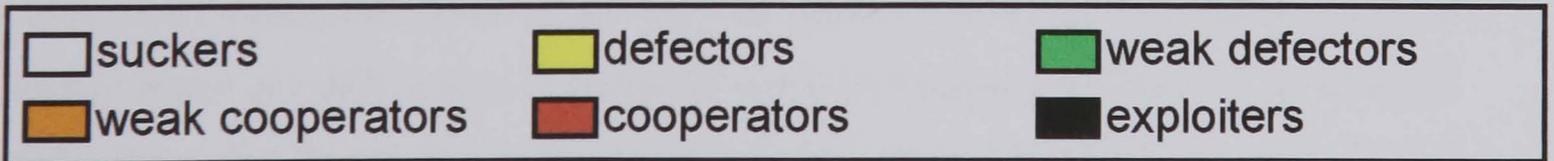


Figure 5.6: Mixed sex interactions, FRC = 2000 (continued)

5.3.3 Discussion

The first experiment in this section (5.3.1) looked at the effect of resource quality on cooperative strategies in the absence of sex differences in energetic costs. The principal finding was that cooperation is most likely when resource quality is low, and least likely when resource quality is high. This finding is not significantly altered when sex differences in energetic costs are added to the model (section 5.3.2). Cooperation decreases as resource quality increases in both male-male and female-female interactions. This is also true of mixed sex interactions, except when MRC is very low. In this case non-reciprocal altruism evolves: scores are biased in favour of females and resource quality has a relatively minor effect on strategy choice.

Sex differences in energetic costs had little effect on female-female strategies. Female cooperation appears to be more dependent on resource quality than any other feature of the model. Surprisingly, males were more cooperative with each other than would be expected. This may be because males generally score so poorly in the mixed sex interactions (especially at very low values of MRC). However, overall levels of male-male cooperation are still fairly low. Mixed sex interactions are characterised by non-reciprocal altruism when male energetic costs are less than 20% of female energetic costs. Otherwise, male-female interactions are quite competitive although cooperation is more likely the higher the value of MRC and the lower the resource quality. Overall, these results mirror those found in chapters 2 and 3 for the more basic model. This is probably due to the close and inverse relationship between the energetic cost of reproduction and resource quality (see fig. 5.2). In effect, increasing resource quality decreases the energetic cost of reproduction. Therefore, all the conclusions reached in chapters 2 and 3 regarding the effect of energetic costs of reproduction on strategy choice also hold true for resource quality.

A single, simple conclusion can be drawn from these two experiments: the likelihood of cooperation increases as resource quality decreases. Or inversely, the likelihood of defection increases as resource quality increases. This result is robust whether or not sex differences in energetic costs are considered. Hauser and Schuster (1997) have also found that in the Prisoner's Dilemma, the likelihood of defection increases as the pay-off for defection increases. In human terms, this result makes a lot of sense. Most of us are more willing to lend an acquaintance £5.00 or buy her a drink, than we are to lend her £100.00 or to buy her a three-course meal. The higher

the value of the altruistic act, the greater the importance of factors such as past relationships with that person, and expectations of future reciprocation. The key element here may be relative risk. When resource quality is low the difference between the highest and lowest scores is 5 points, but when resource quality is high this difference increases to 15 points. That is, the potential benefits of defection and costs of cooperation increase as resource quality increases.

In wild populations cooperation would be expected to be greatest when the value of the contested resource is lowest. Recent research on the African mole rats lends support to this prediction (Faulkes *et al.* 1997). There is considerable inter-specific variation in cooperation among African mole rats. The least cooperative species are solitary, while the most cooperative are communal breeders in which the whole group assists in offspring care. Faulkes *et al.* (1997) used the comparative method to examine the relationship between cooperation and habitat quality and found that the most social species lived in habitats in which mean annual rainfall (a proxy for habitat quality) was lowest. Faulkes *et al.* suggest that cooperation is particularly important when habitat quality is low, because of the increased energetic costs of locating resources.

Among primates, the resource-quality hypothesis requires formal testing under controlled conditions. On a broad level it is possible to make some predictions. Leaves, which contain indigestible items such as cellulose and lignin, are the least nutritious and thus lowest quality food on which primates feed (Dunbar 1988). Fruits, especially when ripe, are a rich source of energy. The richest energy source, and thus highest quality foods, are insects and meat. Therefore, cooperation is expected to be most common when folivorous resources are involved, less frequent when frugivorous resources are involved and least frequent when meat based resources are involved. This prediction is particularly hard to test since there are sharp contrasts in the distributions of these different resource types. As discussed in the introduction, folivory is associated with an egalitarian social system in which competition for resources is low (van Hooff and van Schaik 1992). This may be because of low diet quality, but it is also likely that the even distribution of leafy resources makes competition pointless. Resources such as fruit, which tend to be located in large, defensible clumps, can support larger groups and thus pre-select for greater food-related competition.

Mitchell *et al.* (1991) found that food-related aggression was 70 times more common in a Peruvian group of squirrel monkeys, compared to a Costa Rican group. The Peruvian group was also strongly female-bonded, unlike the Costa Rican group. The main ecological difference between the two groups was the size and quality of the fruiting trees. In Peru, trees tend to be large and bear large amounts of fruit and an average of 17 animals at a time would occupy a single tree. In Costa Rica trees are small and bear few fruits each, and groups of only 3-5 animals would cluster on each tree. Van Hooff and van Schaik (1992) suggest that Mitchell *et al.*'s study supports the resource-distribution hypothesis: increased competition and the formation of cooperative alliances in the Peruvian group occurs because of the presence of large patches of defendable resources. Yet, it is also possible that competition increased as a response to the presence of valuable, higher quality, resources. This study illustrates two difficulties in testing these models. Firstly, it is very difficult to dissociate resource distribution and resource quality effects. Secondly, when competition increases primates will often respond by forming alliances. Thus, increased cooperation is expected in the same context as increased competition.

Very few studies have examined the effect of resource quality on cooperative behaviours in the absence of other confounding variables. De Waal (1996 p.140) reports that while chimpanzees are willing to share leafy foods, they are "hopeless" at sharing favoured plant foods such as bananas. In fact, de Waal reports that competition over bananas is so intense that individuals sometimes become violent (however, see the discussion below for exceptions to this). In another study de Waal (1997) examined food-sharing behaviour in capuchin monkeys with respect to two different foods, apple and cucumber. Apple was found to be the preferred food for twelve of the thirteen subjects. Therefore, food sharing ought to be greater for cucumber than apple. Contrary to this prediction, de Waal found that the rate of food transfer between individuals was greatest when apple was the food item. However, this result may be due to the consistency of the food rather than its quality or desirability. De Waal concludes (1997 p.376):

"The higher rate of food transfer when possessors had apple compared with cucumber was most likely due to the fact that apple crumbles easily when eaten or manipulated, whereas cucumber does not. As a result, many more fragments of apple were laying around by the end of a test than fragments of cucumber, which resulted in more reach-throughs by the partner to collect scraps."

Another study on captive brown capuchin monkeys, by Verbeek and de Waal (1997), examined the effect of food quality on post-conflict behaviour. They found that reconciliations were more frequent following social disputes in the presence of low quality foods. Reconciliations were less common following aggressive disputes over highly attractive food items. This result appears to support the prediction that competition is greater, and cooperation (reconciliation) is lower, when higher quality resources are in dispute. In contrast, in chimpanzees reassuring behaviours such as embraces and kisses, are particularly common in the presence of attractive food. Chimpanzees appear to use appeasement gestures to dampen competition for desirable food items. De Waal (1989b) found that aggressive competition for food increased in chimpanzees when they were unable to perform their usual appeasement behaviours.

Across primate species animal products appear to be more widely shared than any other food. Both capuchin monkeys (Perry and Rose 1994) and chimpanzees (Boesch and Boesch 1989) share meat more readily than any other food item. In both cases meat sharing is most prominent among adults (Rose 1997). This observation is difficult to square with the prediction that cooperation should be lowest when high quality food items, such as meat, are involved. However, in both capuchins and chimpanzees meat sharing may be better described as “tolerated theft” (Blurton-Jones 1987) than true altruism. When an individual allows another to take a portion of food because the costs and practicalities of defending it are too great, it is described as tolerated theft. For example, capuchin monkeys occasionally capture coati pups, which are quite large and are eaten alive (Perry and Rose 1994). The screams of the coati attract the attention of other groups members who beg for a portion of the meat. The sharing of meat by capuchin monkeys may simply be unavoidable under these circumstances.

In contrast to capuchins, hunting in chimpanzees often involves many individuals. The extent to which such group hunting is really cooperative appears to vary between chimpanzee populations. Busse (1978) argues that Gombe chimpanzees do not hunt cooperatively. Busse found that hunting success was not improved by hunting in groups, and that ‘group’ hunting was probably due to many individuals simultaneously attempting to catch the same animal. In this case meat sharing that occurred after capture was more akin to tolerated theft. However, in other populations group hunting and food-sharing does appear to be cooperative. Tai

chimpanzees appear to coordinate their hunting efforts, in the sense that different individuals take on different but complementary roles in the group hunt (Boesch and Boesch 1989). Meat is shared among the hunters, while males that were uninvolved in the kill receive little if anything. Females also receive a share and hunting is most frequent when females are in estrous (Stanford *et al.* 1994). This suggests that males are sharing their food with females, in the hope of gaining mating opportunities. Tutin (1979) found that males who shared meat were preferred as sexual partners and it is possible that access to meat improves female reproductive success (McGrew 1992). But, a firm link between male hunting success and male mating success is yet to be demonstrated. None the less, these observations indicate that meat sharing in Tai chimpanzees may be one aspect of a wider range of reciprocal, cooperative strategies.

Food-sharing in non-human primates is most common between adults and infants. In captive capuchins adults allow infants to take food, although in the wild food sharing, especially of plant foods, is reported to be uncommon (Fragaszy and Barb 1997). Sharing of plant foods mainly occurs between adults and infants in chimpanzees although McGrew (1992) reports occasional sharing by adults males with females. As noted earlier, bananas, a highly valued food source, often provoke aggressive competition in chimpanzees. However at Gombe provisioned bananas are frequently shared between mothers and offspring (Rose 1997). Nishida and Turner (1996) found that in the Mahale mountains infants succeeded in their attempts to procure food from their mothers on 65% of occasions. Interestingly, the greatest success rate occurred when infants solicited items that were difficult for them to obtain themselves. Fragaszy and Barb (1997) suggest that food sharing is particularly important for weanling chimpanzees, which depend upon the same food items as adults, but are inexperienced foragers and dentally immature. They note that maternal sharing of food items is particularly common during the nursing period and the first year after weaning.

Adult cotton-top tamarins actively share food with infants, and allow infants to take food from them (Feistner and Price 1990). The sharers include the mother, the father and older siblings. Feistner and Price found that begging success increased when a highly preferred food was involved in the transaction. In fact, in callitrichids in general, food-sharing increases when preferred food items are involved (Feistner and Chamove 1986; Feistner and Price 1990). This result defies expectations, since

we would expect food-sharing to decrease when food quality is increased. Obviously, in this context food-sharing yields inclusive fitness benefits to the sharers. However, if the benefits of food-sharing are simply measured in terms of kin-selection then we would expect it to be a common behaviour. In fact, across primate species food-sharing is extremely rare, even between mothers and offspring. Why then is food-sharing so prevalent in callitrichids? The nature of the shared food, often live prey, may be the key to understanding this behaviour. Live prey are the most frequently transferred food items in buffy-headed marmosets (Ferrari 1987), tassel-eared marmosets (Feistner and Price 1990), cotton-top tamarins (Feistner and Price 1990) and black-mantled tamarins (Izawa 1978). Feistner and Price (1990 p.43) comment on the great importance of food-sharing to callitrichid infants:

“Prey capture requires skill, and weanlings in need of protein and fat (which will be provided only in steadily decreasing amounts by their mother’s milk) are unable to capture large insects and small vertebrates. Thus, their only means of acquiring food is from others.”

The crucial factor here is that weanlings are unable to forage for themselves due to the nature of the food resource. Sharing of food items such as fruit is of less importance since these are easily acquired. Significantly, the only other non-primate mammals which practice extensive food sharing are the social carnivores (Macdonald and Moehlman 1982). The link between an animal-based diet and cooperation is clearly demonstrated in brown hyenas.

Brown hyenas live in clans of several adult females, a dominant male, and several subordinate males, adolescents and infants. Emigration and immigration by both sexes means that not all clan members are related. All infants older than 3 months are raised in a communal den (Owens and Owens 1979, 1984). Owens and Owens describe female cooperation as the glue that holds the clan together, and all females participate in offspring care, regardless of rank or kinship. Lactating females suckle all cubs, regardless of whether they are their own, and all clan females bring food to the communal den, feeding pups indiscriminately. As in many primate species, the social life of the hyena is of paramount importance. Strong bonds develop between group members and protracted greeting and appeasement displays maintain group harmony. It is the hyena’s dependence upon meat that appears to make cooperation a vital part of their reproductive strategy. Meat is an elusive

resource, and scavenger hunts may take females more than 30 kilometres away from the den. Furthermore, it takes a long time to become an effective hunter or scavenger, which means that weanlings are unable to acquire food for themselves and are reliant on adults for up to two years (Owens and Owens 1979, 1984). Without communal provisioning, few hyena pups would survive.

Thiollay (1991) uses a similar line of reasoning to explain communal living in the red-throated Caracara, *Daptrius americanus*. These raptors share food, cooperate in group mobbing of predators and guard the communal nest as a group. These birds are primarily insectivorous (rather than carnivorous) feeding mostly on insect nests. This is a scarce resource and considerable experience is required to become a proficient hunter. Adults help young birds find their own food by signalling prey locations, partial food sharing and allofeeding. A similar teaching process occurs in blackbacked jackals, in which helpers teach young pups to hunt (Moehlman 1979).

Observations of social carnivores suggest, therefore, that communal care has evolved because of the necessities of provisioning inexperienced weanlings. Alternatively, Riedman (1982) suggests that it is the necessities of group hunting or foraging that select for communal rearing. Many communal breeders are cooperative foragers or hunters, for example mongooses, lions, hyenas, coyotes, jackals, African wild dogs and wolves. Bednarz and Ligon (1988) believe that the necessities of cooperative hunting have determined social structure in Harris' hawk. These hawks live in social units of up to six birds (Bednarz, 1988) . They rely on highly coordinated attacks such as 'the surprise pounce' and 'relay attack' to capture their prey. Typically four birds will participate in the attack, and once caught the prey is divided between the members of the group. Most of the adult birds participate in rearing the young, regardless of relatedness and Bednarz and Ligon believe that this cooperation is an outcome of group hunting. The group members benefit through cooperative hunting of large and potentially dangerous prey, such as jackrabbits which may be three times heavier than a male hawk. Bednarz and Ligon emphasise the influence of group hunting, rather than offspring care, in shaping social structure. However, they also comment on the importance of cooperation to young hawks who have yet to become experienced hunters. In fact, the young are allowed first access to carcasses.

While most team hunters are social breeders, not all social breeders are team hunters. For instance the highly cooperative brown hyena, described above, is a solitary hunter. In fact, group hunting is often no more profitable individually than solitary hunting, and it is likely that in most cases co-ordinated hunting is a consequence, not a cause of communal living (Macdonald, 1983; Packer and Rutten 1988). Most predators are also scavengers, and scavenging from con-specifics is common (Packer and Rutten 1988). Letting other individuals take the risks of hunting is clearly an attractive strategy and potential for cheating is high. In conclusion, it seems most likely that communal living evolved firstly as a response to the needs of weanlings in species in which skill and experience is required in order to capture food. Communal care may help to establish the ground rules of cooperation that some species have then harnessed for the purposes of hunting.

In summary: This discussion has focused on the prediction that cooperation is least likely when resource quality is high, and most likely when resource quality is low. Little support has been found for this hypothesis. Fruits may provoke greater competition than folivorous resources due to their high energetic value. However, because the distributions of frugivorous and folivorous resources are so different it is not possible to determine whether this result is due to the quality of the foods involved, or their spatial distribution. Animal resources, which are of high energetic value, are predicted to be less widely shared than other foods. This expectation is contradicted by the available evidence which suggests that animal and insect prey are more widely shared than any other resource. However, the sharing of animal prey appears to be a special case for one very important reason: weanlings are unable to forage for these food items themselves. Infants simply would not survive to an age in which they have the necessary skills to hunt for themselves, without provisioning from older individuals. Finally, food sharing almost always occurs in the context of other cooperative behaviours such as group hunting and communal care of offspring (e.g. defence of the den in brown hyenas, infant carrying in callitrichids). The necessity of providing food for inexperienced young provides an environment in which other types of cooperative behaviours can develop.

5.4 Cooperation in a Seasonal Environment

The models developed in the previous section suggest that the quality of the resource under dispute affects the types of cooperative strategies that individuals employ. Cooperation is less likely the higher the quality of the resource. In a seasonal environment resource quality fluctuates in a fairly regular manner. Therefore, we might expect individuals to be most cooperative during the poorest months and least cooperative during the richest months. This hypothesis will be tested in the following models. The first, in section 5.4.1, looks at the effect of seasonality on cooperation when male and female reproductive costs are equal. The second, in section 5.4.2, develops this model by looking at how sex differences in reproductive costs effect the results. The basic format of these simulations is exactly the same as in the first two experiments (see section 5.2). However, instead of having the same resource quality throughout each simulation, resource quality was programmed to fluctuate over a 12 month cycle in the following way:

Months 1-3: Poor quality
Months 4-5: Medium quality
Months 6-8: High quality
Month 9: Medium quality
Months 10-12: Poor quality

When the 12 month cycle is complete, it begins again at month 1. When a new generation begins, the cycle starts again from month 1. For each month, the appropriate pay-off matrix is used to reflect resource quality (see figure 5.1).

The average pay-offs were calculated each month, and these pay-offs were then combined to provide three average scores: one each for poor, medium and high resource qualities. For example, over 20,000, generations the average score was calculated for months 1, 2, 3, 10, 11 and 12 to provide an average score when resource quality is poor. Note that only those scores for the first 12 months of each generation were taken into consideration when the average scores were calculated, even though some generations lasted considerably longer than this. Simulation

lengths vary depending on the magnitude of the reproductive costs, and the strategy used. Also, generation times vary within a simulation. If, for instance, agents are very uncooperative at the start of the experiment then generations take many months to complete (let's say, for example, that they take 20 months). If agents become more cooperative, generation times will be considerably shorter (let's say they take 10 months). This means that the average scores for the later months (in this example months 11-20) will only reflect those generations in which individuals were uncooperative. By only taking into account the first 12 months of each generation, this problem is avoided. This is an acceptable solution, since if individuals are being uncooperative, this will be apparent within the first 12 months of the simulation.

5.4.1 Equal male and female reproductive costs

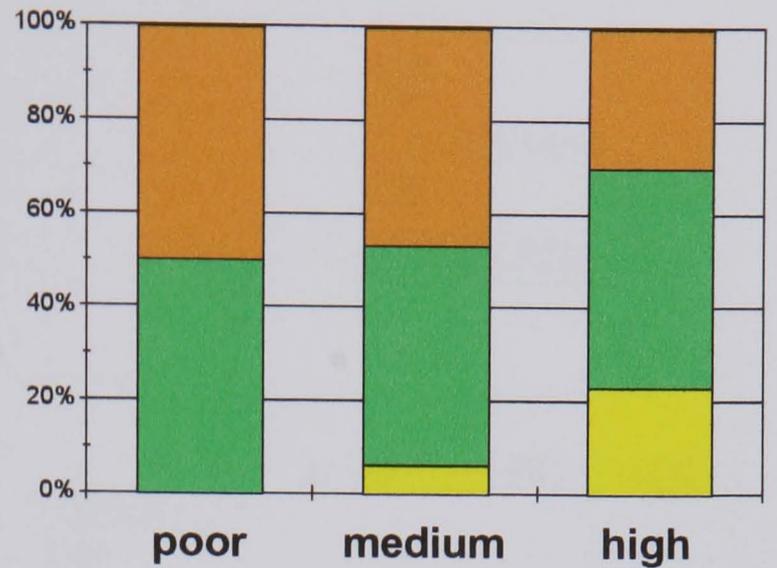
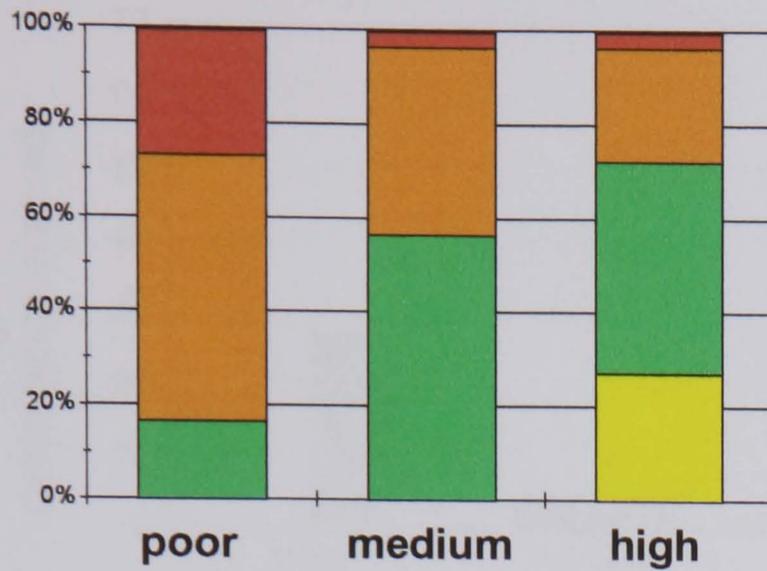
In these runs male reproductive cost is equal to female reproductive cost. The experiment was run 30 times using each of the following reproductive costs: $MRC = FRC = 1000, 2000$ and 3000 . For each set of experiments the average scores were calculated for poor, medium and high quality months. These scores were then translated into strategies using table 5.1. Actual results were compared to expected results. Expected results were drawn from the first experiment, in which resource quality was stable over the whole simulation. For instance, during those months in which resource quality is poor, the same amount of cooperation is expected as occurred when resource quality was poor over the whole simulation for the same reproductive cost (see section 5.3.1). Although the results were analysed for each interaction type (male-male, female-female, male-female), because males and females have identical reproductive costs the results for each type are very similar. To avoid repetition only the results for male-male interactions are discussed here.

Figure 5.7 compares expected and observed results. We would expect that: (1) cooperation will be more likely at higher reproductive costs (RC); and (2) cooperation will be greatest when resource quality is poor, and least when resource quality is high. The first prediction is upheld. Cooperative strategies evolve at the greatest frequency when $RC = 3000$, and the lowest frequency when $RC = 1000$. However, in the seasonal model resource quality does not have the expected effect whatever the value of RC. While there is a slight tendency for agents to be less cooperative when resource quality is high, overall strategies are very similar whether

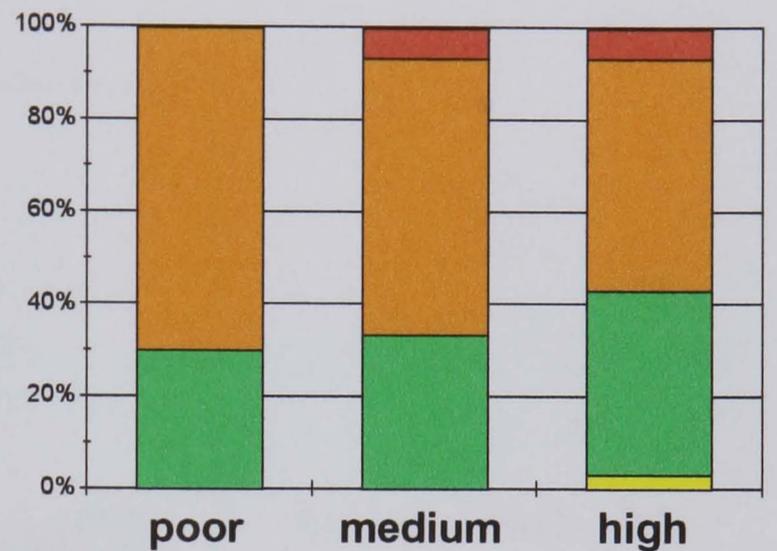
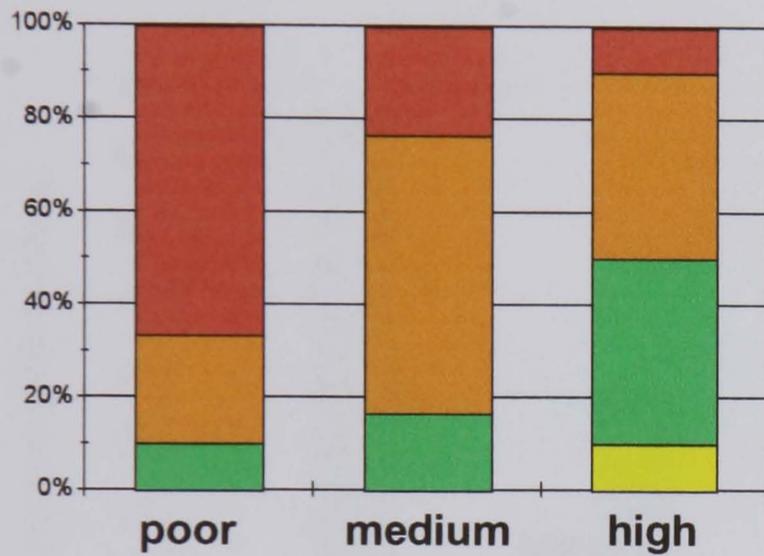
Expected

Observed

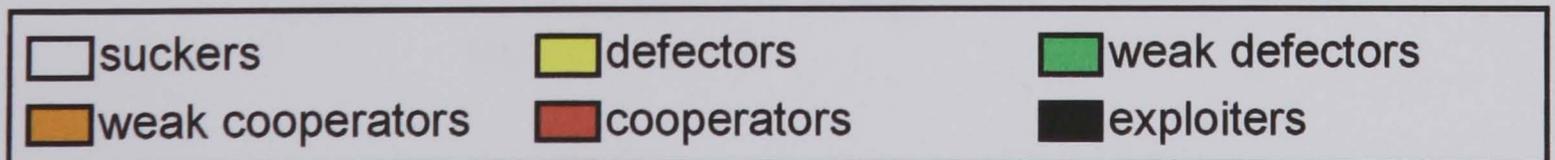
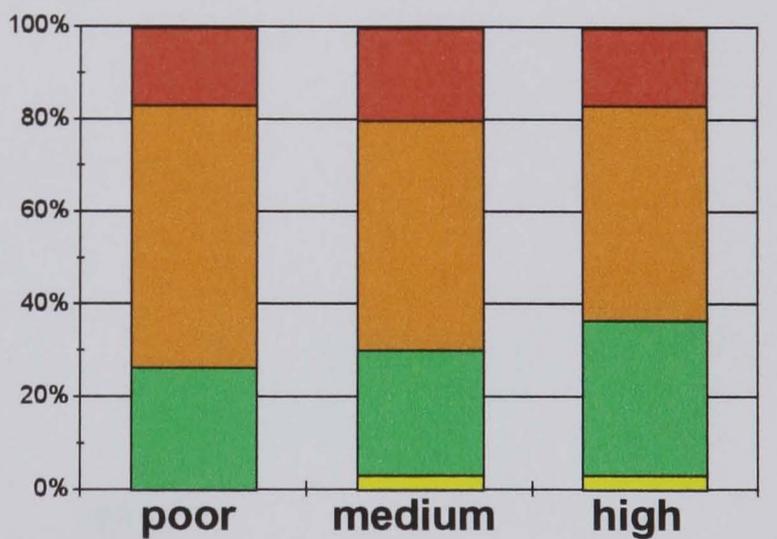
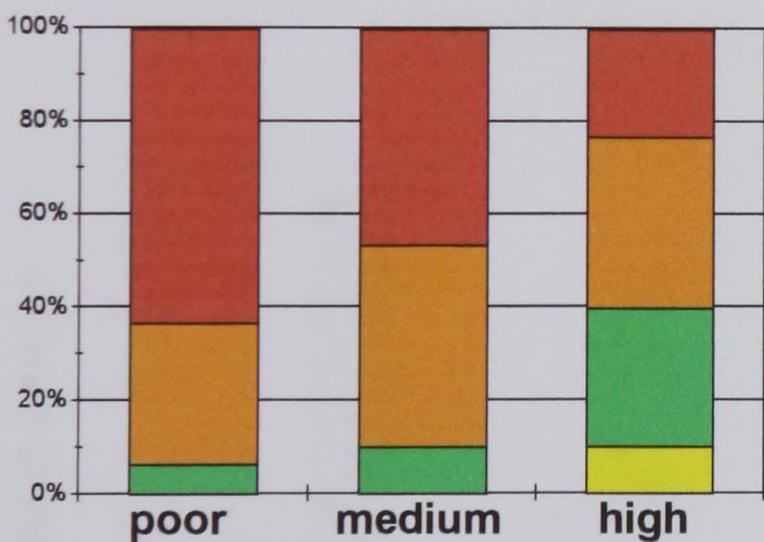
(a) RC = 1000



(b) RC = 2000



(c) RC = 3000



5.7 Expected versus observed strategies in the seasonal model (MRC = FRC)

Figures show the range of expected and observed strategies at different reproductive costs (RC).

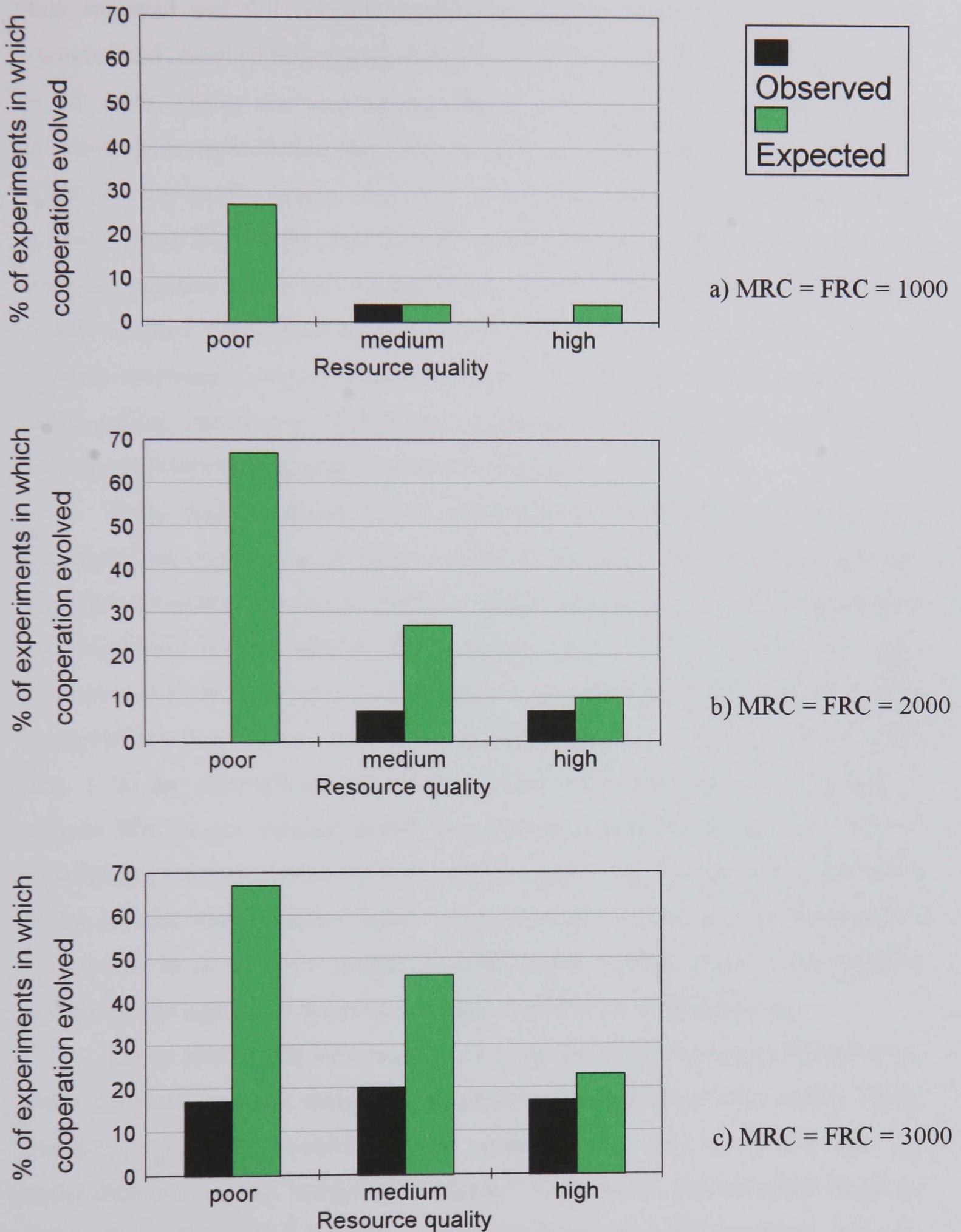


Figure 5.8: Cooperation in a seasonal environment (MRC = FRC)

Figures compare the expected percentage of runs in which cooperation evolves, with the actual percentage of runs in which cooperation evolves. Cooperation is much lower than expected in each case.

resource quality is poor, medium or high. Moreover, strategies are less cooperative than expected and full cooperation is very unusual. Figure 5.8 compares the expected and observed frequencies of experiments in which full cooperation evolved. In all cases, agents are very uncooperative in comparison to expectations. For instance, when reproductive cost (RC) is 1000 (fig. 5.8a), cooperation is expected when resource quality is poor in at least 25% of runs, but in fact cooperation never evolves. When $RC = 2000$ (fig 5.8b) high levels of cooperation are expected for all resource qualities but in fact cooperation is minimal. For instance, when resource quality is poor cooperation would be expected in 65% of experiments, but in practice cooperation never evolves. Only at $RC = 3000$ (fig 5.8 c) does cooperation really appear, and then at much lower levels than expected: cooperation occurs in less than 20% of runs, regardless of resource quality.

These results indicate that in a seasonal environment, in which resource quality varies, cooperation is much harder to establish than in a non-seasonal environment in which resource quality is stable. Interestingly, the observed amount of cooperation is very similar when resource quality is low, medium or high. Moreover, the observed level of cooperation is most similar to the expected level of cooperation when resource quality is high. For instance, when $MRC = FRC = 3000$ (fig. 5.7c) the expected amount of cooperation when resource quality is high is around 20%. In the seasonal model, cooperation evolves in between 15 - 20% of experiments, no matter what the environment quality. The likelihood of cooperation in the months when resource quality is high appears to determine the likelihood of cooperation in all the other months. In other words, strategy choice when resource quality is high appears to determine strategy choice in all other situations.

Let us assume that individuals can choose one of four strategies (cooperation, weak cooperation, weak defection and defection) for each resource quality (poor, medium, high) over the course of a 12 monthly cycle. This means that there are many different possible 'compound strategies'. For instance, players could cooperate during the 'poor' part of the cycle, weakly cooperate over the 'medium' part, and defect over the 'high' part. Alternatively, they could defect during poor, medium and high phases. Or they could cooperate over the poor phase and defect over the other two phases of the cycle, and so on. In total there are 64 different compound strategies that players could use. However, only a very small sub-set of these are actually used. Table 5.2 shows the compound strategies that evolved when

reproductive cost was 3000. Only 9 out of the possible 64 compound strategies ever evolved. The most common compound strategy, which evolved in 37% of experiments, was to weakly cooperate over all resource qualities. The next most common strategy, which evolved in 13% of experiments, was to weakly defect over all resource qualities. Full cooperation over all resource qualities evolved in 7% of experiments. In other words, in more than half of the experiments, the same strategy evolved for each resource quality. Mixed compound strategies only ever involved two different strategy types, for instance cooperation and weak cooperation. These results support the proposition, made above, that strategy choice during periods of high quality resources determines strategy choice during other parts of the cycle. This results in very similar strategies for each resource quality. Most of these strategies involve a combination of weak defection and weak cooperation. Full cooperation only features in 20% of the compound strategies (see table 5.2).

Resource Quality			Percentage of experiments
Low	Medium	High	
Weak cooperation	Weak cooperation	Weak cooperation	37
Weak defection	Weak defection	Weak defection	17
Weak cooperation	Weak defection	Weak defection	13
Weak defection	Weak cooperation	Weak cooperation	10
Cooperation	Cooperation	Cooperation	7
Weak cooperation	Cooperation	Cooperation	7
Cooperation	Weak cooperation	Weak cooperation	3
Weak cooperation	Cooperation	Weak cooperation	3
Weak cooperation	Weak cooperation	Weak defection	3

Table 5.2: Compound strategies used in a seasonal environment

Out of 64 possible compound strategies, only these nine evolved. The table shows the percentage of experiments in which each type of compound strategy evolved. For definitions of strategy types (i.e. ‘weak cooperation’, ‘weak defection’ etc.) see table 5.1.

Why should strategy choice during high quality periods have such a strong effect on strategy choice at other times? The answer lies in the high temptation to defect during periods when resource quality is high. As shown in section 5.3.1, cooperation is least likely when resource quality is high. Therefore, even if two players have cooperated when resource quality is low and medium, there is a good chance that they will defect when resources switch to high quality. However, strategy choice at any time depends not only on resource quality, but also on the history of interactions between two players. If an agent defects during periods of high quality resources, its opponent will remember that defection and will respond accordingly in the following months. If the players are using any kind of TIT-FOR-TAT strategy, the occasional defection during the periods of high pay-offs will result in recriminating defections in the months that follow. This means that strategy choice, and the likelihood of defection when pay-offs are high, sets the tempo for the rest of the simulation.

In summary, variability in resource quality dramatically lowers the likelihood that cooperation will evolve, even at very high reproductive costs. Big temptations to defect when resource quality is high makes cooperation very difficult to establish. The result of this is that strategies are very similar in poor, medium and high quality situations. Most commonly, strategies involve weak defection and weak cooperation.

5.4.2 Male reproductive costs lower than female reproductive costs

The previous experiment was repeated, except in this case female reproductive cost was kept stable at $FRC = 1000$, while male reproductive cost was varied. As before, resource quality fluctuated in a 12-monthly cycle. Average pay-offs were calculated for poor, medium and high quality months (see beginning of this section). Expected pay-offs were derived from experiment 2 (section 5.3.2), in which there were also sex differences in reproductive costs but resource quality was held constant. For example, the pay-offs for male-male interactions at $MRC = 100$ during the poor months of the seasonal model are predicted to be identical to the pay-offs at $MRC = 100$ when resource quality was poor all year round. Results will be analysed by interaction type.

Female-female interactions

The results for female-female interactions are very similar to expectations (fig. 5.9). The value of MRC has very little effect on the outcomes, females employ very similar strategies whatever the value of MRC. Seasonality in resource quality has the expected effect on outcomes. That is, females are most cooperative during poor quality months, and least cooperative during high quality months. In the previous experiment it was found that a high temptation to defect when resource quality is high causes low levels of cooperation throughout the whole cycle. This does not seem to occur here, although full cooperation almost never evolves.

Male-male interactions

Male-male interactions do not differ greatly from expectations (fig. 5.10). As with female-female interactions, the likelihood of cooperation depends on resource quality. Males are most cooperative during the low quality months of the cycle. However, full cooperation is unusual.

Mixed sex interactions

The results for mixed sex interactions are quite dramatically different from expectations (fig. 5.11). Resource quality, as well as male and female reproductive costs, have a marked effect on the outcomes.

When $MRC = 100$ (fig. 5.11a) non-reciprocal altruism is expected no matter what the resource quality, and the likelihood of males being non-reciprocal altruists is expected to diminish as resource quality increases. The observed results are absolutely opposite to these expectations. This is most clearly demonstrated by the pattern of pay-off to females (pay particular attention to the black bars which indicate very high pay-offs). When resource quality is poor non-reciprocal altruism evolves in about 30% of experiments, less than expected. Males, on the other hand, receive more points than expected. As resource quality increases, non-reciprocal altruism becomes more and more likely: when pay-offs are highest, males are non-reciprocal altruists in all but one experiment. Note the very low pay-offs to the male and very high pay-offs to the female when resource quality is high.

These results are repeated for $MRC = 200$ (fig. 5.11b). When resource quality is low, males and females score similar numbers of points. In comparison with expectations, females score less highly than expected while males score more highly

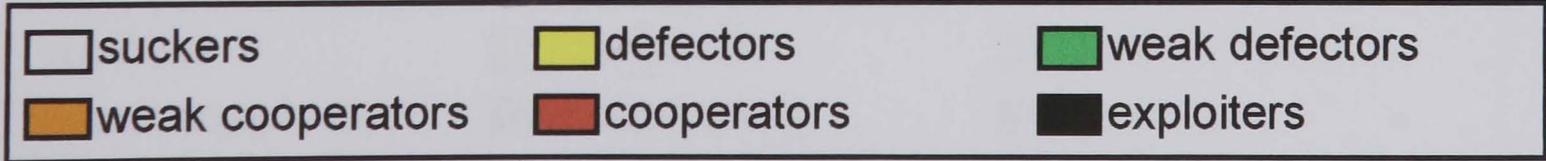
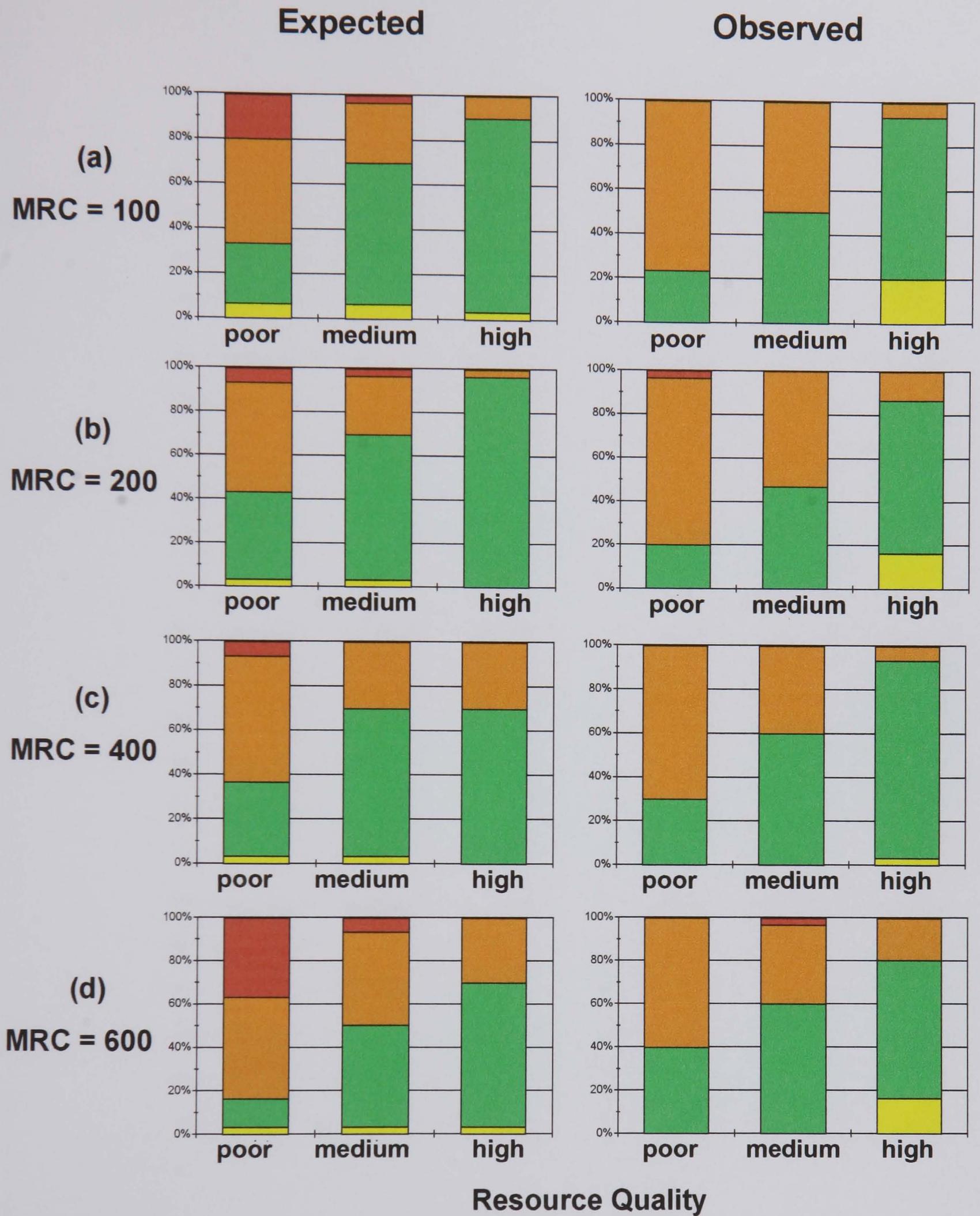


Figure 5.9: Female-female interactions in a seasonal habitat FRC = 1000

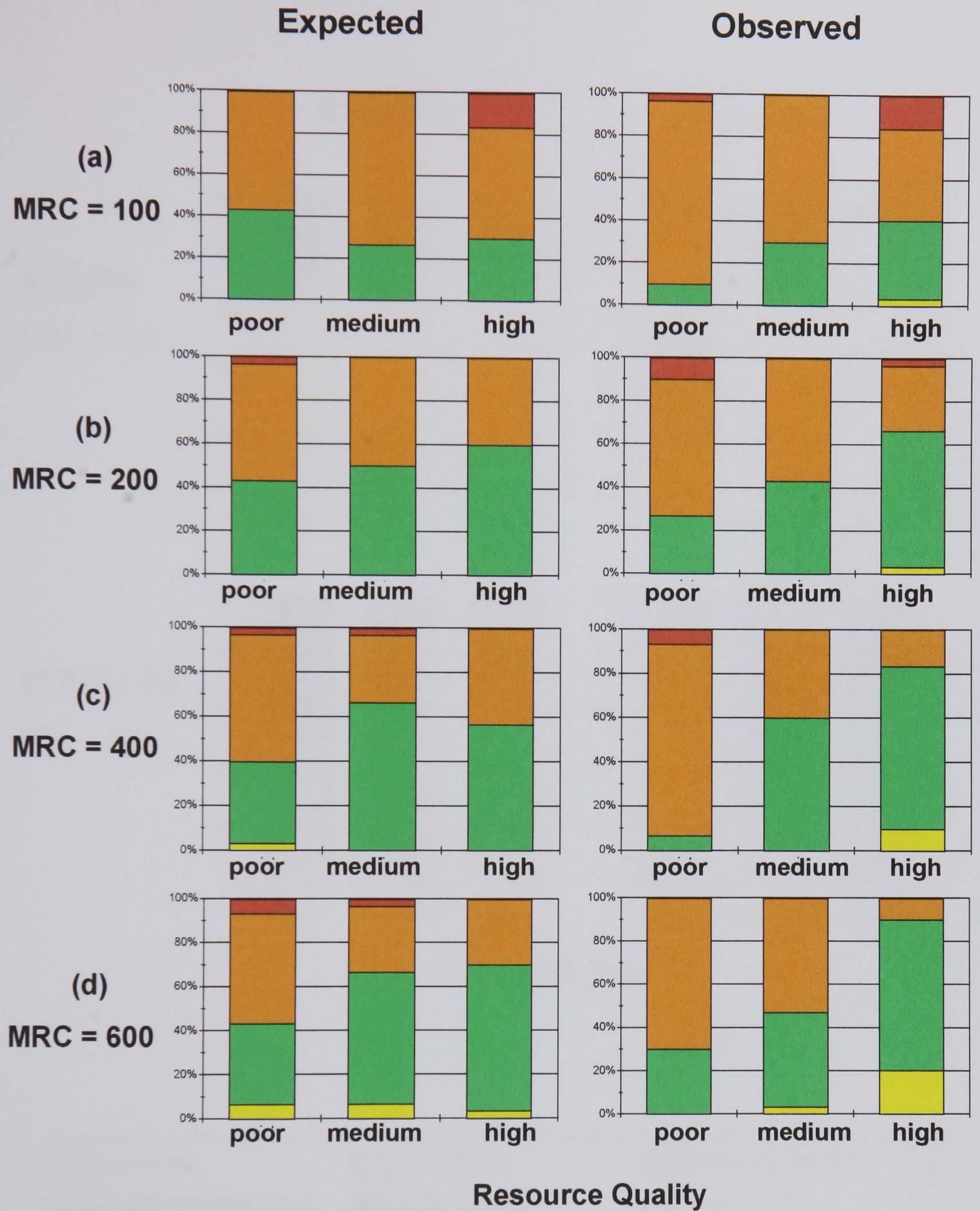


Figure 5.10: Male-male interactions in a seasonal habitat FRC = 1000

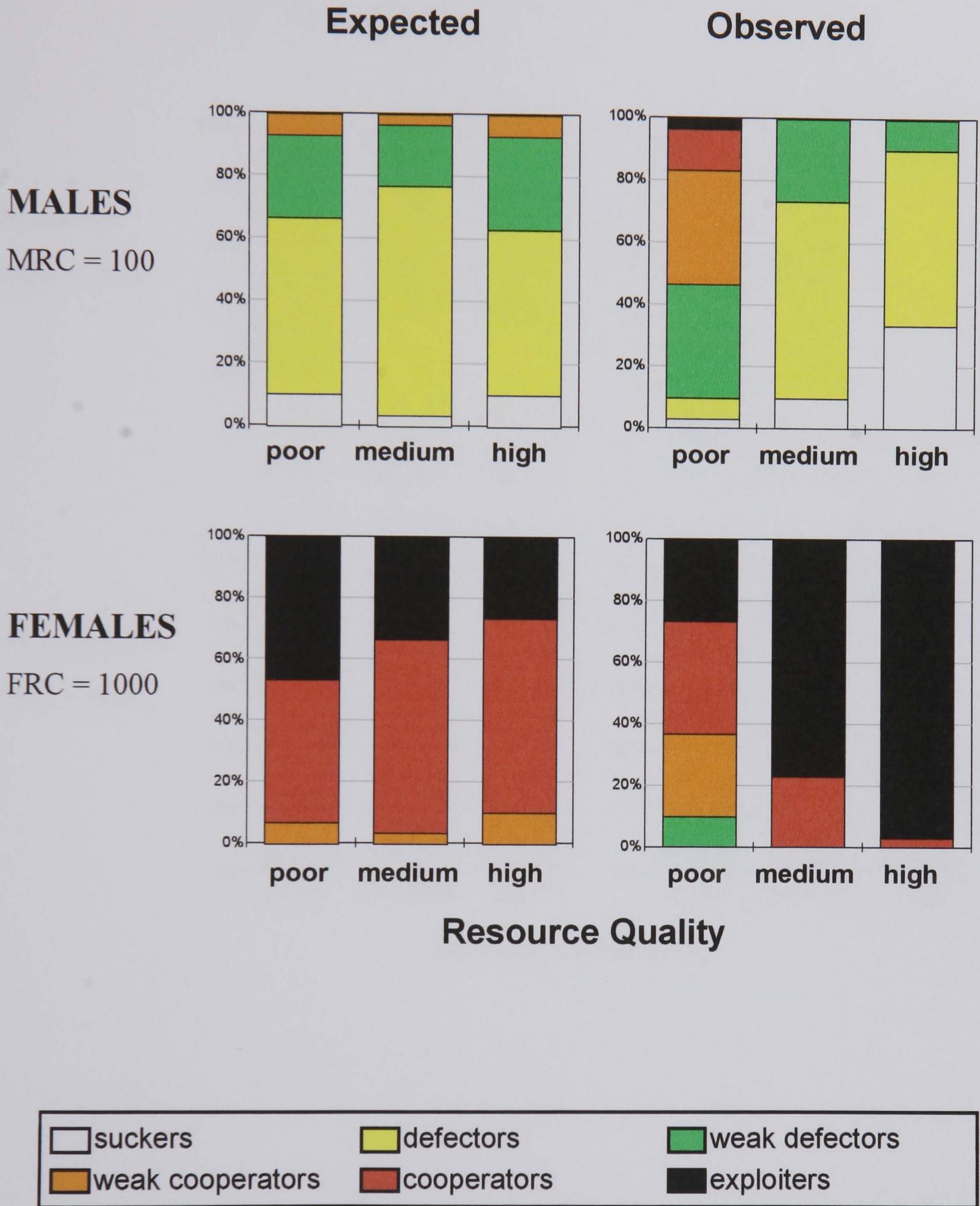


Figure 5.11 (a): Mixed sex interactions in a seasonal habitat, FRC = 1000, MRC = 100

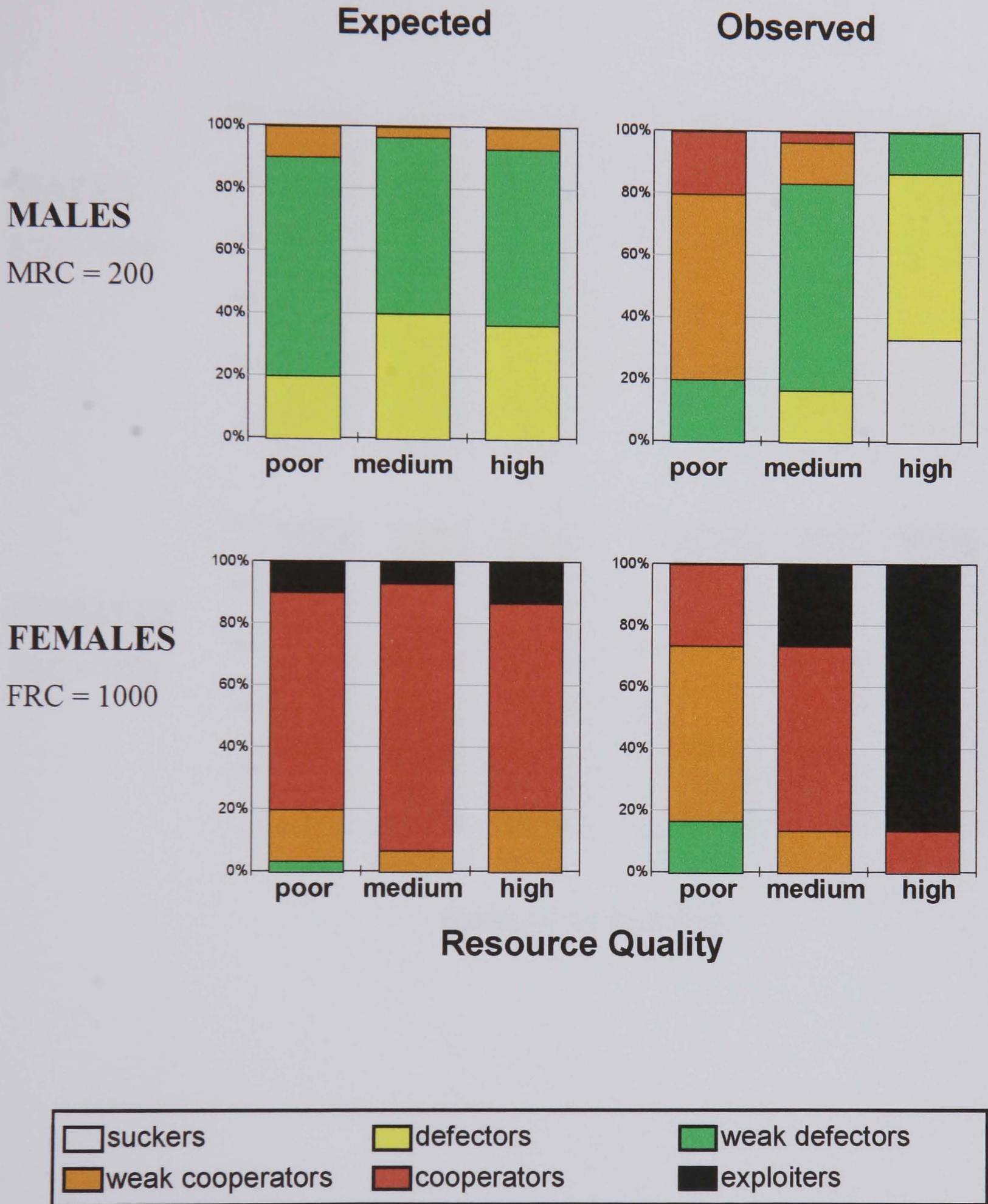


Figure 5.11 (b): Mixed sex interactions in a seasonal habitat, FRC = 1000, MRC = 200

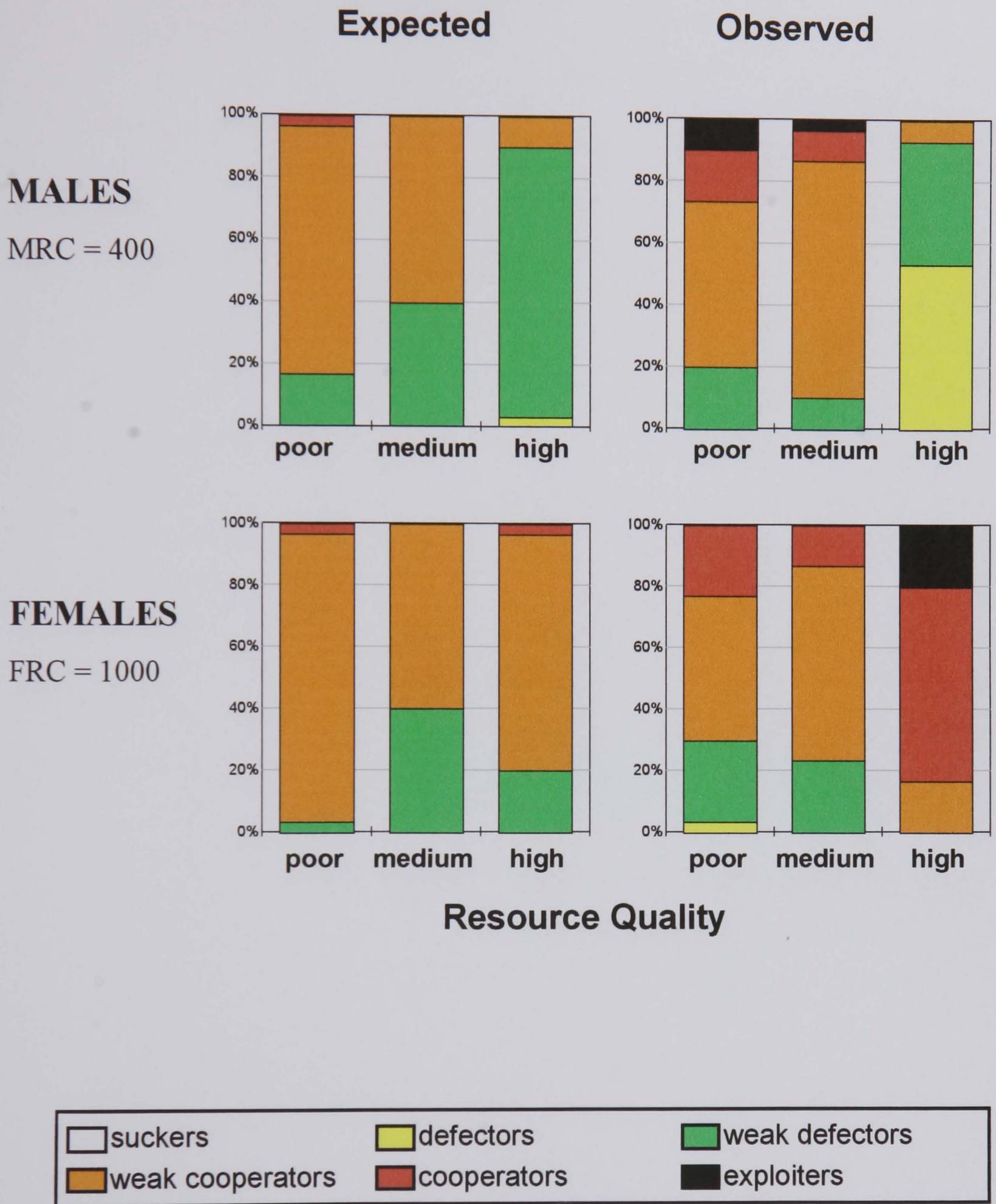


Figure 5.11 (c): Mixed sex interactions in a seasonal habitat, FRC = 1000, MRC = 400

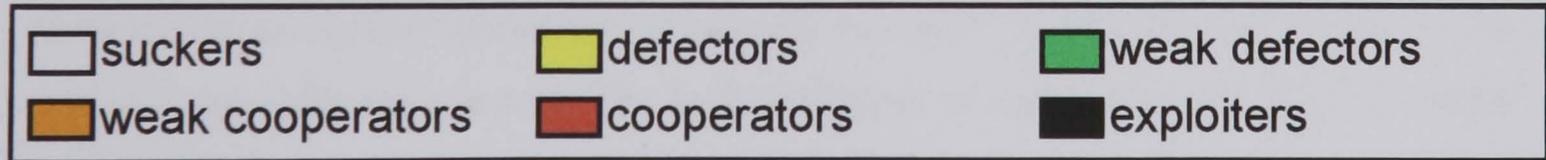
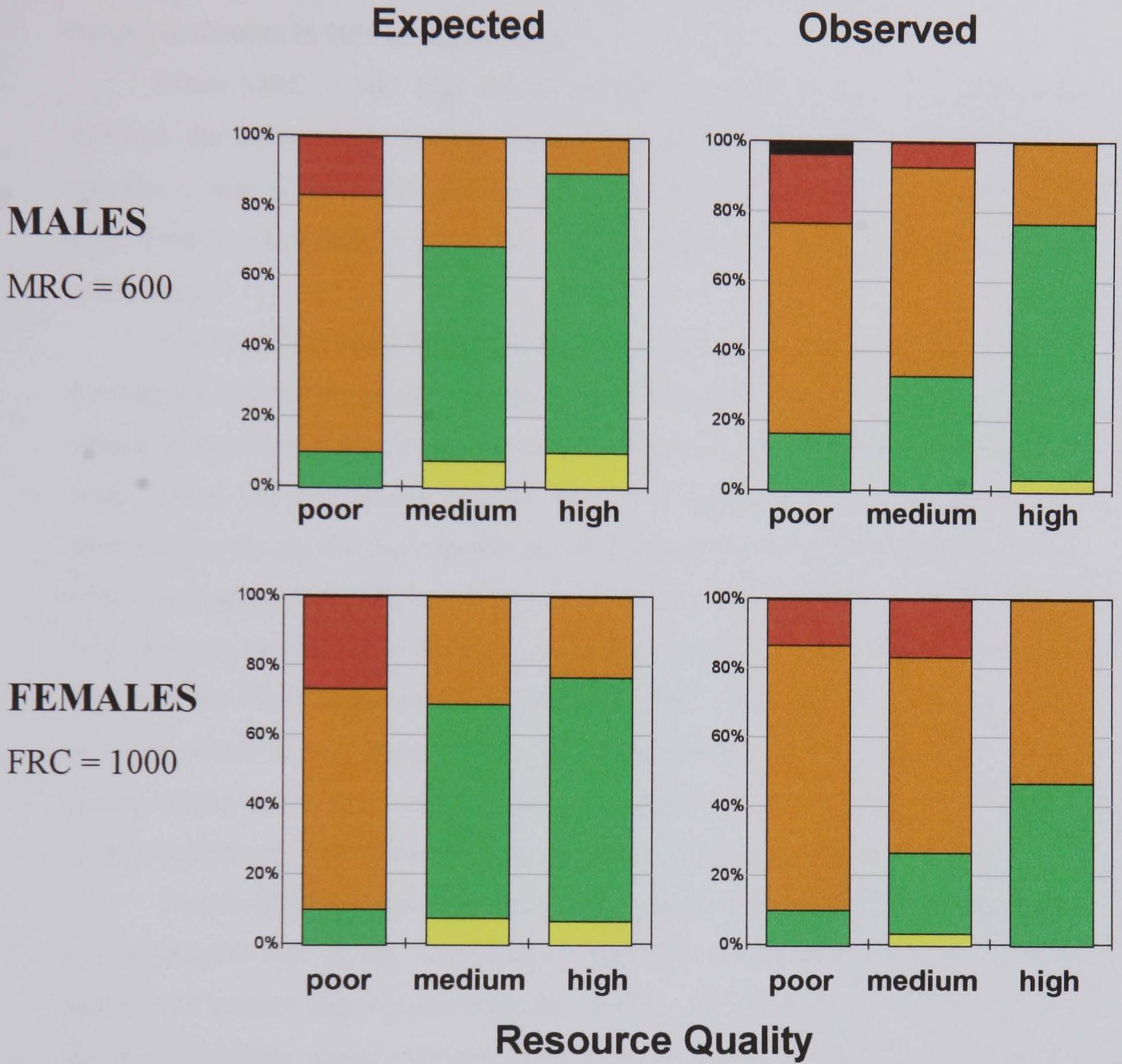


Figure 5.11 (d): Mixed sex interactions in a seasonal habitat, FRC = 1000, MRC = 600

than expected. As resource quality increases, female scores increase while male scores decrease. Quite remarkably, when resource quality is high males are non-reciprocal altruists in 90% of experiments.

When $MRC = 400$ (fig. 5.11c), results are much closer to expectations, although the same trends emerge: males tend to do better than expected when resource quality is low, while females get higher pay-offs when resource quality is high. Finally, when $MRC = 600$ (fig. 5.11d), the observed results are very similar to expectations.

The most interesting result that emerges from this experiment is that seasonal fluctuations in resource quality can have a profound effect on the pattern of male-female interactions. When male reproductive costs are low females cooperate with males during the poor quality months. In return, males are extremely cooperative with females during the high quality months. Males appear to help females during those times when they will benefit the most. This result is extremely robust. Figure 5.12 plots the results of the first six simulations performed when $MRC = 200$ and $FRC = 1000$. The simulations are extremely similar³. During those months in when resource quality is low, males and females obtain very similar scores. As resource quality increases the scores diverge, so that in the months when resource quality is highest (months 6-8) females obtain vastly greater scores than males.

It is possible that the observed strategies are a result of the simulation design. A reproductive cost of, say, 200 points is very low. Even if all individuals defect, males will acquire this number of points by the end of month 4. Therefore, the number of points scored after this time may be irrelevant. This means that the strongest selection pressures on males are at the start of the yearly cycle, when resource quality is low. For males, scoring as many points as possible, and as soon as possible, during this initial period is of prime importance. Selection pressures on females are strong throughout the simulation, especially during the high season when potential pay-offs are greatest. The high incidence of non-reciprocal altruism when resource quality is high may be the result of the high temptation for females to defect at this time, rather than any genuine altruism on the part of the male. In short, if all males have to do is gain 200 points, then there is no real cost to being a non-

³ Note that the other 24 simulations done for $MRC = 200$ were also very similar.

reciprocal altruist when resource quality is high. However, as we shall see, this argument is incorrect.

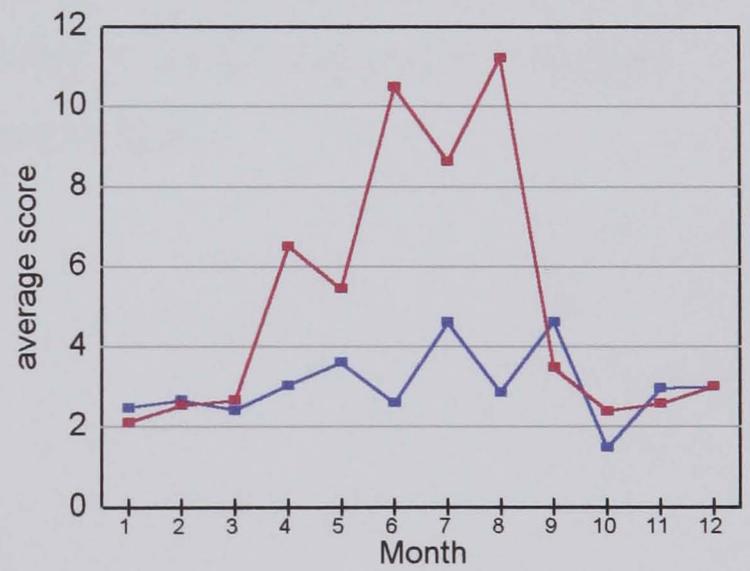
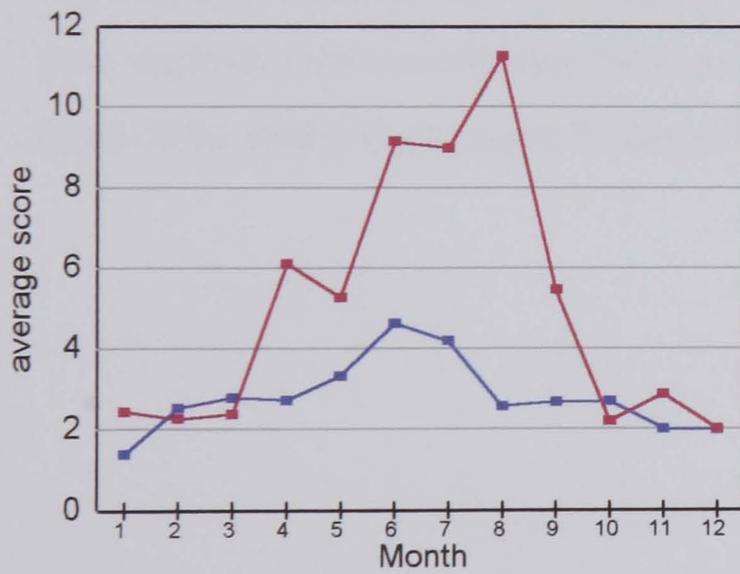
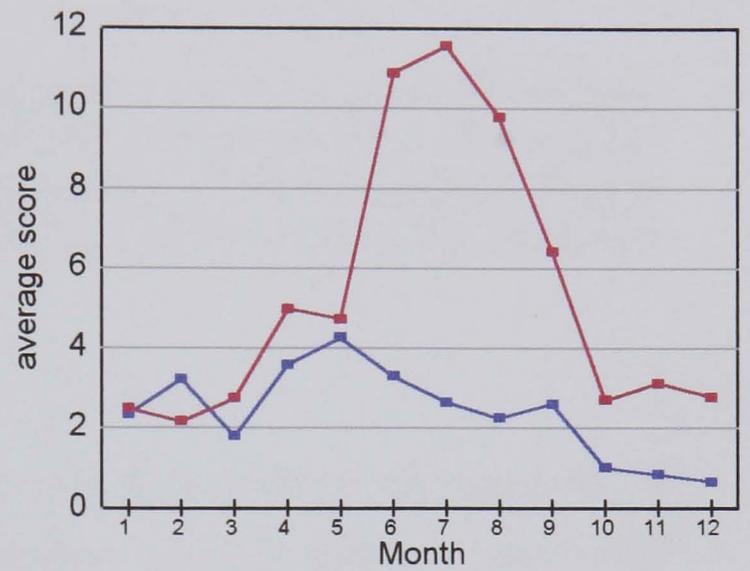
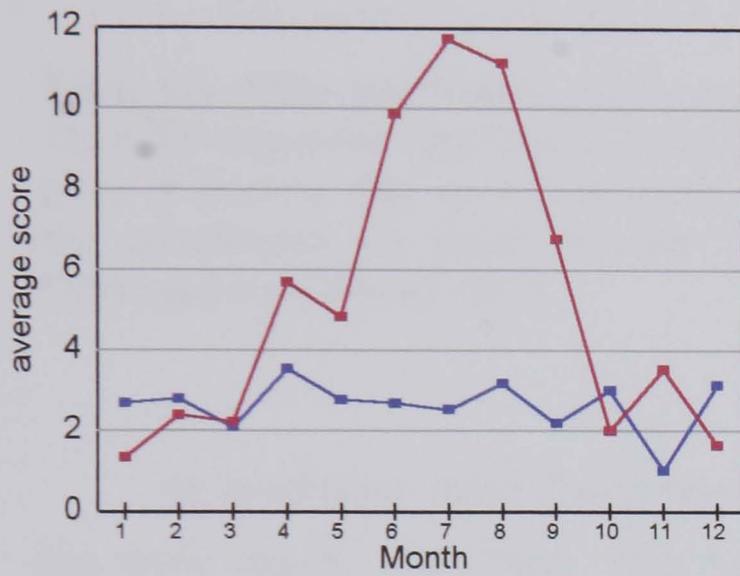
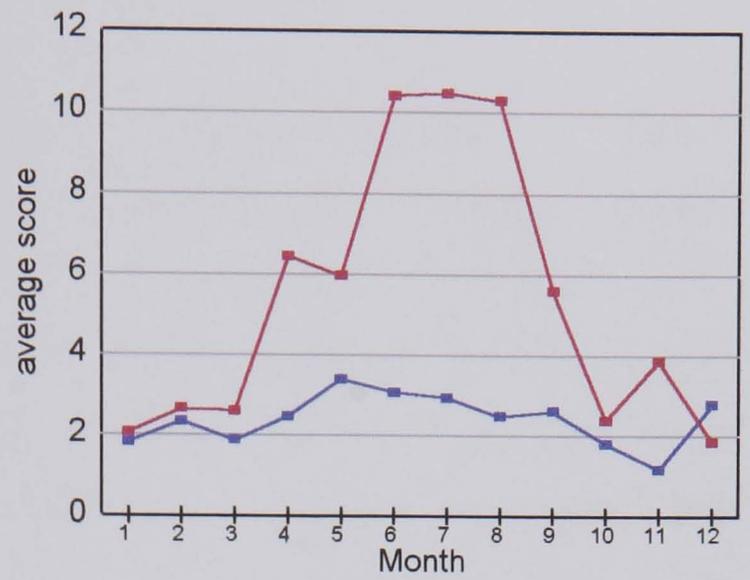
In chapter 3 (section 3.4) it was shown that when male reproductive costs are less than female reproductive costs there is more variation in male reproductive success than female reproductive success: the most successful males sired 5 offspring in a generation while the most successful females sired just 3 offspring. It was argued that it is not enough for a male to acquire enough points to reproduce just once. Successful males will be those that acquire enough points to sire many offspring. The same is true here. The model is designed in such a way that during reproduction, pairs of males and females are chosen at random from all those males and females that have enough points. After reproduction, the cost of reproduction is deducted from each agent's score. If they still have enough points to reproduce they are returned to the population of "fertile" agents. Every month pairs are chosen at random to reproduce until either the number of fertile males or fertile females is zero (see section 5.2). This means that at $MRC = 200$, a male with 600 points could produce 3 offspring in a single month (if there are enough fertile females available). In other words, even though the cost of reproduction for males may be low, it is still an advantage to acquire as many points as possible.

The key to the high level of non-reciprocal altruism in the high season (when resource quality is greatest) may lie in the high levels of cooperation between males and females in the low season (when resource quality is lowest). Let us consider a population which contains two types of males: cooperators and defectors. Cooperators cooperate with females when resource quality is low and, assuming that this cooperation is reciprocated, score highly. Defectors defect at all times and, assuming that females defect in return, receive comparatively low scores. At the end of the low season, the cooperative male will have acquired many more points than the defector. However, the cooperator can only take advantage of his high point scoring if there are fertile females available. This means that it is in the cooperator's interest for females to be fertile as soon as possible. The best way to do this is to be a non-reciprocal altruist when resource quality is high. From the female's point of view cooperating with males when resource quality is low is an excellent strategy, since this provides an incentive for males to be non-reciprocal altruists when resource quality is high.

I am arguing that non-reciprocal altruism can be a good strategy for both sexes. Female cooperation with males in the low season provides males with enough points to produce several offspring, while male non-reciprocal altruism in the high season allows females to reproduce sooner. This appears to be a very robust strategy at low values of MRC (figure 5.12). But, at what value of MRC should males stop being non-reciprocal altruists? In order to answer this question a few simplifying assumptions need to be made:

- 1) During periods of low and medium quality resources males and females cooperate. Both males and females score 3.0 points per game in low quality months, and 6.0 points per game in medium quality months.
- 2) During periods of high quality resources males are non-reciprocal altruists. Therefore, in high quality months males score 4.5 points per games, females score 12.0 points per game.
- 3) Females always play weak-cooperation against each other, scoring 2.0, 4.0 and 6.0 points per game in poor, medium and high quality months respectively.
- 4) Males always defect against each other, scoring 1.0, 2.0 and 3.0 points per game in poor, medium and high quality months respectively.
- 5) There are 25 males and 25 females in the population.

On the basis of these assumptions, it is possible to calculate the cumulative score for each sex each month. These are shown in table 5.3. The crucial factor is that females would be expected to obtain enough points to reproduce (1000) at the end of month 6. At this point, if males are non-reciprocal altruists, they will have gained 878 points. If $MRC = 200$, males already have enough points to reproduce 4 times. But, if $MRC = 400$, males can only reproduce twice. Worse still, at $MRC = 600$ males can only afford to reproduce once. Assuming that successful males will be those that can reproduce many times over, non-reciprocal altruism is a risky strategy at values of MRC greater than 400.



■ males ■ females

Figure 5.12: Variation in male and female average scores when FRC = 1000 and MRC = 200

The graphs plot average scores per player per game over 6 typical simulations. Each graph tells a very similar story: During months 1-3, when resource quality is low, males and females score similar numbers of points. During months 4, 5 and 9 resource quality is medium, and during months 6-8 resource quality is high. During periods of high quality resources females always gain substantially higher scores than males.

Month (quality)	Female score	Male score
1 (low)	48 (FF) + 75 (MF) = 123	24 (MM) + 75 (MF) = 99
2 (low)	123 + 48 (FF) + 75 (MF) = 246	99 + 24 (FF) + 75 (MF) = 198
3 (low)	246 + 48 (FF) + 75 (MF) = 369	198 + 24 (FF) + 75 (MF) = 297
4 (medium)	369 + 96 (FF) + 150 (MF) = 615	297 + 48 (MM) + 150 (MF) = 495
5 (medium)	615 + 96 (FF) + 150 (MF) = 861	495 + 48 (MM) + 150 (MF) = 693
6 (high)	861 + 144 (FF) + 300 (MF) = 1305	693 + 72 (MM) + 113 (MF) = 878
7 (high)	1305 + 144 (FF) + 300 (MF) = 1749	878 + 72 (MM) + 113 (MF) = 1063

Table 5.3: Male and female scores assuming males are non-reciprocal altruists. The table shows the cumulative scores for each sex, on the basis of the assumptions given in the text. The scores are based on a population of 25 males and 25 females, and calculations are shown by interaction type: female-female (FF), male-male (MM) and male-female (MF).

In conclusion, these results have built upon those from previous chapters. It has been shown, once more, that non-reciprocal altruism evolves when male reproductive costs are considerably less than female reproductive costs. In addition, in a seasonal environment non-reciprocal altruism is strongly selected during those parts of the yearly cycle in which resource quality is high.

5.4.3 Discussion

These two experiments have examined the effect of seasonal variation in resource quality on the development of cooperation. It has been shown that when resource quality fluctuates, strategy choice at the times of highest quality resources determines strategy choice at all other times (section 5.4.1). Because there is a high temptation to defect when resource quality is high, overall levels of cooperation in a seasonal environment are less than would be expected. This is true even during periods when resource quality is low. In stark contrast to this, cooperation between males and females increases in a seasonal environment (section 5.4.2). If male reproductive costs are considerably less than female reproductive costs, a special kind of non-reciprocal altruism evolves. During periods of low resource quality males and females cooperate with each other, then when resource quality improves males cooperate while females defect (non-reciprocal altruism). Therefore, it is possible to make two predictions regarding cooperation in a seasonal environment:

- 1) Cooperation is more difficult to establish when the quality of the resource in question varies over time.
- 2) In a seasonal environment, males are most likely to be non-reciprocal altruists when resource quality is high.

These predictions will be discussed here. As in previous chapters, an extensive search of the literature has been conducted in order to ascertain the potential value of these predictions. Overall, I found it very difficult to find any studies that clearly support or contradict either of them. The main problem is that seasonality can have a multitude of effects on behaviour which are very difficult to untangle. First of all there is the problem (already discussed at length in sections 5.1 and 5.3.3) that changes in resource quality are almost always accompanied by changes in resource distribution. Large patches of high quality resources are able to support more individuals, and thus create more opportunities for both competition and cooperation. Moreover, large food patches may promote group defence of resources from other competing groups.

A second difficulty in interpreting these results is that in seasonal habitats there is usually a distinct breeding season during which male-male competition for females is intense (Bernstein 1993). Increased rates of male transfer during the breeding season in some primate groups (e.g. rhesus macaques) would also lead to increased competition at this time (Bernstein 1993). The manner in which breeding season effects competitive and cooperative interactions will vary between groups. For instance, when males are much bigger than females, males may behave quite aggressively towards females and thus coerce them into sexual interactions (Smuts and Smuts 1993). On the other hand, when females and males are similar in size, females usually approach males to initiate copulations (Stevenson *et al.* 1994). In rhesus monkeys, changes in both female-male and female-female behaviours such as grooming, sexual behaviour, aggression and proximity occur in the transition to the breeding season (Maestriperi and Scucchi 1989). The problem is that affiliative and competitive behaviours that arise because of breeding season effects will obscure possible affiliative and competitive behaviours that arise because of seasonal changes in resource quality. Few studies have been able to dissociate these effects (but see Schiml *et al.* 1996). Despite these problems, the following discussion attempts to bring together a number of studies that have looked at aspects of cooperation and competition in a seasonal environment.

1) Cooperation is more difficult to establish when the quality of the resource in question varies over time.

The experiments performed here strongly suggest that cooperation is difficult to establish when resource quality fluctuates, as it does in a seasonal habitat. The high temptation to defect when resource quality is high prevents future cooperation when resource quality is low. In effect, the level of cooperation when resource quality is high determines how much cooperation is expected at all other times. Therefore, in a seasonal habitat cooperation should be more or less the same throughout the year. Moreover, cooperation should be greater in less seasonal environments. Intra-population differences in food sharing in capuchin monkeys appear to support this hypothesis. Rose (1997) has observed that meat sharing in capuchins is more frequent in less seasonal habitats. Also, Gould (1996) found no

differences in male-female agonistic and affiliative interactions in ringtailed lemurs with respect to seasonal availability of food. On the other hand, Stevenson *et al.* (1994) found that feeding tolerance in woolly monkeys varied with respect to food availability. During periods of food scarcity males excluded non-lactating females and juveniles from fruiting trees.

One possible test of the model is to look at how cooperative relationships such as grooming vary over the wet and dry season. Dunbar (1988) found no differences in grooming time between the wet and dry seasons for a large number of baboon populations. Taken at face value, this result would appear to support the model. However, such a conclusion would be premature. Grooming is a very important activity in baboon groups (see figure 4.1 and discussion in section 4.4.2). Dunbar (1988) believes that baboons use grooming as a way of servicing their social relationships, establishing friendships and forming alliances. In fact, baboons will sacrifice feeding and resting time rather than lose time spent grooming. This indicates that baboons have very good reasons for maintaining high levels of grooming throughout the year that have nothing to do with resource quality. Furthermore, it is not at all clear that the pay-offs associated with cooperative behaviours such as grooming vary in any predictable way with habitat quality. This means that, it is unlikely that grooming itself confers greater benefits to the recipient or incurs greater costs to the donor at certain times of the year, unless it can be shown that the number of parasites in the fur varies according to season. Bitetti (1997) found that in *Cebus apella* grooming sessions were less frequent during the winter than at other times of the year. However, Bitetti concluded that this was due to seasonal differences in the opportunities for grooming created by different resource distributions. This model only applies if the pay-offs for different cooperative acts vary in a seasonal manner. Unless it can be definitively shown that the costs and benefits of grooming vary in this way, this method of testing the hypothesis is invalid.

At this point, attempts to apply the model directly to living populations have been disappointing. However, the model will apply to any situation in which the pay-offs of cooperation and competition vary. Therefore, its power may lie not in looking at cooperation in seasonal environments, but at looking at cooperation in groups where individuals regularly cooperate/compete over different resources with different pay-offs. In some situations the benefits and risks associated with

cooperation and competition may be low, this is similar to the poor resource quality situation. In other situations, the benefits and risks of cooperation and competition may be high, as in the high resource quality situation. As we have already seen in chapters 1, 2 and 3, most group living primates cooperate in a wide variety of situations: infant care, coalitionary support, tolerance at a feeding site, coordinating activities, grooming, food sharing and so on. This model would predict that if individuals establish a cooperative relationship in a high risk / high pay-off situation (e.g. coalitionary support) they should also cooperate in a low risk / low pay-off situation (e.g. grooming). Conversely, failure to cooperate in a high risk / high pay-off situation should cause the break-down of cooperation in the low risk / low pay-off situation. Chimpanzees may be aware of this type of social rule. Verbeek and de Waal (1997) found that chimpanzees engage in reassuring behaviours in the presence of particularly attractive food items, such as bananas. They suggest that chimpanzees are careful to ensure cooperation in the presence of highly desirable resources, in order to ensure that cooperation is maintained in other social contexts.

Reconciliation following aggressive disputes occurs in wide variety of primate species including chimpanzees, capuchins, macaques, guenons and patas monkeys (Verbeek and de Waal 1997). In some species special 'peace-making' gestures have evolved. For instance, stump-tailed macaques have a special hip-holding gesture that is used to ease social tensions following conflicts (de Waal 1996). It appears that primates have evolved mechanisms to promote good relations even in high cost/high benefit situations such as aggressive contests so that social harmony can be maintained at other times. After all, simply staying together as a group involves cooperation in terms of group coordination of activities such as, when and where to eat, sleep and travel. In other words, the occurrence of reconciliation in many primates species is evidence that the most crucial aspect of a good cooperative strategy is to ensure that competition in high cost/high benefit situations does not ruin the chances of cooperation in low cost/low benefit situations.

2) In a seasonal environment, males are most likely be non-reciprocal altruists when resource quality is high.

The model presented in section 5.3.2 confirmed the finding of previous chapters that non-reciprocal altruism is most likely to evolve when male reproductive costs are much less than female reproductive costs. If non-reciprocal altruism is likened to male care giving then we can now make the additional prediction that, in a seasonal environment, seasonal patterns of paternal care will emerge. In a seasonal environment male care giving is most likely during periods when resource quality is high. Most seasonal environments can be roughly divided into a wet and a dry season. According to the model, male care giving should peak in the wet season, when resource abundance is greatest. Therefore, if females give birth in the wet season they stand a greater chance of extracting male care giving than they would if they gave birth in the dry season.

Male care giving occurs most in New World monkeys, all of which live in a seasonal habitat and are seasonal breeders (Kinzey 1997). Among the New World monkeys there are approximately equal numbers of species in which females give birth in the wet and dry seasons. Male care giving never occurs in those species which give birth in the dry season. In contrast, male care giving does occur in most of the species which give birth in the wet season (*Lagothrix* species being the exception). These observations appear to support the model. That is, species from genera such as *Aotus*, *Callicebus*, *Pithecia*, *Leontopithecus* and *Saguinus* time their birth season to coincide with (a) the period of highest resource availability, and (b) the period in which males are most likely to provide parental care.

Why do females from genera such as *Alouatta*, *Brachyles*, *Cacajao*, *Saimiri* and *Chiropotes* time births to coincide with the dry season, rather than the wet season when the likelihood of male care giving is greatest? Very little work has been done in this field. Among the Old World monkeys, rhesus macaques also give birth in the dry season (Koenig *et al.* 1997). Koenig *et al.* suggest that in this case females are constrained by the energetic demands of conception, rather than lactation. It may be that certain New World monkeys are unable to meet the energetic requirements of conception in the dry season and thus are forced to conceive in the wet season. This indicates that dry season birth peaks may be unavoidable and have the effect of militating against male care giving.

Observations of New World monkeys support the prediction that male care giving will be greatest when resource quality is greatest. That is, in New World monkeys, male care giving only occurs when females give birth during the wet season. Of course, this is not a sufficient condition for male care. Energetic costs for females must be considerably greater than energetic costs for males if paternal care is to evolve (in chapter 4 it was shown that this condition is satisfied in many New World monkeys). The point is, that if female energetic costs are very much higher than male energetic costs then seasonal birth peaks at times of resource abundance enhance the opportunities for male care giving.

Male care giving in chacma baboons, which peaks during times of food scarcity, appears to contradict the model. Anderson (1992) studied male care giving in chacma baboons at the Süikerobsrand nature reserve in South Africa. These baboons live in a harsh, mountainous and seasonal habitat. The severe environment puts the baboons under high energetic stress, especially during the winter when food is low in both quality and quantity. At these times resting metabolic rate is around 14% higher than expected. Furthermore, during the winter travel time increases greatly and, given the mountainous terrain, locomotor costs are high. Given these environmental constraints, it would be fair to surmise that this is a low quality, highly seasonal habitat, where energetic costs are high. Male assistance in infant transport and protection occurs in some, but by no means all, chacma baboon populations. Levels of paternal care-giving in Anderson's study group are high, and the advantages to females are clear. Male investment alone has greater influence on improving survival rates and shortening inter-birth interval than any other factor. In this case, male care appears to be a response to high female energetic costs in a poor quality habitat. Anderson found that male carrying was greatest in the winter, and when predation risk is high. Furthermore, males were more likely to carry the heavier, more burdensome infants. In other words, males tailor their cooperation to the times of greatest female need. Overall, the results of this study contradict our expectations that male care will be greatest during times of resource abundance. It seems that the severe winter conditions overwhelm all other considerations.

At this point it would be premature to draw any firm conclusions on the basis of these models. The simulations themselves are fairly complex, involving 12 different strategy strings and variable pay-off matrices. However, in the real world,

variation in resource quality has far reaching effects, which are considerably more complex and inter-dependent than can be captured in these models. Controlled experiments are required to investigate cooperative and competitive strategies when pay-offs vary, as they do in the seasonal model. It has been suggested here that the model may be particularly relevant in looking at paternal care in New World monkeys, all of which live in highly seasonal habitats. Male care giving only occurs in those species that give birth in the wet season. Males may be less able to afford the costs of care giving when females give birth in the dry season. It is not clear why females should give birth in the dry season at all, since this means that the energetically costly lactation period coincides with the period of low resource availability. It is suggested here that these females may be less able to conceive in the dry season, although this hypothesis remains to be tested. The available literature indicates that very little consideration has been given to the possible effects of seasonality on male care giving or cooperation in general. The simulations discussed in this chapter suggest that future research into the relationship between resource quality, seasonality and cooperation would yield interesting results.

CHAPTER 6

Cooperation and the Evolution of Human Social Intelligence

6.1 Introduction

Previous chapters have emphasised the extent to which human societies are similar to those of other animals, especially other primates. The social world of most primates is complex, involving cooperative and competitive interactions between individuals of different age, sex and rank. Yet, the structure of human social groups involves larger numbers and types of cooperative relationships than are seen in any other single primate group. Humans live in large multi-male, multi-female societies which involve extensive cooperative networks. Within these groups, human males and females form pair-bonds which are almost always formalised by marriage (Buss and Schmitt 1989). The cooperative bonds between marriage partners differ in quality and permanence across human societies. None the less, marriage is almost always associated with a division of labour between husband and wife, and male investment in his wife and her offspring. However, Deacon (1997) points out that male care giving and pair bonding are extremely unlikely within the context of large multi-male, multi-female societies because the opportunities for extra-pair matings are great.

This research has shown that in order to understand the evolution of such an unusual social system, we need to consider how the energetic costs of reproduction have changed for males and females over the course of human evolution. In this section we will briefly review how changes in climate, sexual dimorphism, diet and brain size may have led to profound changes in the energetic costs to *Homo* females and how these changes may have led to changes in social structure. However, the main purpose of this chapter is to show that the evolution of human cooperative strategies must have been accompanied by the co-evolution of cognitive support mechanisms. As we shall see, the development of cooperative relationships between males and females in particular, may have placed special cognitive demands on our hominid ancestors.

6.1.1 The evolution of human social groups

In the previous chapter it was argued that the environmental context in which animals exist effects the kinds of cooperative strategies that evolve. This suggests that the climatic context of hominid evolution may yield important clues with regard to the evolution of cooperative behaviour. While researchers differ in the extent to which they regard climatic change during human evolution as important in shaping speciation and extinction events (see, for example, Vrba 1988, Foley 1994), there is a general consensus regarding the kinds of climatic changes that were involved. *Homo erectus* almost certainly lived in a drier, more open habitat than the australopithecines (Reed 1997; Ruff 1991), who appear to have lived in more closed, wooded environments. The australopithecine skeleton exhibits a number of adaptations to a partially arboreal lifestyle (Ruff 1991; Stern and Susman 1983) and is short and squat when compared with a human skeleton, possibly reflecting adaptations to a wetter environment. In contrast, the postcranial skeleton of *Homo erectus* shows no arboreal adaptations and is considerably taller and slimmer than that of the australopithecines. Ruff (1991) argues that these body proportions indicate that *Homo erectus* lived in an open, arid environment. Wheeler (1994) also argues that the body shape of *Homo erectus* is a thermoregulatory adaptation. The larger, slimmer and taller *Homo* would have been able to withstand greater heat stress, and would have been able to conserve water better than its shorter, squatter ancestors.

There are a number of reasons to believe that the transition from a closed wet habitat to open, dry conditions would have promoted an increase in cooperation. Firstly, the models used in the previous chapter predict that cooperation is more likely when resource quality is low. It follows, that the arid conditions in which *Homo erectus* evolved would have selected for more cooperative strategies. Secondly, Aiello and Dunbar (1993) point out that predation pressures tend to be greater in open environments and that other primates, such as baboons, respond to this by increasing group size. Aiello and Dunbar suggest that the move to more open habitats by early *Homo* may have selected for larger group sizes, and intensified the need for cooperative strategies that promote group cohesion. Thirdly, Hawkes *et al.* (1998; pers. comm.) suggest that in a more arid environment there may be an increased reliance on embedded food resources, such as tubers, that are difficult for young

children to acquire for themselves. Food sharing, especially with young weanlings, may have become an important part of the behavioural repertoire of *Homo erectus*. Finally, the transition from the closed, wet environments of the australopithecines to the open, dry habitats of early *Homo* also involved considerable skeletal adaptations, including an increase in body size (McHenry 1992a, 1992b, 1996). While both males and females increased in size, the change was most marked in females. McHenry (1996) estimates that *Australopithecus afarensis* males were 50% bigger than females. *Homo erectus* males were just 20% heavier than females, indicating an important shift in the balance of energetic costs between the sexes. The increased energetic load on females, in comparison to males, would have contributed to a change in social behaviour involving more cooperation both between females and between males and females.

In addition to changes in climate and postcranial anatomy, the other major change during human evolution has been a three-fold increase in the size of the brain (see figure 1.1). This has had important energetic implications (Aiello and Wheeler 1995; Aiello 1997). Because brain tissue is metabolically expensive, Aiello and Wheeler argue that brain expansion must have involved a trade off with another energetically expensive tissue: the gastrointestinal tract. This would only have been possible if the changes in gut size were accompanied a change to a diet containing a higher percentage of animal products which are less bulky, of higher quality and are more easily digested than plant foods. The adaptive complex of an increase in brain size and a reduction in gut size, mediated by a change to an animal-based diet, implies a profound change in the energetic costs of reproduction for females. This is due to the direct costs to the mother of providing enough energy to her infant for brain growth (Foley and Lee 1991; Martin 1981, 1983, 1996). In addition, a change to a diet with a high meat component requires that females provision their offspring until they have gained the necessary skills to acquire meat for themselves (see discussion in section 5.3.3; Aiello 1998). The dual loads of extensive food-sharing between mother and offspring, and the training necessary for the offspring to find its own resources would significantly increase the period of maternal investment beyond the weaning period.

There were two main periods of brain size increase during hominid evolution. The first occurred during the transition from australopithecines to early *Homo*. This

period of brain expansion also coincided with changes in climate and body size and taken together these factors are indicative of a considerable change in hominid energetic and cooperative strategies. I believe that at the very least, *Homo erectus* societies would have involved extensive cooperation between females. The second period of brain expansion occurred from around 500,000 – 100,000 years ago. Brain expansion during this time was exponential, indicating rapidly increasing female energetic costs. In chapter 4 it was argued that the archaic *Homo sapiens* living during this time must have lived in highly cooperative social groups in which male provisioning played an important role. Skeletal evidence that Neandertal males led more active lives and were more skeletally robust than females supports the proposition that there was a sexual division of labour at this time (Ruff 1987). Thus, I am proposing a two stage model of the evolution of human social organisation. The first transition occurring between the australopithecines and *Homo erectus*, involving increased female cooperation. The second occurring between 500,000 and 100,000 years ago and involving the addition of male care giving, the formation of pair bonds and the sexual division of labour within the context of a wider cooperative network.

Possibly the most important cooperative endeavour in the hominids was the provisioning of offspring, especially young weanlings. Cooperation in the care and feeding of offspring is especially important in the callitrichids and social carnivores because of the special difficulties faced by a weanling who does not have the experience to capture its own food. Similarly, a shift to a meat-based diet or increased reliance on embedded food items is likely to have selected for increased cooperation in the hominids. Hawkes *et al.* (1997a, b, c, 1998) stress the importance of female provisioning of offspring, especially by related females such as aunts and grandmothers. They suggest that menopause and long post-menopausal life spans may have evolved as part of such a cooperative strategy. This hypothesis is based on the finding that senior post-menopausal Hadza women play an important role in provisioning their daughter's offspring. The benefits of this are clear for the child, the mother and the grandmother. With more provisioning the child would be expected to have higher survival. The mother is relieved of some of the burden of providing food, reducing her energetic stress and shortening her inter-birth interval. Finally, the decreased mortality of the child and the increased fecundity of the mother equate to higher inclusive fitness for the grandmother.

Because of the changes in female energetic costs, it seems likely that increased female cooperation would have evolved fairly early in the evolution of the *Homo* genus. There may have been selection for menopause and increased post-reproductive lifespans (Aiello 1998; in press) as well as other features such as concealed ovulation, reproductive synchrony and increases in subcutaneous fat (Power and Aiello 1997; Power *et al.* 1997; Stern and McClintock 1998; Turke 1984). However, paternal investment may also have been important, especially if an increased meat component to the diet is involved. There are a number of reasons why females may be unable to provide meat for their offspring themselves. Firstly, hunting is an unpredictable foraging strategy (Hawkes 1993; Hawkes *et al.* 1997a). Hunting may provide as many calories per day *on average* as other foraging strategies. However, studies of modern hunter-gatherers suggest that there is considerable day-to-day variation in hunting returns, and on any given day there is a high chance of failure. Secondly, hunting especially of large animals is incompatible with childcare. If hominid females were pursuing a hunting strategy, then they must have been dependent on other females for offspring care in their absence. Finally, hunting is an energetically costly activity (see chapter 4) which may prohibit female participation due to the adverse effects that high energy expenditure has on fertility (Bentley 1985). On the other hand, high daily energetic costs on the part of human males appears to reflect a strategy of male investment in females and their offspring.

It seems that climate change provoked changes in the energetic strategies of our hominid ancestors. In response to escalating female energetic costs and deteriorating environment quality, *Homo* spp. must have adopted a range of cooperative strategies including increased female-female and male-female cooperation. Unfortunately, cooperative behaviours do not leave a mark on the fossil record. Yet, I believe that cooperation played such an important role in the evolution of human society, that it has left a mark on the human mind. That is, humans appear to have specially evolved cognitive mechanisms for managing a social world in which balancing the benefits of cooperation, the temptations of cheating and avoiding exploitation is of paramount importance. These cognitive adaptations are in themselves evidence of the kinds of selective pressures that shaped hominid evolution.

Just as cooperative behaviours have their origins in non-human primates, so do the cognitive support mechanisms for these behaviours. Thus, the next section will

briefly review the primate basis of human cognition. This discussion will provide a baseline for looking at human intelligence.

6.2 The Primate Basis of Human Cognition

Most primates live in social groups which contain individuals of different age, sex, rank and kinship. As we have seen throughout this thesis, individuals within groups cooperate and compete over a wide variety of different resources in a wide variety of social situations. However, decisions about when to cooperate or compete depend not only on the age, sex and rank of the two animals directly involved in a situation, but the ages, sexes and ranks of their allies. In vervet monkeys, a fight between two individuals is often followed by aggressive encounters between their relatives (Cheney and Seyfarth 1990, 1992). Therefore, it is very important for each animal to know who is related to who, and who is allied with whom (Cheney and Seyfarth 1986). The evidence suggests that primates are well aware of the relationships between other group members. Dasser (1988a, b) showed macaques pictures of adult females and juveniles from their social group and found that they could classify pictures based on relatedness. Cheney and Seyfarth (1990) used vocal play-back experiments to show that when an infant screams, adults look to the infant's mother for a response. Cheney and Seyfarth suggest (1992 p.142):

“in their social interactions monkeys do not simply associate some individuals with others but instead classify relationships into types. “Mother-offspring bonds” or “bonds between the members of family X” are abstractions that allow different relationships to be compared with one another..... the monkeys' ability to represent social relationships has evolved because it offers the most accurate means of predicting the behaviour of others.”

In other words, monkeys appear to have a cognitive map of the social relationships within their group which they use to predict the consequences of their social interactions.

Apes may have a more sophisticated social intelligence than monkeys. De Waal and Luttrell (1988) examined reciprocal altruism in monkeys and apes, and

found an interesting difference. While monkeys would reciprocate cooperative acts, they would not necessarily punish noncooperative behaviours. Apes, on the other hand, not only reciprocate cooperation but they also appear to have a “system of revenge” (de Waal 1996 p.157). That is, chimpanzees will punish those who have opposed them. Even females will occasionally attack a dominant male that has failed to support them during a confrontation. De Waal and Luttrell (1988) suggest that the lack of revenge system in monkey groups may either reflect differences in cognition or in social flexibility. The latter explanation may be the most likely. In species such as macaques there is a strict dominance hierarchy, and retaliation for a wrong-doing may be very costly. For instance, if a subordinate challenges a dominant animal, then he or she is likely to face the aggression of the whole of the dominant animal’s kin-group. Chimpanzee groups tend to have a much looser dominance hierarchy than macaque groups and chimpanzees may simply have more freedom to express their anger than a macaque does. Subordinate macaques will sometimes attack the less-dominant relative of the animal with which they had a confrontation. This suggests that it is social rather than intellectual factors that prevent macaques from reciprocating nasty as well as nice behaviours.

One area in which apes are almost certainly more advanced than monkeys is theory of mind. The term ‘theory of mind’ refers to the ability to understand the mental state of others (Premack and Woodruff 1978). An individual that has a theory of mind is able to interpret and respond to the beliefs and desires of another individual. Monkeys appear to be very good at recognising and reacting to different social relationships and they attempt to manipulate the behaviour of others. However, there is little evidence that monkeys are aware of, or attempt to influence, the mental states of other animals (Cheney and Seyfarth 1990, 1992). Cheney and Seyfarth assert that monkeys are unable to distinguish between their own state of mind, and the state of mind of other animals. They are unable to recognise another animal’s ignorance or that another animal has knowledge that they do not have. This is reflected in the fact that while monkeys use observation and trial-and-error to learn new tasks, they never imitate or teach each other. Monkeys appear to find it very difficult to take on the role of others in manipulative tasks. Furthermore, while monkeys almost certainly experience emotions such as fear and grief, there is little evidence that they recognise these emotions in others. Cheney and Seyfarth conclude that (1992 p.144) “monkeys

do not know what they know and cannot reflect upon their knowledge, their emotions or their beliefs.”

The evidence that apes, especially chimpanzees, have a theory of mind is much stronger than it is for monkeys. Premack and Woodruff (1978) conducted the first experiments on chimpanzee theory of mind. They showed a chimpanzee a film of a human unsuccessfully attempting to solve a problem. They then presented the chimpanzee with several photographs, one of which showed the solution to the problem. Chimpanzees were found to be quite good at selecting the appropriate solution, indicating that they had understood the problem from the human’s point of view. Other ‘seeing and knowing’ experiments indicate that chimpanzees understand that different individuals have different states of mind (Premack 1988). The experimental set-up involves two trainers and a chimpanzee. A piece of food is hidden, and the chimpanzee is able to observe that one of the trainers sees the food being hidden, while the other is prevented from doing so (this trainer was either excluded from the room, hidden behind a screen or had a bag over his or her head). The chimpanzee must then choose one of the trainers. Premack found that the chimpanzees recognised which humans were knowledgeable about the whereabouts of the food, and which were ignorant. In other words, the monkeys were able to understand that the two trainers had different states of mind. Povinelli *et al.* (1990) conducted a similar series of tests on chimpanzees, and reached the same conclusion. However, Povinelli (1994) later reanalysed the data and found that in the first trial, the success rate of the animals was no better than would have been achieved by chance. This indicates, that chimpanzees may have learnt to succeed in the test through associative learning, rather than by understanding mental states.

The extent to which chimpanzees and other apes possess a theory of mind remains a point of considerable debate. However, there is less doubt that there are differences between monkeys and apes in their abilities to attribute mental states to others. These differences have been demonstrated in a test by Povinelli *et al.* (1992a, b) who set rhesus monkeys and chimpanzees a cooperative task involving a special apparatus with several handles. Two individuals are required to work the apparatus successfully: one individual can see which handle to pull in order to deliver food to both animals but is unable to operate it; the other cannot see which handle is appropriate but can reach all the handles. Pairs of rhesus monkeys and pairs of

chimpanzees were taught to operate the machine successfully. The individual roles within the pairs were then switched, so that viewers became pullers and visa versa. Here the cognitive differences between monkeys and chimpanzees became apparent. Each monkey had to be trained from scratch in their new role. However, the chimpanzees were able to assume their new roles without training. It seems that the chimpanzees were able to imagine themselves in the other role and behave appropriately, although Byrne (1995) questions the extent to which this requires an understanding of the mental state of another animal.

Byrne and Whiten (1992) collated anecdotal evidence of deception in primates. They found that most cases of deception in monkeys could be explained without attributing theory of mind to the perpetrator. However, there were instances of deception in the apes which were difficult to explain without attributing some knowledge of mental states to the performer. As an example, consider the following anecdote reported by Savage-Rumbaugh (1980). The scenario concerns two male chimpanzees, Austin and Sherman. Sherman would often bully Austin, but Austin discovered that Sherman was afraid of noises from outside their sleeping quarters. Thereafter, whenever Sherman became overly aggressive Austin would run outside and make a commotion and then return indoors, whimpering. Austin's pretence at being scared was successful, and Sherman would invariably respond with panic, looking to Austin for comfort. Byrne and Whiten (1992) argue that it is more parsimonious to conclude that Austin was aware of and was manipulating Sherman's view of the world, than to try to explain such a scenario simply by reference to learned behaviours.

There are two possible advantages of having a theory of mind. Firstly, theory of mind increases an individual's ability to manipulate the state of mind of other animals. For this reason, theory of mind is often associated with 'Machiavellian' intelligence (Byrne and Whiten 1988; Whiten and Byrne 1997) and the most convincing demonstrations of theory of mind involve deception. However, theory of mind may also enhance an individual's opportunities for cooperation since it allows a better assessment of another individual's intentions, whether cooperative or exploitative (Byrne and Whiten 1997b). It is of prime importance for cooperators to be able to identify fellow cooperators and to avoid individuals who might exploit them. The extent to which theory of mind is relevant to cooperative interactions in

non-human primates is unknown, principally because it is much harder to observe theory of mind at work in a cooperative, as opposed to a deceptive, context.

The preceding discussion indicates that haplorhine primates have evolved special mental abilities for negotiating the social world, although these abilities may differ between monkeys and apes. Therefore, we should expect that there will be parts of the brain that are specifically adapted for social problem-solving. Dunbar (1992, 1993) argues that social intelligence is located primarily in the neocortex and that the larger, and more complex the social world, the larger the neocortex that is required (see section 1.1.2). To support this, Dunbar (1993) shows that the size of the neocortex, relative to the size of the rest of the brain (the neocortex ratio), is closely correlated with group size (Dunbar 1993). Furthermore, neocortex ratio is also related to the use of tactical deception (Byrne 1996).

The 'social intelligence hypothesis' suggests that managing social relationships is a considerable cognitive challenge. For this reason primates have evolved a sophisticated social intelligence with which to negotiate the social world. This is not to deny the importance of ecological problems in shaping the primate brain. Frugivores, for instance, appear to have larger brains than folivores, due to the greater difficulties in locating fruit compared with leaves (Barton 1996; Clutton-Brock and Harvey 1980). Tool use may also contribute to cognitive differences between apes and monkeys (Byrne 1997; Parker and Gibson 1979; Tomasello and Call 1994; see also discussion in section 1.1.2). The point is, that social intelligence is a very important aspect of primate cognition and appears to be limited by brain size, or more specifically neocortex size. Not only has the human brain expanded three-fold over the course of human evolution, but the neocortex in particular is considerably larger than would be expected. In fact, the human neocortex is around 200% larger than would be expected for a primate of our body size (Deacon 1997). Under these circumstances, we should not be surprised that social intelligence may also have played an important role in the evolution of the human brain.

6.3 The Evolution of Human Cognition

“We need an explanation for why we are moral. How did our moral rules evolve? Having evolved, why do they survive? The theory of repeated games has contributed enormously to our understanding of these questions. If moral rules did not exist, game theorists would have to invent them in order to shift society from equilibria with bad properties to equilibria with good ones.”

(Binmore *et al.* 1993a p.5)

Cooperation is a fundamental aspect of human behaviour. In fact part of the appeal of models such as the Prisoner’s Dilemma, and concepts such as reciprocal altruism, is that they describe a social situation which most of us find ourselves in every day. As has been shown in this research, there are many possible outcomes to the repeated Prisoner’s Dilemma game. Reciprocal altruism is by no means the only solution. Moreover, when pay-offs vary then cooperation is actually very hard to achieve (section 5.4). None the less, reciprocal altruism is part and parcel of human life. Binmore comments (1990 p.24):

“Those who live in New York may not agree, but to a considerable extent people tell the truth, keep their word, respect property rights, and help old ladies across the road. Why do they behave this way?”

Why do humans cooperate? It is unlikely that humans become reciprocal altruists through some process of rational deduction, in the sense used by game theorists (Binmore 1993). The social world is so complex that it is impossible to have complete information about the problem at hand and thus to calculate the possible consequences of different actions, or the rationality and motivation of other individuals. Even in experimental situations in which it is possible to acquire complete information, Binmore (1993) reports that subjects use ‘rules of thumb’ or notions of ‘fairness’ to make strategic decisions, rather than a logical process of deduction. This leads Binmore (1993; Binmore *et al.* 1993a,b), to suggest that humans have in-built rules, or morals, that help us to achieve good solutions, such as reciprocal altruism. The advantage of game theory, is that it helps assess what these ‘good solutions’ might be.

Binmore (1991) suggests that social rules, or morals, may be hard-wired directly into our minds and behaviour, but that in humans they are more likely to be socially transmitted. Because the calculations required to assess the appropriate action in a given situation are complex, and vary from one situation to the next, it would be very difficult to imagine how appropriate rules could be hard-wired into our genetic code by evolutionary processes. None the less, in this section it will be shown how biological (as well as social) evolution has equipped us with the mental apparatus required for solving social problems specifically related to cooperation. Theory of mind, for instance, may have evolved for exactly this purpose. We will return to the question of social versus biological conditioning at the end of this section. First, this section examine why cooperation may have become so important in human societies. We will then examine the kinds of cognitive mechanisms required to support this cooperation.

Cashdan (1985) views reciprocity as a kind of insurance against lean times. By sharing resources, especially food items, there is less risk that on any given day someone will go hungry. Cashdan (1985) found that amongst the Nata, sharing of food items, especially grains, increased during the poorest parts of the season. This observation accords well with the prediction that cooperation is most likely when resource quality is low (see section 5.3). Cashdan (1980) points out that food-sharing is particularly important in hunter-gatherer groups whose lifestyle prevents the long-term storage of food items. This type of cooperative relationship is a kind of ‘generalised’ exchange (Sahlins 1972). Food is given and received by many different members of a community, and is not restricted to directly reciprocal exchanges between two individuals. In fact, Sahlins comments that interactions over food are explicitly non-reciprocal (1972 p.215):

“direct and equivalent returns for food are unseemly in most social settings: they impugn the motives both of the giver and of the recipient.”

There is, however, a fundamental flaw in this food-sharing strategy. A system of generalised exchange is open to exploitation by ‘freeloaders’ who can take the benefits of sharing without paying the costs (Smith 1988). Smith argues that the only way to prevent cheating is if the system is supported by mechanisms for monitoring

and punishing freeloaders. As we shall see, the ability to detect cheats and identify cooperators appears to be a part of our evolved psychology.

The view that food-sharing is not reciprocal may be false. This is because reciprocity is difficult to distinguish from unconditional altruism unless it is disrupted in some way. An example of this is provided by Dwyer and Minnegal (1997) who studied the sharing of sago flour in a village in lowland Papua New Guinea. By custom, village residents (land-owners) share sago flour with 'guests' who may remain in the village for several years. At first sight, the guests would appear to be freeloaders, since in the short-term they do not return the favour. However, over the course of several years villages are disbanded, and reformed on new land. This means that former residents become guests in a new community and former guests may reclaim previously owned land. Dwyer and Minnegal (1992) hypothesised that in the long term the sharing of sago flour was reciprocated. However, the most convincing support for this hypothesis only emerged when the community they had been researching met with unusual circumstances (Dwyer and Minnegal 1997). Usually a village will dissolve within a few years, however, by 1995 this particular community had remained stable for nine years. Dwyer and Minnegal found that under these new circumstances cooperation between residents and guests was severely diminished. They conclude that (1997 p.89): "once the potential for reciprocation was lost the "sago game" broke down."

The advantages of food-sharing extend beyond the immediate nutritional benefits identified by Cashdan. Sahlins (1972) points out that food sharing is a way of establishing and maintaining good social relationships. Equally, not sharing food may damage previously good relationships. He notes (1972 p.215):

"Food dealings are a delicate barometer, a ritual statement as it were, of social relations, and food is thus employed instrumentally as a starting, a sustaining, or a destroying mechanism of sociability."

Human cooperative relationships are multidimensional. Humans create a vast web of cooperative relationships, each of which supports the others. Failure to cooperate in one circumstance may lead to the breakdown of cooperation in many other circumstances. The models presented in the previous chapter (section 5.4) showed that the high temptation to cheat when resource quality is high can destroy what

would otherwise have been a cooperative relationship. In humans it is very important to resist the short-term temptation to cheat, in order to preserve longer-term cooperation. This point is emphasised by Palmer (1991) who studied information sharing among Maine lobstermen. The lobstermen sometimes exchange information regarding the location of good fishing sites. This information is clearly highly beneficial to the recipient, and is costly to the giver, since it will lead to a depletion the stock of fish available to him. Palmer found that while kin selection and reciprocal altruism explain some of the situations in which individuals either exchanged or withheld information, the rules of reciprocation were more strongly mediated by the costs of deceit. Palmer explains that the consequences of deceit may have severe effects on other aspects of an individual's social relationships, beyond the fishing context (1991 p.231):

“the consequences of secrecy and deceit may go far beyond the economic loss of future information exchanges..... Blatant lies and selfish secrecy, even if economically advantageous, are likely to be incompatible with the diplomacy needed in such social environments Southern Harbor lobstermen have a high percentage of competitors who are also friends and neighbours.”

Palmer provides us with the following example (1991 p.232):

“I have observed one lobsterman's brother helping another lobsterman's neighbour's son find a job, while another lobsterman repairs a different lobsterman's cousin's car. Such interactions may involve people beyond the local community, and may influence interactions of individuals who have never met either of the two lobstermen.”

In many instances humans cooperate because they understand that not doing so could lead to the break-down of other cooperative relationships. By foregoing the short-term benefits of cheating, it is possible to harvest the long term benefits of cooperation. The pervasiveness of cooperation in human societies is quite striking. In fact, sometimes humans are almost “irrationally” cooperative. In experimental games in which there is no chance that an individual who chooses the highest paying, deceptive strategy will be discovered, human subjects are still likely to cooperate (Caporael *et al.* 1989; Frank 1988; Frank *et al.* 1993). For example, Frank (1988)

conducted an experiment in which wallets containing money and personal papers were left lying around in the street for passers-by to find. People who found the wallets could keep the money without being found out. None the less, 45% of the wallets were returned by post.

The pervasive cooperation that is so typical of human societies is a puzzle. Although cooperation is a good strategy in the long term, in the short term it requires foregoing immediate benefits. Ainslie (1975) has shown that in many instances people are more attracted to short term benefits that are certain, compared with long term benefits that may be uncertain. This is because of a factor known as the 'matching law' (Ainslie 1975). Ainslie conducted the following two experiments. In the first, subjects were offered either \$100 in 28 days time, or \$120 in 31 days times. Most subjects chose the second option. In the second experiment, subjects were offered either \$100 today, or \$120 in three days time. This time, even though the amounts and days apart were the same as in the first experiment, most subjects chose the immediate pay-off of \$100. The subjects were obeying the matching law, whereby the attractiveness of the reward is inversely related to its delay. The matching law explains why, for instance, dieting or giving up smoking is so difficult. The short term rewards of a chocolate bar or cigarette often appear more attractive than the long term benefits of resistance. According to the matching law, people will always be attracted by the short term benefits of cheating, compared with the long term, less certain, benefits of cooperation. How, then, do humans manage to maintain cooperative relationships?

Humans vary in cooperative and deceptive tendencies. Tests for 'Machiavellian' intelligence are designed to reveal how manipulative people are (Wilson *et al.* 1996, 1998)¹. People who score highly on these tests (high-Machs), are more deceptive in nature compared with those who gain low scores (low-Machs). Wilson *et al.* (1996) argue that high-Machs use more deceptive strategies in social situations, and compare them to defectors in the Prisoner's Dilemma game. Low-Mach individuals tend to use nicer social strategies, following a rule similar to TIT-

¹ These tests assume that Machiavellian intelligence refers only to those aspects of intelligence that are involved with manipulation or deception. However, in some instances Machiavellian intelligence may also refer to cooperative aspects of cognition (see, for example, Byrne and Whiten 1988 and Whiten and Byrne 1997).

FOR-TAT. These different strategies were demonstrated by Harrel and Hartnagel (1976) who conducted an experiment in which subjects were given the opportunity to steal in the presence of a supervisor. The supervisor was portrayed as being either distrustful or trusting. The behaviour of people who were rated as high-Machs was unaffected by the disposition of the supervisor. The majority of high-Machs (more than 80%) stole from the supervisor in both situations. However, the behaviour of the low-Machs was very different depending on how trustful the supervisor was perceived to be. While the majority of low-Machs (more than 80%) stole from the distrustful supervisor, only 24% of them stole from the trusting supervisor. Wilson *et al.* comment that (1996 p.290):

“Low-Machs seem to be guided by a tit-for-tat strategy in which the distrustfulness of the supervisor is perceived as an act of defection which calls for overt retaliation.”

High-Machs, by contrast, will defect whenever there is an opportunity. Moreover, high-Machs are perceived by others as social charmers. High-Machs are judged to be more attractive and intelligent than other people, and perform well in bargaining and alliance-forming situations. Christie and Geis (1970 p.339) comment that:

“high Machs are preferred as partners, chosen and identified as leaders, judged as more persuasive, and appear to direct the tone and content of interaction – and usually the outcome.”

Because high-Machs are socially attractive, their manipulative tendencies may be difficult to identify, especially in the short term. Wilson *et al.* (1998) conducted an experiment that was designed to uncover the ‘real’ motivations of high-Machs that are usually well disguised. Subjects were asked to write fantasy stories and the main characters in these stories were then judged by other subjects. Wilson *et al.* report that low-Mach authors created characters that were trustworthy, cooperative and helpful. In sharp contrast, high-Mach authors created characters that were selfish, uncaring, judgmental, untrustworthy, aggressive, undependable and suspicious. Not surprisingly, most people felt that they would prefer a character created by a low-Mach, rather than a high-Mach author as a social partner.

The preceding discussion presents us with the following paradox. The matching law suggests that it is always more attractive to cheat in the short term than cooperate in the long term. Furthermore, human society contains people that are both socially attractive and manipulative (i.e. high-Machs) and are likely to exploit cooperators. But despite this, cooperation is pervasive throughout human societies. How then, do cooperators overcome the short-term temptation to defect? Furthermore, how do cooperators guard against exploitation? In the following discussion I argue that a whole range of cognitive mechanisms have evolved as scaffolding for cooperative strategies, these include: a) inhibition mechanisms; b) emotional constructs such as guilt, trust, anger and honour; c) cheat detection mechanisms; and d) social intelligence including theory of mind.

Humans appear to be able to inhibit cheating behaviours. That is, faced with a situation in which cheating is not only possible, but highly advantageous, many people will resist the temptation. Of course, this is not true of everyone, as we have already seen people vary in their tendency to be cooperative. But even high-Machs will commonly find themselves in situations in which it is advantageous to inhibit cheating. Deacon (1997) suggests that the prefrontal cortex is extremely important in inhibiting behavioural responses. The greatly expanded human prefrontal cortex stops us from literally doing the first thing that comes into our minds. Other animals have much smaller prefrontal cortex's for their body size, and are very poor at inhibiting behaviour responses. For example, Savage-Rumbaugh and Lewin (1994) discuss an experiment involving a language-trained bonobo, Kanzi, who had to choose between two piles of sweets, one of which was larger than the other. Whichever pile Kanzi chose was given to another bonobo. Kanzi himself was given the pile of sweets which he *did not* choose, and so it was to his advantage to choose the smaller pile. However, no matter how many times the test was repeated Kanzi always chose the larger pile. The look of disappointment on Kanzi's face when the larger pile was then given to the other animal indicates that Kanzi was not being altruistic! Rather, Kanzi was simply unable to inhibit his immediate attraction to the larger pile of sweets.

The greatly expanded human prefrontal cortex may be involved in inhibiting the desire to cheat in cooperative contexts. Interestingly, inhibition may also be involved in the development of language, symbolism (Deacon 1997) and sexual strategies (Bjorklund and Kipp 1996) although such a discussion is tangential to the

immediate concerns of this chapter. However, while Deacon (1997) stresses the importance of inhibition in helping us to ‘stop and think’ about our actions, it is not clear that inhibition alone would be enough to stimulate a cooperative response. According to the matching law, short-term considerations tend to outweigh long term benefits. Frank (1988) argues that cooperation is far more likely to be established if cheating bears short-term costs and cooperation short-term benefits. That is, humans need short-term incentives to cooperate. Frank argues that we have an emotional system which fulfils exactly this requirement. In simple terms, cooperation makes us feel good and deception makes us feel bad. Frank provides the following example (1988 p.53 his italics):

“Consider, for example, a person capable of strong guilt feelings. This person will not cheat even when it is in her material interests to do so. The reason is not that she fears getting caught but that she simply does not *want* to cheat. Here aversion to feelings of guilt effectively alters the payoffs she faces.”

The point is, that most people suffer from a guilty conscience if they deceive someone else. If cheating makes us feel bad, then this may be enough to ensure that in most instances we will refrain. On the other hand, giving gifts, returning a lost wallet, giving to charity and sharing a meal are all actions that make us feel good. Furthermore, these types of acts establish an individual’s reputation as a cooperator (Frank 1988 p.82):

“It is often prudent to refrain from cheating, as the tit-for-tat and reciprocal altruism theories have ably demonstrated. On such occasions, there will be advantage in being able to suppress the impulse to cheat. We can thus imagine a population in which people with consciences fare better than those without. The people who lack them would cheat less often if they could, but they simply have greater difficulty solving the self-control problem. People who have them, by contrast, are able to acquire good reputations and cooperate successfully with others of like disposition.”

If you are a cooperator, it is important to gain a reputation as such in order to attract other cooperators with whom to interact. In fact, Roberts (1998) describes a scenario in which individuals compete for cooperative partners by being altruistic. Roberts calls this ‘competitive altruism’ and describes altruism as a handicap (after

Zahavi 1977). The handicap principal provides an explanation for traits that are seemingly maladaptive, such as the peacock's tail. These traits indicate that the bearer of the trait is of such high quality that they can afford to send out very costly signals. By extension, an altruist who performs an act, such as giving blood, is sending out the signal "look at me: I am so willing to cooperate that I will even give my blood to a total stranger." It is important to understand that humans do not cooperate because they wish to establish a good reputation, or because they feel guilt if they cheat (Binmore 1990). Rather, because cooperation is a good strategy in situations like the Prisoner's Dilemma, the desire to establish a good reputation and guilt have evolved to ensure that this good strategy is executed.

Frank argues that a person who cooperates, even when it would pay them to be selfish and defect, unconsciously develops verbal and facial signals of their willingness to cooperate. For example, an individual who blushes or stammers when they think they have done something wrong sends a clear signal that they are conscientious. Thus, even if we have not observed a person cooperate or cheat, we may be able to judge their character by other means. Frank points out that there are numerous cues to another person's feelings (Frank 1988 p.8):

"Posture, the rate of respiration, the pitch and timbre of the voice, perspiration, facial muscle tone and expression, and movement of the eyes, are among the signals we can read. We quickly surmise, for example, that someone with clenched jaws and a purple face is enraged, even when we do not know what, exactly, may have triggered his anger. And we apparently know, even if we cannot articulate, how a forced smile differs from one that is heartfelt."

Humans appear to be very good at interpreting these signals. Frank *et al.* (1993) found that when human subjects are given half an hour to get to know each other, their ability to predict which people will defect and which will cooperate in the Prisoner's Dilemma is much better than would be expected by chance. The way we speak, our body language, our facial expressions and our behaviour signal our cooperative tendencies to others. But, by signalling their willingness to cooperate, altruists are very vulnerable. Selfish individuals will be easily able to identify cooperators and may exploit them. If these exploiters are able to mimic cooperators,

then it may be very difficult to avoid them. Therefore, cooperators must also have a defence system.

Exploiters are more likely to be found outside of a group, than within it. Individuals within a group interact with each other on a daily basis, and are able to assess each others cooperativeness by their behaviour. Because the chances of interacting again are high, cooperation is more likely to develop. In the first instance, therefore, we tend to expect individuals within our own group to be cooperative. On the other hand, Sahlins (1972) notes that reactions to strangers are often negative, and that altruistic relationships are unlikely to emerge. This is because it is easier to exploit a stranger who has not had the opportunity to witness past encounters and may not have the opportunity in the future to punish any misdemeanours (Dugatkin and Wilson 1991). This reasoning suggests that it is very important to recognise and cooperate with individuals from within your group. A feeling of group belonging, even on the most superficial grounds, substantially enhances cooperation in experimental games (Caporael *et al.* 1989). For example, Tajfel (1970; see also Tajfel and Billig 1974) randomly assigned subjects into two groups, on the pretext that they were divided on the basis of a task (e.g. whether they had over- or underestimated the numbers of dots in a display). Even though none of the subjects ever met each other, they still behaved preferentially towards other members of their own group. If group members are allowed to interact then cooperation increases even more. In experimental situations discussion between individuals can increase the incidence of cooperation to nearly 100%, even when there is no possibility of cheating being detected (Caporael *et al.* 1989).

Language itself may be a very interesting facilitator of cooperation. Dunbar (1993; see also Aiello and Dunbar 1993) argues that language in humans serves the same function as grooming does in primates, that is language is used to establish and maintain social relationships. The advantage of language, over grooming, is that it is much more efficient, since it is possible to talk to many people at one time and talk to more people over a period of time. Dunbar argues that language may have evolved first as a sort of 'vocal grooming' through which social cohesion could be maintained within large groups. Furthermore, dialects may help us to identify individuals with whom we wish to cooperate (Nettle and Dunbar 1997). Because dialects are difficult to fake, they provide a reliable indicator of social origin. Thus, even in large groups,

language and dialect make it possible to establish and maintain cooperative relationships.

By selectively interacting with group members it is possible to establish cooperative relationships within social groups. None the less, even within groups it is important for cooperators to be able to identify potential cheats. Tooby and Cosmides (1992; Cosmides 1989) believe that over the course of evolution the human mind has evolved mechanisms specifically for cheat detection. They show that while humans are very poor at solving abstract problems, they are very good at solving social problems particularly those that involve identifying cheats. Similarly, Mealey *et al.* (1996) found that people are better at remembering the faces of people they perceive to be potential cheats, compared with faces that are judged to be neutral or trustworthy.

Binmore (1990; see also Binmore *et al.* 1991) points out that in cooperative/competitive situations, it is important to be able to assess the strategies of others in order to determine which strategy is best for oneself. In order to do this, it is necessary to see the situation from the other person's view point. This requires theory of mind. In the previous section it was argued that apes may have some theory of mind abilities. The apes are capable of more elaborate deceptive tactics than monkeys, and Byrne and Whiten (1992) suggest that theory of mind plays an important role in this. While there is still considerable debate as to the extent to which apes have theory of mind, there is no doubt that most humans have theory of mind abilities that surpass those of both apes and monkeys (Dunbar 1996; Frith 1989; Happé 1994). Most humans acquire a theory of mind at around 3-4 years of age. Most adults regularly use this ability to see the world from another individual's point of view. Clearly, theory of mind could greatly enhance an individual's ability to assess the motivations of others. This would be useful for high-Machs who wish to deceive gullible low-Machs, and low-Machs who need to be able to identify and avoid exploitative individuals. Furthermore, theory of mind may play an important role in purely cooperative exchanges. For example, Davis notes that when exchanging gifts it is very important to assess the needs and desires of the other person and to provide a gift of appropriate value (1992 p.11):

“We expect that givers put themselves in our shoes, and they should try to calculate our utility. It is not a matter of calculating the true or objective value, but of imagining someone else’s evaluation: in jargon, it involves inter-subjectivity.”

In other words, providing gifts requires a theory of mind.

This discussion indicates that many different cognitive mechanisms have evolved to help humans deal with a complex social world. Emotions, inhibition mechanisms, language and dialects, predispositions towards members of one’s own group, cheat detection mechanisms and theory of mind may all be parts of human social intelligence. Some of these processes, such as theory of mind and inhibition, are biological characteristics that have been shaped by biological evolution. Other processes, such as in-group favoritism, the tendency to be manipulative, or feeling guilty following deception, may be more strongly controlled by the social environment. In most cases, it is likely that both evolutionary and social forces shape cooperative and competitive behaviours.

The point is, that evolution has armed our minds with the skills required to solve the problem of when to cooperate, and when to cheat. These skills may have evolved as an evolutionary arms race between high-Machs (who need to seek out gullible cooperators) and low-Machs (who need to seek out fellow cooperators while defending themselves against exploiters). Indeed Trivers (1971) suggests that the expansion of the human brain may have been the result of a cognitive arms race fuelled by the evolution of cooperation. But, as we have already seen, other primates live in a “complex social world”, and also have sophisticated social intelligence. Why, then, do human cooperative relationships require this extra cognitive support? Many of the elements that have contributed to the evolution of human cooperation have already been discussed. Hominid evolution occurred in an arid environment, in the context of increased dependency on animal based products and escalating female energetic costs. This research has shown that all of these factors have contributed to the evolution of cooperation in humans, and thus the evolution of human social intelligence. However, I believe that it was the evolution of cooperation between males and females in particular, that placed the greatest cognitive demands on our hominid ancestors. This reasons for this will become clear in the next section.

6.4 The Mental Battle of the Sexes

In the previous section it was shown that people differ in their cooperative and manipulative tendencies. Because of this, it was argued that the necessities of assessing the social strategies of others has driven many different aspects of human intelligence. If this is the case, it implies that there are features of the human social world that are more complex than the social worlds of other primates, including the chimpanzee. Dunbar (1993) argues that the greater complexity of human social lives is due to the large size of human social groups. Humans require a more advanced social intelligence simply to keep track of large numbers of different social relationships. However, many New World monkeys live in groups as large as, or larger than, those of humans and do not appear to require larger brains in order to keep track of other group members. More importantly, it is not clear why a greater quantity of social relationships would select for specific cognitive devices such as theory of mind. It seems more likely that different types of social relationships will impose different cognitive demands. For instance, the rules “always cooperate with sisters” or “always defect against strangers” may be very effective without requiring sophisticated mental processes. In contrast, the rule “only cooperate with non-relatives if they cooperated with you in the past over a resource of similar value” may require rather more sophisticated mental processes to employ successfully.

Which types of social relationships are the most cognitively demanding? Barber and Raffield (unpublished text, cited in Wilson *et al.* 1996) looked at different types of social relationships in order to assess how manipulative they tend to be. They found that female-female interactions were the least manipulative and that male-male interactions tended to be highly manipulative. Most interestingly, manipulative behaviour by both sexes was greatest during male-female interactions. This suggests that inter-sex interactions may be more cognitively demanding than same sex interactions. This section explores why this should be, and examines some of the mental mechanisms that may have evolved in order to support inter-sex relationships.

I have argued in this thesis that the sexual division of labour, whereby males provide animal food for females and their offspring, evolved as a response to high female energetic costs (compared with male energetic costs). That is, male

provisioning is a paternal care strategy. Hawkes (1990, 1991, 1993, see also Hawkes *et al.* 1991) argues that large animal hunting by males is not a paternal care strategy at all. Rather, it is a method of intra-sexual competition, whereby successful hunters hope to gain status and attract mates (Hawkes 1993 p.341):

“If those who provide public goods [large game] are listened to and watched more closely than others and favored as neighbors and associates, they have a larger, readier pool of potential allies and mates.”

Hawkes and her co-workers argue that among the Hadza the purpose of hunting is to attract females. This hypothesis is based on their analysis of Hadza foraging strategies. Among the Hadza, hunting large game benefits the group as a whole by providing more calories per head than other hunting or foraging strategies. But, at an individual level it is a risky strategy because the likelihood of catching an animal on any given day is very low. The problem is that big game hunting is unpredictable. Among the Hadza, big game hunting yields average returns of 4.9 kg per day. However, as a group, hunters killed or scavenged only one large animal every four days, and each individual hunter could only expect to take one large animal per month (Hawkes *et al.* 1991). Hawkes *et al.* argue that other foraging strategies such as pursuing small game or gathering plant products would provide more reliable returns than big game hunting. They point out that men appear to target resources that are widely shared (Hawkes 1991, 1993; Hawkes *et al.* 1991). For instance, while Ache men gain about 1,340 kcal/hr through hunting large animals and gathering honey only 13% of these food sources provision their own family (Hawkes 1993). In contrast, Ache women earn about 1,220 kcal/hr gathering plant foods but around 48% is consumed by their own family. Since men seem to pursue large game at the expense of more reliable foraging strategies, Hawkes *et al.* conclude that the purpose of hunting is to “show off” to potential mates.

Hill and Kaplan (1994) disagree with Hawkes and colleagues. They argue that among the Ache large game hunting is a very successful foraging strategy. Because meat is widely shared Ache men contribute greater than 85% of the total caloric intake of the group (Hill *et al.* 1987). Hill and Kaplan emphasise the nutritional benefits of large game hunting, and stress its importance as part of a network of reciprocal relationships which may also involve sexual access. In contrast, Hawkes

and her co-workers play down the nutritional benefits of big game hunting, stressing that meat is an unpredictable, and thus unreliable resource. However, it is difficult to understand why hunting would be a good way of “showing off” your value as a mate, if meat was not a resource desired by females. Riches explicitly links meat, prestige and mating success in Northwest Coast Indian societies, arguing (1984, p.240):

“hunters who claim prestige competitively advance their superiority as food suppliers. Since the provisioning of food – and especially the meat of ‘prestigious’ big game – reflects the complementarity of male and female tasks, the reason for which hunters promote prestige values is, I argue, to distinguish themselves as especially desirable partners in marriage.”

It seems clear that in some societies, such as those described by Hawkes and Riches, hunting is a good mate-attraction strategy. In these societies, males tend to devote little time to direct child care (e.g. holding, playing and carrying), concentrating their efforts on hunting (Hurtado and Hill 1992). Draper and Harpending (1988, see also Draper 1989) refer to these groups as ‘father absent’ and point out that among hunter-gatherers they are most common in rich, stable environments. Other hunter-gatherer groups which are ‘father present’ tend to be found in harsher, highly seasonal or less stable habitats. An example of a father-present society is the Hiwi of Southwestern Venezuela (Hurtado and Hill 1992). These people live in an environment in which food availability is low, and malnutrition is a considerable risk. Male provisioning is an important determinant of child mortality among the Hiwi, and during the poor season males provide around 90% of the food items consumed. Hiwi males participate in other aspects of child care, such as holding and monitoring, in addition to their provisioning activities. Other populations in which paternal investment appears to be high are the Iflaluk (Betzig and Turke 1992) and the Aka pygmies (Hewlett 1992).

Hurtado and Hill (1992) compared the social systems of the Hiwi and the Ache and concluded that both mating and paternal investment are important aspects of male reproductive strategies. Whether males choose to be show-offs (or Cads in Dawkins’ (1989) terminology) or provisioners (Dads) depends upon the socioecological context. If the opportunities for extra-pair matings are great, then it pays for males to invest more time and energy in attracting mates. On the other hand, under harsh environmental conditions male investment may be essential in order to

insure offspring survival. It is interesting to note, in this context, that the models presented in the previous chapter would also predict that paternal care is most likely in poorer and/or more seasonal habitats.

The literature on male mating strategies seems to suggest that each human group can be characterised by a single male strategy, whether Cad or Dad (see, for example Draper 1989; Draper and Harpending 1988; Hawkes 1990, 1991, 1993; Hawkes *et al.* 1991; Hewlett 1992; Hurtado and Hill 1992). However, it is likely that both Cads and Dads will be found within single populations. For instance, Bleige Bird and Bird (1997) have found the presence of both male strategies among the Merriam of the Torres Strait. A large part of the Merriam diet is made up of turtle meat, and turtle hunting is carried out all year round. During the turtle's feeding and mating season turtle hunting can be risky and expensive, involving (Bleige Bird and Bird 1997 p.54): "long travel times, high speed pursuits in motorised craft and dangerous hand-capture methods." Only a few, usually young, males participate in these hunts and the fruits of their labour are widely shared during feasts, rather than being used for household consumption. During the nesting season the energetic costs of hunting and the risks involved are low, since turtles are easy to find and capture. During this season the majority of the turtle meat is shared only with close neighbours for household consumption. Bleige Bird and Bird conclude that two different reproductive strategies are practised by the Merriam men, which are associated with age and marital status. Young, unmarried men engage in high-risk hunting from which they gain very little nutritional reward, but great social status through their generous distribution of the meat. Married men, on the other hand, concentrate on low risk hunting through which they can provide meat for their family and closest neighbours.

Males, therefore, appear to hunt for two rather different reasons: showing off (the Cad strategy) or provisioning (the Dad strategy). Some males may follow one or other strategy for the whole of their lives. Other males may switch strategies depending on age, status and opportunity. These two hunting strategies correspond with the two sexual strategies identified by Buss and Schmitt (1993, see also Buss 1989). Buss and Schmitt describe males as either short-term strategists, who pursue short-term relationships with the aim of mating with as many females as possible, or alternatively, as long term strategists who invest heavily in a single female with a view to long-term, exclusive mating access. Both long-term and short-term strategies have

costs and benefits (Buss and Schmitt 1993), and both strategies may be practised by a single male at different life stages.

In the previous section it was argued that the presence of low-Machs and high-Machs in the same population creates complex social conundrums. Similarly, the presence of two male strategies presents complex reproductive scenarios for both sexes (Buss 1989; Buss and Schmitt 1993). Male short-term strategists require the social skills to deceive females into believing they are willing to provide resources in the long-term. A female who mates with a short-term strategist faces high costs, since there will be little investment from the male and she may deter other potential long-term strategists. Thus, females require the skills necessary to identify and avoid male Cads. On the other hand, the ideal scenario for a female may be to mate with a short-term strategist (for his 'good genes') but to form a long-term relationship with a long-term strategist (for his investment). This in turn presents a problem for male long-term strategists who must avoid being cuckolded, a strong possibility in a large, mixed sex group. For both males and females it is important to be able to identify the real motivations of potential mates. Just as humans appear to have evolved psychological mechanisms for dealing with cooperative relationships in general, we also appear to have mental processes designed specifically for our interactions with members of the opposite sex.

Both males and females appear to have evolved mate preferences which reflect sex differences in mating strategies. Buss (1989) in a study spanning 37 different cultures, found that females consistently prefer males who possess traits associated with high resource acquisition potential. That is, females seek those males who will best be able to invest in themselves and their offspring. Males, on the other hand, tend to seek females who possess attributes, such as youth, that signal high fertility. However, Buss and Schmitt (1993) found that when males were divided into short-term and long-term strategists there were some telling differences. Short-term strategists rated physical attractiveness as a more desirable trait in a mate than long-term strategists did. Furthermore, short-term strategists rated previous sexual experience as a positive trait. In contrast, long term strategists rated commitment, faithfulness and sexual loyalty as very important traits in potential partners.

The deceptive tactics employed during courtship appear to have evolved to exploit the sexual strategies of others. Males attempt to persuade females of their

resource acquisition potential, while females seek to enhance features that indicate fertility. Tooke and Camire (1991) found that in inter-sexual interactions male deceptive tactics include feigned commitment, sincerity, trust and resource acquisition ability. Female deceptive tactics focus on physical appearance, particularly those aspects linked to youth. Tooke and Camire describe female deception as passive, in contrast to the active attempts at deception performed by males. This is not to imply that all male reproductive strategies involve deception. It is to the advantage of males who wish to enter into long term partnerships to advertise their intentions honestly. Hirsch and Paul (1996a,b) asked male subjects to rate different male courtship behaviours as either honest or deceitful and as pursuing a long-term or a short term mate. Strategies used to pursue long-term relationships were judged to be honest. These included interacting with friends and family on dates, talking about plans and goals, discussing children and wanting a friendship before embarking on a sexual relationship. Particularly important was the amount of time, energy and money invested in the relationship. Hirsch and Paul argue that high investment is an honest signal of a man's commitment to the relationship. In contrast, behaviours attributed to short term strategists were judged to be manipulative, exploitative and threatening.

Hirsch and Paul (1996b) point out that when males are pursuing a long-term strategy then the interests of males and females are congruent. However, when males pursue a short-term strategy, the interests of males and females are likely to be diametrically opposed. Thus, it is particularly important for females to be able to detect deception in males. Tooke and Camire suggest that over the course of evolution male deception tactics and female detection abilities have co-evolved (1991 p.361):

“As deceptive self-presentation by males in ancestral environments became a more and more successful strategy for obtaining copulations, it is reasonable to assume that it was countered by an increase in the ability of females to detect increasingly more subtle verbal and non-verbal cues correlated with male deception.”

While female success at detecting the true intentions of males is mixed (Tooke and Camire 1991), several lines of evidence suggest strong selection for detection mechanisms in females. Females are consistently better than males at picking up on non-verbal cues associated with deception (Tooke and Camire 1991). Females are

also better than males at verbal tasks (Kimura 1993). In the face recognition tests, discussed in the previous section, Mealey *et al.* (1996) found that females were particularly good at remembering the faces of low-status threatening males and high-status trustworthy males. Females in this experiment may be picking out males that they perceive to be short-term or long-term strategists. Overall, these observations suggest that females may be better than males at using verbal and non-verbal behaviour to ascertain motivations.

Tooke and Camire (1991) suggest that females may have better theory of mind abilities than males. They assert that the ability to accurately appraise another person's intentions may be particularly important to females during mixed sex interactions. While there is no clear evidence that females do have superior theory of mind ability, females are more likely than males to take another person's view during interactions (Tooke and Camire 1991). However, theory of mind would clearly also be advantageous to males during inter-sexual interactions. Male Cads need to be able to identify gullible females, while Dads need to be able to assess the potential fertility and faithfulness of prospective mates. At the bottom line, the consequences of failing to accurately determine the intentions of a prospective mate could be dire for long-term strategists of both sexes: Male Dads could end up investing in another male's offspring; females who mate with Cads could be stranded with minimal investment from the male and with diminished prospects of attracting a long-term mate. It would seem difficult to underestimate the usefulness of theory of mind when choosing a mate.

In conclusion, there is considerable variation in the sexual strategies used by males and females both between and within populations. Male hunting strategies may serve two rather different purposes: provisioning or mate-competition. Similarly, male mating strategies may be categorised as seeking 'quality' or 'quantity'. When mixed sexual strategies are present within a population, it is very important for individuals to be able to identify the true intentions of others. This is especially true when pair-bonding occurs within groups containing many other adults of both sexes, as it does in humans. Avoiding mate desertion and ensuring paternity certainty are considerable problems for females and males respectively. For these reasons, interactions between males and females may be the most cognitively challenging of all. Failure to successfully manage these relationships may have more disastrous consequences in

terms of reproductive success, than failure in relationships with individuals of the same sex. I proposed earlier that male provisioning would have become an important aspect of human social organisation between 500,000 and 100,000 years ago. If this is true, then the ‘mental battle of the sexes’ would also have taken place at this time. As brain size began to increase, and the energetic costs of reproduction for females increased, then so began the co-evolution of mate attraction strategies, deceptive strategies, detection techniques and theory of mind. These abilities in themselves may have also selected for increasing brain size creating a feedback loop between these different processes.

6.5 Concluding Remarks

This thesis has demonstrated the usefulness of game theory in investigating the evolution of social groups in humans and other animals. It has also shown the importance of recognising that individuals differ in their motivations due to differences in characteristics such as age, sex and status. It is these differences that create the complex behaviours that we see in the living world. This research has focused on just one of these differences: sex. It has shown that we should expect males and females to differ in their cooperative and competitive strategies, both with their own sex and in their interactions with the opposite sex. This is because the energetic cost of producing offspring differs for males and females. It has also been shown that the evolution of paternal care can be understood as part of this cooperative framework. That is, when the energetic cost of reproduction for the female greatly exceeds that for the male, then male care giving may evolve.

In seeking to understand the evolution of any animal society, it is vital to study male and female anatomy, biology, behaviour and cognition not as individual entities but in terms of how they relate to each other. This research has shown that this approach can be constructive in studying the evolution of hominid social groups. In the transition from the australopithecines to early *Homo* there were likely to have been profound changes in hominid social structure due to changes in the relationship between male and female energetic costs of reproduction. Female energetic costs are predicted to have increased, compared with male energetic costs, due to changes in body size dimorphism, brain size and diet. To compensate for these elevated female costs, it is proposed that at this time there was an increase in female cooperation. An increase in male cooperation is likely to have occurred between 500,000 to 100,000 years ago due to further increases in female energetic costs related to an exponential increase in brain size. This suggests that the social groups of archaic *Homo sapiens* involved male care giving, the formation of pair bonds and the sexual division of labour. In this final chapter it has been proposed that this new social structure would have presented new cognitive challenges to both sexes. Future research in this area should yield interesting results.

APPENDICES

The following appendices provide the computer codes for the models used in this thesis. All the programs were written in C, and compiled using the Borland Turbo C++ compiler. An outline is given for each program in English. These outlines are not comprehensive, but serve as a basic guide to the programs.

Each program has several parts: (1) A main program which manages the flow of the code; (2) a definitions file (e.g. dilemdef.h) which defines basic structures and variables; (3) one or more calls files (e.g. dilcalls.h) which activates all the sub-routines.

Appendix 1: Control Program

A1.1. Basic Outline

start

user sets cost of reproduction (RC)

set *run counter* = 0

While *run counter* < 30 do this:

{

Generate 650 agents at random, where each agent has

- 1 strategy string

- score = 0

set *generation counter* = 0

set *offspring counter* = 0

While *generation counter* < 20,000 do this:

{

while *offspring counter* < 650 do this:

{

1. Pick two agents at random

2. These agents play 100 games of the Prisoner's Dilemma according to their strategy strings. Each game is scored according to the Prisoner's Dilemma pay-off matrix. Points gained are added to each agent's score

3. Pick two new agents at random

4. If each agent has enough points to reproduce (RC) they reproduce by crossover and mutation of their strategy strings

Two new offspring are added to a separate offspring

RC is subtracted from each player's score

The *offspring counter* is increased by +2

}

Replace adult population with offspring

Set *offspring counter* = 0

Set all scores = 0

Generation counter is increased by +1

}

Collate and print results

run counter is increased by +1

}

End

A1.2. Main program

```

#include <stdio.h>
#include <stdlib.h>
#include <time.h>
#include "dildef1.h"
#include "dilcall1.h"

int size; /* population size (= 650) */

main(int argc, char *argv[])
{
    size = atoi(argv[1]);

    Agents *adults = (Agents *) calloc(size, sizeof(Agents)); /*create arrays of agents & offspring */
    Agents *offspring = (Agents *) calloc(size, sizeof(Agents));
    Sumstrat *stratarray = (Sumstrat *) calloc(RUN, sizeof(Sumstrat));
    Avgscore *avgarray = (Avgscore *) calloc(RUN, sizeof(Avgscore)); /*to calculate results
*/

    check_arrays(adults, offspring, stratarray, avgarray); /* check memory space */

    int rescount = 0; /* results conter */

    int gen = 1; /* generation counter */
    int reprocost; /* cost of reproduction, RC */
    int end; /* no. generations to run (= 20000) */
    int i,j; /* general counters */
    int offno = 0; /* offspring counter */
    int run = 0; /* run number */
    int a = 0; /* to keep track of results */
    int lasta = 0;

    float average = 0;
    int avgcount = 0;

    float stratsummary[STRATSIZE]; /* records strategies used */

    srand(time(NULL)); /* seed random number generator*/

    user(&reprocost, &end); /* set parameters */

    init_files(); /* initialise results files */

    while (run < RUN) /* RUN = 30 */
    {
        printf("\nRUN %d: ", run); /* start of a new run */
        init_adults(adults, size); /* generate adult strategies at random*/

        while (gen <= end) /* start of new generation */
        {
            while (offno < size)
            {
                while (offno < size)
                {
                    i = 1+ (rand()%(size-1)); /* pick pairs at random to interact */
                    do{
                        j = 1+ (rand()%(size-1));
                    } while (j==i);

                    average += dilemma(adults, i, j); /* play Prisoner's Dilemma
*/
                }
            }
        }
    }
}

```

```

    avgcount +=2;                                     /* and calculate results */

    i = 1+ (rand()%(size-1));                          /* pick pairs at random to reproduce */

    do{
        j = 1+ (rand()%(size-1));
    } while (j==i);

    /* Have the agents gained enough points to reproduce? */
    if ((adults[i].score >= reprocost) && (adults[j].score >= reprocost))
    {
        reproduction(adults, i, j, offspring, offno);    /* reproduction */
        adults[i].score -= reprocost;                    /* Players score decreased by RC
        adults[j].score -= reprocost;
        offno += 2;                                       /* increase offspring counter */
    }
}

/* record results every ten generations */
if ((gen ==1) || (gen%50 == 0))
{
    avgarray[run].avg[a] = (float) average/avgcount;
    a++;
    countmoves(adults, stratarray, size, run);
    rescount++;
}

if (gen%1000 == 0)
    printf("GEN %d, ", gen);

    average= 0;                                       /* reset values */
    avgcount = 0;
    swap(adults, offspring, size);
    offno = 0;
    gen++;
}

/* end of run, print results */

for (i=0; i < STRATSIZE; i++)
{
    stratarray[run].strat[i] = (float) stratarray[run].strat[i] / rescount;
}
printstratsum(stratarray, run);

run++;                                               /* reset values */
rescount = 0;
lasta = a;
a = 0;
gen = 1;
}

printavg(avgarray, run, lasta);
return (0);
}

```

A1.3. Definitions [dildef1.h]

```
#define STRATSIZE 22          /* Length of Strategy string (21 +1) */
#define LASTROUND 100       /* Number of rounds of PD */
#define RUN 30              /* Number of runs

struct agents {
    int strategy[STRATSIZE]; /* for playing Pris. dilem. */
    int score;               /* tally of score */
};
typedef struct agents Agents;

struct avgscore{            /* For results */
    float avg[500];
};
typedef struct avgscore Avgscore;

struct sumstrat{           /* For results */
    long float strat[STRATSIZE];
};
typedef struct sumstrat Sumstrat;
```

A1.4. Functions [dilcall1.h]

```
/* Function prototypes */
```

```
void check_arrays(Agents *A, Agents *off, Sumstrat *strat, Avgscore *avg);
void init_adults(Agents *adults, int size);
void user(int *cost, int *last);
float dilemma(Agents *player, int one, int two);
int score(int p1, int p2);
void reproduction (Agents *parents, int male, int female, Agents *child, int childno);
void swap(Agents *parents, Agents *children, int size);
void countmoves(Agents *chromosome, Sumstrat *sum, int size, int run);
void printavg(Avgscore *adults, int lastrun, int gencount);
void printstratsum(Sumstrat *strat, int run);
void init_files(void);
```

```
// check_arrays: Check that there is enough memory for the arrays
```

```
void check_arrays(Agents *A, Agents *off, Sumstrat *strat, Avgscore *avg)
{
    if (A == NULL){
        printf("Error allocating memory for adults\n");
        exit(1);
    }

    if (off == NULL){
        printf("Error allocating memory for offspring\n");
        exit(1);
    }

    if (strat == NULL){
        printf("Error allocating memory for strategy array\n");
        exit(1);
    }

    if (avg == NULL){
        printf("Error allocating memory for average array\n");
        exit(1);
    }
}
```

```
/* init_adults: initialise adults */
```

```
void init_adults(Agents *adults, int size)
{
    int i, j;

    for(i=1; i < size; i++)
    {
        for (j=1; j < STRATSIZE; j++)           /*randomly fill array with 1s and 0s*/
        {
            adults[i].strategy[j] = rand()%2;
        }

        adults[i].score = 0;                    /* initial score = 0 */
    }
}
```

```
/* init_files: open results files */
```

```
void init_files(void)
{
    FILE *avgptr;                               /* files to store results */
```

```

FILE *stratptr;

stratptr = fopen("sumstrat.dat","w");
avgptr = fopen("average.dat", "w");
fclose(stratptr);
fclose(avgptr);
}

/* user: asks user for variables i.e. cost of reproduction, number of generations */
void user( int *cost, int *last)
{
    printf("\nEXPERIMENT ONE\n");
    printf("\n\nPlease enter the cost of reproduction:\n");
    scanf("%d", cost);
    printf("\nHow many generations would you like to run?\n");
    scanf("%d", last);
}

/* dilemma: playing the Prisoner's Dilemma */
/* Note: 'round two' and 'score ref' are game templates which indicate to the players which
position on their strategy array they should refer to for their next move. eg. In the score ref
array: position 1 = mymove; position 2 = my opponents move; position3 = my move on
previous round; position 4 = opponents move in previous round. 1 = cooperation, 0 =
defection . Position 5 tells me where to look on my strategy array for my next move, position
6 tells my opponent where to look on its array.*/

float dilemma(Agents *player, int one, int two)
{
    int round = 1;
    int moves[4] = {0}; /* records last two moves of each agent */
    int roundtwo[4][4] = {{1,0,2,3},{0,1,3,2},{1,1,4,4},{0,0,5,5}};
    int scoreref[16][6] = {{1,1,1,1,6,6}, {0,1,1,1,7,8}, {1,0,1,1,8,7}, {1,1,0,1,9,10},
                          {1,1,1,0,10,9},{1,1,0,0,11,11}, {0,0,1,1,12,12}, {1,0,0,1,13,14},
                          {0,1,1,0,14,13}, {0,1,0,1,15,16},{1,0,1,0,16,15}, {1,0,0,0,17,18},
                          {0,1,0,0,18,17}, {0,0,1,0,19,20}, {0,0,0,1,20,19}, {0,0,0,0,21,21}};

    int i;

    int initscore1 = player[one].score; /* initial scores */
    int initscore2 = player[two].score;

    float addavg = 0; /* for results */

    /* take first turn */
    /* agents refer to first position in their strategy array */

    if (round == 1)
    {
        moves[0] = player[one].strategy[1];
        moves[1] = player[two].strategy[1];
        player[one].score += score(moves[0], moves[1]); /* Add points won to scores */
        player[two].score += score(moves[1], moves[0]);
        moves[2] = moves[0];
        moves[3] = moves[1];
        round++;
    }
}

```

```

/* Round 2 */
/* Previous moves are compared to 'roundtwo' reference array to determine behaviour
in this round */

if (round == 2)
{
    for(i=0; i <=3; i++)
    {
        if((roundtwo[i][0] == moves[2]) && (roundtwo[i][1] == moves[3]))
        {
            moves[0] = player[one].strategy[(roundtwo[i][2])];
            moves[1] = player[two].strategy[(roundtwo[i][3])];
            break;
        }
    }

    player[one].score += score(moves[0], moves[1]);    /* Add points won to scores */
    player[two].score += score(moves[1], moves[0]);
    round++;
}

/* All other rounds */
/* The moves made by each player in the last two rounds are compared to
the scoreref reference array to determine behaviour in the current round*/

for (round = 3; round <= LASTROUND; round++)
{
    for (i=0; i <=15; i++)
    {
        if((scoreref[i][0] == moves[0]) && (scoreref[i][1] == moves[1]) &&
            (scoreref[i][2] == moves[2]) && (scoreref[i][3] == moves[3]))
        {
            moves[2] = moves[0];
            moves[3] = moves[1];
            moves[0] = player[one].strategy[(scoreref[i][4])];
            moves[1] = player[two].strategy[(scoreref[i][5])];
            break;
        }
    }

    player[one].score += score(moves[0], moves[1]);
    player[two].score += score(moves[1], moves[0]);
}

/* calculate average score per player per game, and return value to main program */
addavg = ((float)(player[one].score - initscore1)/LASTROUND);
addavg +=((float)(player[two].score - initscore2)/LASTROUND);

return addavg;
}

/* score: calculate scores */
int score(int p1, int p2)
{
    int addscore = 0;

    if ((p1 == 1) && (p2 == 1))    /* both cooperate */
    {
        addscore = 3;
    }
}

```

```

}

if ((p1 == 1) && (p2 == 0))          /* P1 cooperates, opponent does not.
                                     P1 receives suckers payoff */
{
    addscore = 0;      /*0*/
}

if ((p1 == 0) && (p2 == 1))          /* P1 defects, its opponent  coops */
{
    addscore = 5;      /*5*/
}

if ((p1 == 0) && (p2 == 0))          /* both defect */
{
    addscore = 1;
}

return (addscore);
}

/* Reproduction */
/* Two agents cross their strategy codes to create two new offspring.*/
/* There is a small chance of mutation */

void reproduction (Agents *parents, int male, int female, Agents *child, int childno)
{
    int crossno = 0;
    int c,i;
    int mutate;

    crossno = rand()%STRATSIZE;          /* randomly select crossover point */
    for(c=1; c <=crossno; c++)
    {
        child[childno].strategy[c] = parents[male].strategy[c];          /* crossover */
        child[childno+1].strategy[c] = parents[female].strategy[c];
    }

    for(c= crossno+1; c < STRATSIZE; c++)
    {
        child[childno].strategy[c] = parents[female].strategy[c];
        child[childno+1].strategy[c] = parents[male].strategy[c];
    }

    if (rand()%10000 <= 2)              /* mutation?? */
    {
        mutate = (1+ rand()%21);
        if (child[childno].strategy[mutate] == 0)
            { child[childno].strategy[mutate] = 1; }
        else
            { child[childno].strategy[mutate] = 0; }
    }

    if (rand()%10000 <= 2)
    {
        mutate = (1+ rand()%21);
        if (child[childno+1].strategy[mutate] == 0)

```

```

    { child[childno+1].strategy[mutate] = 1; }
  else
    { child[childno+1].strategy[mutate] = 0; }
}
}

```

/* Swap: Replace parent generation with offspring */
/* When enough offspring have been created to replace the parent generation,
then offspring become the new adults */

```

void swap(Agents *parents, Agents *children, int size)
{
  int i,j;

  for(i=1; i< size; i++)
  {
    for(j=1; j < STRATSIZE; j++)
    {
      parents[i].strategy[j] = children[i].strategy[j];
    }
    parents[i].score = 0;
  }
}

```

/* Countmoves: Calculates the percentage of agents cooperating for each gene in the
strategy array */

```

void countmoves(Agents *chromosome, Sumstrat *sum, int size, int run)
{
  float onecount = 0;
  int i,j;

  for(i=0; i < STRATSIZE; i++)
  {
    for(j = 0; j < size; j++)
    {
      if(chromosome[j].strategy[i] == 1)
      { onecount++;}
    }
    onecount = ((onecount/size)*100);
    sum[run].strat[i] += onecount;
    onecount = 0;
  }
}

```

/* Printavg: Records the average scores in results files */

```

void printavg(Avgscore *adults, int lastrun, int gencount)
{
  FILE *avgptr;

  int i=0;
  int run = 0;

  if((avgptr = fopen("average.dat", "a")) == NULL)
    printf("the average male file cannot be opened\n");
  else

```

```
for(i=0; i < gencount; i++)
{
    for(run=0; run < lastrun; run++)
        fprintf(avgptr, " %.2f,", adults[run].avg[i]);
    fprintf(avgptr, "\n");
}
```

```
fclose(avgptr);
}
```

```
/* Printstratsum: Records the %cooperate alleles at each locus on the strategy string  
*/
```

```
void printstratsum(Sumstrat *strat, int run)
{
    FILE *stratptr;

    int i;

    if((stratptr = fopen("sumstrat.dat", "a")) == NULL)
        printf("file cannot be opened");
    else
    {
        for (i=0; i < STRATSIZE; i++)
            fprintf(stratptr, " %.2f,", strat[run].strat[i]);
    }
    fprintf(stratptr, "\n");

    fclose(stratptr);
}
```

Appendix 2: Model 1 (The Prisoner's Dilemma in a Mixed Sex Environment)

A2.1. Basic Outline

start

user sets cost of reproduction for males (MRC) and females (FRC)

set *run counter* = 0

While *run counter* < 30 do this:

{

Generate 650 agents at random, where each agent has

- sex (M/F)

- 4 strategy strings

- score = 0

set *generation counter* = 0

set *offspring counter* = 0

While *generation counter* < 20,000 do this:

{

while *offspring counter* < 650 do this:

{

1. Pick two agents at random

2. These agents play 100 games of the Prisoner's Dilemma according to their strategy strings. The strategy strings used depend on the sex of each player. Each game is scored according to the Prisoner's Dilemma pay-off matrix. Points gained are added to the each agent's score

3. Pick two new agents at random

4. If the agents are of opposite sex, and each agent has enough points to reproduce (FRC or MRC) they reproduce by crossover and mutation of their strategy strings

Two new offspring are added to a separate offspring
FRC is subtracted from the female's score, and MRC is subtracted from the male's score

The *offspring counter* is increased by +2

}

Replace adult population with offspring

Set *offspring counter* = 0

Set all scores = 0

Generation counter is increased by +1

}

Collate and print results

run counter is increased by +1

}

End

A2.2. Main program

```

#include <stdio.h>
#include <stdlib.h>
#include <time.h>
#include "dildef2.h"
#include "dilcal2.h"

int size;

main(int argc, char *argv[])
{
    size = atoi(argv[1]);                // reads size from command line

    int rcmale, rcfemale;                // costs of reproduction, set by user
    int end;                              // no. generations to run (= 20,000)
    int i,j;
    user(&rcmale, &rcfemale, &end);      // user sets parameters
    int run = 0;

    // Define variables for adults, offspring and results. 'Agents' are the basic type, and each
    // agent has four strategy strings corresponding to the four interaction types 1: male-male
    // 2: male-female interactions, 3: female-female, 4: female-male. The results arrays
    record
    // strategies and average scores per game.

    Agents *adults = (Agents *) calloc(size, sizeof(Agents));
    Agents *offspring = (Agents *) calloc(size, sizeof(Agents));
    Strategy *malemale = (Strategy *) calloc(size, sizeof(Strategy));
    Strategy *offmalemale = (Strategy *) calloc(size, sizeof(Strategy));
    Strategy *malefem = (Strategy *) calloc(size, sizeof(Strategy));
    Strategy *offmalefem = (Strategy *) calloc(size, sizeof(Strategy));
    Strategy *femfem = (Strategy *) calloc(size, sizeof(Strategy));
    Strategy *offfemfem = (Strategy *) calloc(size, sizeof(Strategy));
    Strategy *femmale = (Strategy *) calloc(size, sizeof(Strategy));
    Strategy *offfemmale = (Strategy *) calloc(size, sizeof(Strategy));
    Sumstrat *stratmm = (Sumstrat *) calloc(RUN, sizeof(Sumstrat));
    Sumstrat *stratmf = (Sumstrat *) calloc(RUN, sizeof(Sumstrat));
    Sumstrat *stratff = (Sumstrat *) calloc(RUN, sizeof(Sumstrat));
    Sumstrat *stratfm = (Sumstrat *) calloc(RUN, sizeof(Sumstrat));
    Avgscore *avgmm = (Avgscore *) calloc(RUN, sizeof(Avgscore));
    Avgscore *avgmf = (Avgscore *) calloc(RUN, sizeof(Avgscore));
    Avgscore *avgff = (Avgscore *) calloc(RUN, sizeof(Avgscore));
    Avgscore *avgfm = (Avgscore *) calloc(RUN, sizeof(Avgscore));
    Avgscore *males = (Avgscore *) calloc(RUN, sizeof(Avgscore));
    Avgscore *females = (Avgscore *) calloc(RUN, sizeof(Avgscore));

    check_arrays(adults, malemale, offmalemale, malefem, offmalefem, // check memory space
        avgmm, avgmf, males, stratmm, stratmf);

    check_arrays(offspring, femfem, offfemfem, femmale, offfemmale,
        avgff, avgfm, females, stratff, stratfm);

    int gen = 1;                          // generation counter
    int offno = 0;
    int reproflag = 0;                     // reproduce when set to 1
    int rescount = 0;
    int a = 0;
    int lasta;

```

```

float avgarray[6] = {0};
mm    int avgcount[6] = {0};
init_files();

srand(time(NULL));

while (run < RUN)
{
    printf("\nRUN %d..... ", run);
    init_adults(adults, size);
    init_strategies(malemale, malefem, femfem, femmale, size);

    while (gen <= end)
    {
        while (offno < size)
        {
            i = rand()%size;
            do{
                j = rand()%size;
            } while (j==i);

            prisdilem(adults, malemale, malefem, femfem, femmale, i,j, avgarray,
                    avgcount);

            i = rand()%size;
            do{
                j = rand()%size;
            } while (j==i);

            // test if different sex, and have enough points, if 'yes' then reproflag = 1
            // reproduction involves crossover and mutation of all 4 strategy strings

            reproflag = repro_test(adults,i,j, rcmale, rcfemale);
            if (reproflag == 1)
            {
                reproduction(malemale, offmalemale, i, j, offno);
                reproduction(malefem, offmalefem, i, j, offno);
                reproduction(femfem, offfemfem, i, j, offno);
                reproduction(femmale, offfemmale, i, j, offno);
                reproflag = 0;
                offno += 2;
            }
        }

        if ((gen ==1) || (gen%40 == 0))
        {
            for(i=0; i < 6; i++)
            {
                avgarray[i] = (float) avgarray[i]/avgcount[i];
            }
            males[run].avg[a] = avgarray[0];
            females[run].avg[a] = avgarray[1];
            avgmm[run].avg[a] = avgarray[2];
            avgmf[run].avg[a] = avgarray[3];
            avgff[run].avg[a] = avgarray[4];
            avgfm[run].avg[a] = avgarray[5];
        }
    }
}

```

```

    a++;

    countmoves(malemale, stratmm, size, run);           // examine strategies
    countmoves(malefem, stratmf, size, run);
    countmoves(femfem, stratff, size, run);
    countmoves(femmale, stratfm, size, run);
    rescount++;
}

if (gen%100 == 0)
{
    printf("Gen%d, ", gen);
}

gen++;
swap(malemale, offmalemale, size);                   // offspring become new generation
swap(malefem, offmalefem, size);
swap(femfem, offfemfem, size);
swap(femmale, offfemmale, size);
init_newgen(adults, size);
offno = 0;

for (i=0; i < 6; i++)
{
    avgarray[i] = 0;
    avgcount[i] = 0;
}
}

// calculate % alleles at each locus over entire simulation
for(i=0; i < STRATSIZE; i++)
{
    stratmm[run].strat[i] = (float) stratmm[run].strat[i] / rescount;
    stratmf[run].strat[i] = (float) stratmf[run].strat[i] / rescount;
    stratff[run].strat[i] = (float) stratff[run].strat[i] / rescount;
    stratfm[run].strat[i] = (float) stratfm[run].strat[i] / rescount;
}

printstratsum(stratmm, stratmf, stratff, stratfm, run); // print strategies

run++;                                               // reset variables
rescount = 0;
lasta = a;
a = 0;
gen = 1;
}

// all 30 runs complete
// print averages
printavg(males, females, avgmm, avgmf, avgff, avgfm, run, lasta);

return (0);
}

```

A2.3. Definitions [dildef2.h]

```
#define STRATSIZE 21
#define LASTROUND 100 // 100 rounds of prisoners dilemma per game
#define RUN 30 // number of runs

struct agents{
    int score;
    int sex; // 0 = male, 1 = female
};
typedef struct agents Agents;

struct strategy{
    int strat[STRATSIZE];
};
typedef struct strategy Strategy;

struct avgscore{
    float avg[600];
};
typedef struct avgscore Avgscore;

struct sumstrat{
    long float strat[STRATSIZE];
};
typedef struct sumstrat Sumstrat;
```

A2.4. Functions [dilcal2.h]

```

void check_arrays(Agents *A, Strategy *S1, Strategy *S2, Strategy *S3, Strategy *S4, avgscore
    *AS1, Avgscore *AS2, Avgscore *AS3, Sumstrat *SS1, Sumstrat *SS2);
void user(int *mcost, int *fcost, int *last);
void init_adults(Agents *players, int popsize);
void init_newgen(Agents *players, int popsize);
void init_strategies(Strategy *boyboy, Strategy *boygirl, Strategy *girlgirl, Strategy *girlboy,
    int popsize);
void prisdilem(Agents *adults, Strategy *malemale, Strategy *malefem, Strategy *femfem,
    Strategy *femmale, int i, int j, float average[], int avgcount[]);
float homodilem(Agents *adults, Strategy *player, int one, int two);
void heterodilem(Agents *adults, Strategy *player1, Strategy *player2, int one, int two, float
    average[]);
int score(int p1, int p2);
int repro_test(Agents *adults, int p1, int p2, int malecost, int femcost);
void reproduction(Strategy *chromosome, Strategy *child, int p1, int p2, int childno);
void swap(Strategy *parents, Strategy *children, int size);
void countmoves(Strategy *chromosome, Sumstrat *sum, int size, int run);
void printavg(Avgscore *male, Avgscore *fem, Avgscore *mm, Avgscore *mf, Avgscore
    *ff, Avgscore *fm, int run, int gencount);
void printstratsum(Sumstrat *mm, Sumstrat *mf, Sumstrat *ff, Sumstrat *fm, int run);
void init_files(void);

```

// Check_arrays: Check that there is enough memory for the arrays

```

void check_arrays(Agents *A, Strategy *S1, Strategy *S2, Strategy *S3,
    Strategy *S4, Avgscore *AS1, Avgscore *AS2, Avgscore *AS3,
    Sumstrat *SS1, Sumstrat *SS2)
{
    if (A == NULL){
        printf("Error allocating memory for adults\n");
        exit(1);
    }

    if (S1 == NULL){
        printf("Error allocating memory for malemalestrategy\n");
        exit(1);
    }

    if (S2 == NULL){
        printf("Error allocating memory for malemalestrategy\n");
        exit(1);
    }

    if (S3 == NULL){
        printf("Error allocating memory for malefem strategy\n");
        exit(1);
    }

    if (S4 == NULL){
        printf("Error allocating memory for malefem strategy\n");
        exit(1);
    }

    if (AS1 == NULL){
        printf("Error allocating memory for avgcores\n");
    }

```

```

    exit(1);
}

if (AS2 == NULL){
    printf("Error allocating memory for avgscores\n");
    exit(1);
}

if (AS3 == NULL){
    printf("Error allocating memory for avgscores\n");
    exit(1);
}

if (SS1 == NULL){
    printf("Error allocating memory for femmale strategy\n");
    exit(1);
}

if (SS2 == NULL){
    printf("Error allocating memory for femmale strategy\n");
    exit(1);
}
}

// init_files: clear the files for a new set of results
void init_files(void)
{
    FILE *malesptr;
    FILE *femsptr;
    FILE *mmptr;
    FILE *mfptr;
    FILE *ffptr;
    FILE *fmptr;

    FILE *stratmmptr;
    FILE *stratmfptr;
    FILE *stratffptr;
    FILE *stratfmptr;

    malesptr = fopen("males.dat","w"); /* open results files */
    femsptr = fopen("females.dat","w");
    mmptr = fopen("mm.dat","w");
    mfptr = fopen("mf.dat","w");
    ffptr = fopen("ff.dat", "w");
    fmptr = fopen("fm.dat", "w");
    fclose(malesptr);
    fclose(femsptr);
    fclose(mmptr);
    fclose(mfptr);
    fclose(ffptr);
    fclose(fmptr);
    stratmmptr = fopen("stratmm.dat","w");
    stratmfptr = fopen("stratmf.dat","w");
    stratffptr = fopen("stratff.dat","w");
    stratfmptr = fopen("stratfm.dat","w");
    fclose(stratmmptr);
    fclose(stratmfptr);
    fclose(stratffptr);
}

```

```

    fclose(stratfmptr);
}

// user: Set costs of reproduction and number of generations
void user(int *mcost, int *fcost, int *last)
{
    printf("\nEXPERIMENT TWO\n");
    printf("\n\nPlease enter the cost of reproduction for males\n");
    scanf("%d", mcost);
    printf("\n\nPlease enter the cost of reproduction for females\n");
    scanf("%d", fcost);
    printf("\nHow many generations would you like to run?\n");
    scanf("%d", last);
}

// Init_adults: Initialise adults for score and sex
void init_adults(Agents *players, int popsize)
{
    int i;

    for(i=0; i < popsize; i++)
    {
        players[i].sex = rand()%2;           /* 0: male, 1: female */
        players[i].score = 0;               /* initial score = 0 */
    }
}

// new_gen: Each generation, assign each agent a sex and a score
void init_newgen(Agents *players, int popsize)
{
    int i;

    for(i=0; i < popsize; i++)
    {
        players[i].sex = rand()%2;         /* 0: male, 1: female */
        players[i].score = 0;             /* initial score = 0 */
    }
}

// Init_strategies: For first generation only, randomly set strategy strings to 1s and 0s
void init_strategies(Strategy *boyboy, Strategy *boygirl, Strategy *girlgirl, Strategy *girlboy,
                    int popsize)
{
    int i,j;

    for (i=0; i < popsize; i++)
    {
        for (j=0; j < STRATSIZE; j++)
        {
            boyboy[i].strat[j] = rand()%2;
            boygirl[i].strat[j] = rand()%2;
            girlgirl[i].strat[j] = rand()%2;
            girlboy[i].strat[j] = rand()%2;
        }
    }
}
}

```

/* prisdilem: Manages the playing of the Prisoner's Dilemma. Checks each players sex, and then sends the appropriate strategy string to the appropriate sub-routine. The average score per player per game is recorded in a results array.

```

void prisdilem(Agents *adults, Strategy *malemale, Strategy *malefem, Strategy *femfem,
              Strategy *femmale, int i,int j, float average[], int avgcount[])
{
    float addavg = 0;                // addavg: points scored in games

    if ((adults[i].sex == 0) && (adults[j].sex == 0))    // if both players are male .....
    {
        addavg = homodilem(adults, malemale, i, j);        // ... send malemale strategy strings to
                                                         // homodilem sub-routine
        average[0] += addavg;                             // add scores to male results
        average[2] += addavg;                             // add scores to malemale results
        avgcount[0] += 2;
        avgcount[2] += 2;
    }

    if ((adults[i].sex == 1) && (adults[j].sex == 1))    // if both players are female .....
    {
        addavg = homodilem(adults, femfem, i, j);        // ... send femfem strategy strings
    }
    to
                                                         // homodilem sub-routine
                                                         // female scores
                                                         // femfem scores
        average[1] += addavg;
        average[4] += addavg;
        avgcount[1] += 2;
        avgcount[4] += 2;
    }

    if ((adults[i].sex == 0) && (adults[j].sex == 1))    // .. if player1 is male, player 2 female...
    {
        heterodilem(adults, malefem, femmale, i, j, average); //... send strategy strings to heterodilem
                                                         sub-routine, send the male player first
                                                         // add results within sub-routine

        avgcount[0]++;
        avgcount[1]++;
        avgcount[3]++;
        avgcount[5]++;
    }

    if ((adults[i].sex == 1) && (adults[j].sex == 0))
    {
        heterodilem(adults, malefem, femmale, j, i, average);
        avgcount[0]++;
        avgcount[1]++;
        avgcount[3]++;
        avgcount[5]++;
    }
}

```

// homodilem: Prisoner's Dilemma played between agents of the same sex. The main difference between this and heterodilem is that it in the latter case, average scores must be recorded within the program. In this case, calculation can be left to the prisdilem program. In both cases, the logic behind the programming is exactly the same as in the control, described in Appendix 1.

```
float homodilem(Agents *adults, Strategy *player, int one, int two)
{
    int round = 1;
    int moves[4] = {0}; /* records last two moves of each agent */
    int roundtwo[4][4] = {{1,0,1,2},{0,1,2,1},{1,1,3,3},{0,0,4,4}};
    int scoreref[16][6] = {{1,1,1,1,5,5}, {0,1,1,1,6,7}, {1,0,1,1,7,6}, {1,1,0,1,8,9},
                          {1,1,1,0,9,8}, {1,1,0,0,10,10}, {0,0,1,1,11,11}, {1,0,0,1,12,13},
                          {0,1,1,0,13,12}, {0,1,0,1,14,15}, {1,0,1,0,15,14}, {1,0,0,0,16,17},
                          {0,1,0,0,17,16}, {0,0,1,0,18,19}, {0,0,0,1,19,18}, {0,0,0,0,20,20}};

    int i;
    int previousi = 99; /* dummy number. Previous i indicates if
                        agents are 'locked in'to a type of play */

    int initscore1 = adults[one].score; /* initial scores */
    int initscore2 = adults[two].score;
    float addavg = 0; /* for results */

    /* take first turn */
    /* agents refer to first position in their strategy array */

    if (round == 1)
    {
        moves[0] = player[one].strat[0];
        moves[1] = player[two].strat[0];
        adults[one].score += score(moves[0], moves[1]);
        adults[two].score += score(moves[1], moves[0]);
        moves[2] = moves[0];
        moves[3] = moves[1];
        round++;
    }

    /* Round 2 */
    /* Previous moves are compared to 'roundtwo' reference array to determine
    behaviour in this round */

    if (round == 2)
    {
        for(i=0; i <=3; i++)
        {
            if((roundtwo[i][0] == moves[2]) && (roundtwo[i][1] == moves[3]))
            {
                moves[0] = player[one].strat[(roundtwo[i][2])];
                moves[1] = player[two].strat[(roundtwo[i][3])];
                break;
            }
        }

        adults[one].score += score(moves[0], moves[1]);
        adults[two].score += score(moves[1], moves[0]);
        round++;
    }
}
```

```

/* All other rounds */
/* The moves made by each player in the last two rounds are compared to
the scoreref reference array to determine behaviour in the current round*/

for (round = 3; round <= LASTROUND; round++)
{
  for (i=0; i <=15; i++)
  {
    if((scoreref[i][0] == moves[0]) && (scoreref[i][1] == moves[1]) &&
      (scoreref[i][2] == moves[2]) && (scoreref[i][3] == moves[3]))
    {
      moves[2] = moves[0];
      moves[3] = moves[1];
      moves[0] = player[one].strat[(scoreref[i][4])];
      moves[1] = player[two].strat[(scoreref[i][5])];
      break;
    }
  }
  /* calculate scores */
  adults[one].score += score(moves[0], moves[1]);
  adults[two].score += score(moves[1], moves[0]);
}

addavg = ((float)(adults[one].score - initscore1)/LASTROUND);
addavg += ((float)(adults[two].score - initscore2)/LASTROUND);
return addavg;
}

// Heterodilem: Prisoner's Dilemma when agents are of different sex
void heterodilem(Agents *adults, Strategy *player1, Strategy *player2,
  int one, int two, float average[])
{
  int round = 1;
  int moves[4] = {0}; /* records last two moves of each agent */
  int roundtwo[4][4] = {{1,0,1,2},{0,1,2,1},{1,1,3,3},{0,0,4,4}};
  int scoreref[16][6] = {{1,1,1,1,5,5}, {0,1,1,1,6,7}, {1,0,1,1,7,6},
    {1,1,0,1,8,9}, {1,1,1,0,9,8},{1,1,0,0,10,10},
    {0,0,1,1,11,11}, {1,0,0,1,12,13}, {0,1,1,0,13,12},
    {0,1,0,1,14,15},{1,0,1,0,15,14}, {1,0,0,0,16,17},
    {0,1,0,0,17,16}, {0,0,1,0,18,19}, {0,0,0,1,19,18}, {0,0,0,0,20,20}};

  int i;
  int previousi = 99; /* dummy number. Previous i indicates if
agents are 'locked in'to a type of play */

  int initscore1 = adults[one].score; /* initial scores */
  int initscore2 = adults[two].score;

  /* take first turn */
  /* agents refer to first position in their strategy array */

  if (round == 1)
  {
    moves[0] = player1[one].strat[0];
    moves[1] = player2[two].strat[0];
    adults[one].score += score(moves[0], moves[1]);
    adults[two].score += score(moves[1], moves[0]);
  }
}

```

```

    moves[2] = moves[0];
    moves[3] = moves[1];
    round++;
}

/* Round 2 */
/* Previous moves are compared to 'roundtwo' reference array to determine
behaviour in this round */

if (round == 2)
{
    for(i=0; i <=3; i++)
    {
        if((roundtwo[i][0] == moves[2]) && (roundtwo[i][1] == moves[3]))
        {
            moves[0] = player1[one].strat[(roundtwo[i][2])];
            moves[1] = player2[two].strat[(roundtwo[i][3])];
            break;
        }
    }

    adults[one].score += score(moves[0], moves[1]);
    adults[two].score += score(moves[1], moves[0]);
    round++;
}

/* All other rounds */
/* The moves made by each player in the last two rounds are compared to
the scoreref reference array to determine behaviour in the current round*/

for (round = 3; round <= LASTROUND; round++)
{
    for (i=0; i <=15; i++)
    {
        if((scoreref[i][0] == moves[0]) && (scoreref[i][1] == moves[1]) &&
            (scoreref[i][2] == moves[2]) && (scoreref[i][3] == moves[3]))
        {
            moves[2] = moves[0];
            moves[3] = moves[1];
            moves[0] = player1[one].strat[(scoreref[i][4])];
            moves[1] = player2[two].strat[(scoreref[i][5])];
            break;
        }
    }

    /* calculate scores */
    adults[one].score += score(moves[0], moves[1]);
    adults[two].score += score(moves[1], moves[0]);
}

average[0] += ((float)(adults[one].score - initscore1)/LASTROUND);
average[3] += ((float)(adults[one].score - initscore1)/LASTROUND);
average[1] += ((float)(adults[two].score - initscore2)/LASTROUND);
average[5] += ((float)(adults[two].score - initscore2)/LASTROUND);
}

```

```

/* score: calculate scores */
int score(int p1, int p2)
{
    int addscore = 0;

    if ((p1 == 1) && (p2 == 1))    /* both cooperate */
    {
        addscore = 3;
    }

    if ((p1 == 1) && (p2 == 0))    /* P1 cooperates, opponent does not.
                                    P1 receives suckers payoff */
    {
        addscore = 0;    /*0*/
    }

    if ((p1 == 0) && (p2 == 1))    /* P1 defects, its opponent  coops */
    {
        addscore = 5;    /*5*/
    }

    if ((p1 == 0) && (p2 == 0))    /* both defect */
    {
        addscore = 1;
    }

    return (addscore);
}

// reprotest: checks to see if pair are of different sexes and have enough
// points to mate. If yes, points are subtracted from scores.
int repro_test(Agents *adults,int p1,int p2, int malecost, int femcost)
{
    int flag = 0;

    if ((adults[p1].sex == 0) && (adults[p2].sex == 1))
    {
        if ((adults[p1].score >= malecost) && (adults[p2].score >= femcost))
        {
            flag = 1;
            adults[p1].score -= malecost;
            adults[p2].score -= femcost;
        }
    }

    if ((adults[p2].sex == 0) && (adults[p1].sex == 1))
    {
        if ((adults[p2].score >= malecost) && (adults[p1].score >= femcost))
        {
            flag = 1;
            adults[p2].score -= malecost;
            adults[p1].score -= femcost;
        }
    }
    return flag;
}

```

```

// reproduction: reproduction by crossover and mutation of strategy strings
void reproduction(Strategy *parents, Strategy *child, int male, int female, int childno)
{
    int crossno = 0;
    int c,i;
    int mutate;

    crossno = rand()%STRATSIZE;          /* randomly select crossover point */
    for(c=0; c <=crossno; c++)
    {
        child[childno].strat[c] = parents[male].strat[c];
        child[childno+1].strat[c] = parents[female].strat[c];
    }

    for(c= crossno+1; c < STRATSIZE; c++)
    {
        child[childno].strat[c] = parents[female].strat[c];
        child[childno+1].strat[c] = parents[male].strat[c];
    }

    /* mutation, 1/5000 probability */

    if (rand()%10000 <= 2)
    {
        mutate = rand()%21;
        if (child[childno].strat[mutate] == 0)
            { child[childno].strat[mutate] = 1; }
        else
            { child[childno].strat[mutate] = 0; }
    }
    if (rand()%10000 <= 2)
    {
        mutate = rand()%21;
        if (child[childno+1].strat[mutate] == 0)
            { child[childno+1].strat[mutate] = 1; }
        else
            { child[childno+1].strat[mutate] = 0; }
    }
}

// When enough offspring have been created to replace the parent generation,
//then offspring become the new adults
void swap(Strategy *parents, Strategy *children, int size)
{
    int i,j;

    for(i=0; i< size; i++)
    {
        for(j=0; j < STRATSIZE; j++)
        {
            parents[i].strat[j] = children[i].strat[j];
        }
    }
}

```

/* Countmoves: Counts the percentage of agents co-operating for each gene in the strategy array */

```
void countmoves(Strategy *chromosome, Sumstrat *sum, int size, int run)
{
    float onecount = 0;
    int i,j;

    for(i=0; i < STRATSIZE; i++)
    {
        for(j = 0; j < size; j++)
        {
            if(chromosome[j].strat[i] == 1)
            { onecount++;}
        }
        onecount = ((onecount/size)*100);
        sum[run].strat[i] += onecount;
        onecount = 0;
    }
}
```

// printavg: print average scores to files

```
void printavg(Avgscore *male, Avgscore *fem, Avgscore *mm, Avgscore *mf,
             Avgscore *ff, Avgscore *fm, int lastrun, int gencount)
```

```
{
    FILE *malesptr;
    FILE *fempstr;
    FILE *mmptr;
    FILE *mfptr;
    FILE *ffptr;
    FILE *fmptr;

    int i=0;
    int run = 0;

    if((malesptr = fopen("males.dat", "a")) == NULL)
        printf("the average male file cannot be opened\n");
    else
        for(i=0; i < gencount; i++)
        {
            for(run=0; run < lastrun; run++)
            {
                fprintf(malesptr, " %.2f,", male[run].avg[i]);
            }
            fprintf(malesptr, "\n");
        }

    fclose(malesptr);

    if((fempstr = fopen("females.dat", "a")) == NULL)
        printf("the average male file cannot be opened\n");
    else
        for(i=0; i < gencount; i++)
        {
            for(run=0; run < lastrun; run++)
            {
                fprintf(fempstr, " %.2f,", fem[run].avg[i]);
            }
            fprintf(fempstr, "\n");
        }
}
```

```

}
fclose(femsptr);

if((mmptr = fopen("mm.dat", "a")) == NULL)
    printf("the average male file cannot be opened\n");
else
    for(i=0; i < gencount; i++)
    {
        for(run=0; run < lastrun; run++)
        {
            fprintf(mmptr, " %.2f,", mm[run].avg[i]);
        }
        fprintf(mmptr, "\n");
    }
fclose(mmptr);

if((mfptr = fopen("mf.dat", "a")) == NULL)
    printf("the average male file cannot be opened\n");
else
    for(i=0; i < gencount; i++)
    {
        for(run=0; run < lastrun; run++)
        {
            fprintf(mfptr, " %.2f,", mf[run].avg[i]);
        }
        fprintf(mfptr, "\n");
    }
fclose(mfptr);

if((ffptr = fopen("ff.dat", "a")) == NULL)
    printf("the average male file cannot be opened\n");
else
    for(i=0; i < gencount; i++)
    {
        for(run=0; run < lastrun; run++)
        {
            fprintf(ffptr, " %.2f,", ff[run].avg[i]);
        }
        fprintf(ffptr, "\n");
    }

fclose(ffptr);

if((fmptr = fopen("fm.dat", "a")) == NULL)
    printf("the average male file cannot be opened\n");
else
    for(i=0; i < gencount; i++)
    {
        for(run=0; run < lastrun; run++)
        {
            fprintf(fmptr, " %.2f,", fm[run].avg[i]);
        }
        fprintf(fmptr, "\n");
    }

fclose(fmptr);
}

```

// Printstratsum: print strategies to files

```

void printstratsum(Sumstrat *mm, Sumstrat *mf, Sumstrat *ff, Sumstrat *fm, int run)
{
    FILE *stratmmptr;
    FILE *stratmfptr;
    FILE *stratffptr;
    FILE *stratfmptr;
    int i;

    if((stratmmptr = fopen("stratmm.dat", "a")) == NULL)
        printf("file cannot be opened");
    else
    {
        for (i=0; i < STRATSIZE; i++)
            fprintf(stratmmptr, " %.2f", mm[run].strat[i]);
    }
    fprintf(stratmmptr, "\n");

    fclose(stratmmptr);

    if((stratmfptr = fopen("stratmf.dat", "a")) == NULL)
        printf("file cannot be opened");
    else
    {
        for (i=0; i < STRATSIZE; i++)
            fprintf(stratmfptr, " %.2f", mf[run].strat[i]);
    }
    fprintf(stratmfptr, "\n");
    fclose(stratmfptr);

    if((stratffptr = fopen("stratff.dat", "a")) == NULL)
        printf("file cannot be opened");
    else
    {
        for (i=0; i < STRATSIZE; i++)
            fprintf(stratffptr, " %.2f", ff[run].strat[i]);
    }
    fprintf(stratffptr, "\n");
    fclose(stratffptr);

    if((stratfmptr = fopen("stratfm.dat", "a")) == NULL)
        printf("file cannot be opened");
    else
    {
        for (i=0; i < STRATSIZE; i++)
            fprintf(stratfmptr, " %.2f", fm[run].strat[i]);
    }
    fprintf(stratfmptr, "\n");
    fclose(stratfmptr);
}

```

Appendix 3: Generation Times Model

A3.1. Basic Outline

start

user sets cost of reproduction for males (MRC) and females (FRC)

set *run counter* = 0

While *run counter* < 30 do this:

{

Generate 650 agents at random, where each agent has:

- sex (M/F)

- a male-type: defect (D), reciprocal altruist (RC) or
non-reciprocal altruist (NRA)

- score = 0

set *generation counter* = 0, set *generation time counter* = 0

set *offspring counter* = 0

While *generation counter* < 1000 do this:

{

while *offspring counter* < 650 do this:

{

1. Pick two agents at random

2. These agents play 100 games of the Prisoner's Dilemma. Females always score $3 \times 100 = 300$ against each other; males always score $1 \times 100 = 100$ against each other. Mixed sex interactions are scored according to male type: D both score 1; RA both score 3; NRA male scores 1.5, female scores 4. Points gained are added to the each agent's score

3. Pick two new agents at random

4. If the agents are of opposite sex, and each agent has enough points to reproduce (FRC or MRC) they reproduce. The male-type of the male is recorded. FRC is subtracted from the female's score, and MRC is subtracted from the male's score.

The *offspring counter* is increased by +1

4. *Generation time counter* is increased by +1

}

Replace adult population with offspring in the proportions of successful male-types.

Set *offspring counter* = 0

Set all scores = 0

Generation time is recorded, *generation time counter* set to 0

Generation counter is increased by +1

}

Collate and print results (average generation time)

run counter is increased by +1

}

End

A3.2. Program

// Three types of males exist: cooperators, defectors and super cooperators. Which males are best, and how does male strategy affect generation time?

```
#include <stdio.h>
#include <stdlib.h>
#include <time.h>

struct results{
    float prop[3];
    float time;
};

typedef struct results Results;

// Function calls
void init_var(int *female, int *male, int *inter, int *popsize);
void init_score(float *ff, float *mm, float *fm, float *mf);
void init_pop(int sex[], int score[], int popno, int type[], float props[]);
void interact(int sex[], int score[], int p1, int p2, int l, float ff, float mm, float fm,
    float mf, int poptype[]);
int repro_test(int sex[], int score[], int p1, int p2, int malecost, int femcost);
void init_maletype(float prop[3]);
void update_type(int poptype[], int p1, float tally[]);
void create_child(int childtype[], int parenttype[], int dad, int child);
void newpop(int sex[], int score[], int oldtype[], int newtype[], int popsize);
void count_type(int poptype[], int popsize, Results *result, int runno);
int another(void);
void print_results(Results *result, int end);

//main program
main()
{
    Results result[150];
    int popsex[1001];           // 0: male, 1: female
    int popscore[1001];       // records scores
    int poptype[1001];        // Male strategies: 0 (DD), 1 (CC), 2 (NRA)
    int childtype[1001];
    int N = 1000;             // pop. size
    int FRC = 1000, MRC = 1000, l = 100; // female RC, male RC, iteration no.
    float FF = 3, MM = 3;     // scoring between same sex
    float FM = 4.5, MF = 1.5; // scoring for NRA interactions
    long int t = 1;           // time
    long int tavg = 0;        // average generation time
    int childno = 0;
    int gametype = 0;

    srand(time(NULL)+550);    /* seed random number generator*/

    int i, j;
    int reproflag = 0;
    int gen = 1;
    int lastgen = 1;
    float maletype[3];        //Records props.0 defects, 1 coops, 3 NRAs
```



```

    count_type(poptype,N,result,run);
    if(run%10 == 0)
        printf("\nExpt %d.....", run);
    run++;
}while(run <= lastrun);

print_results(result, lastrun);

return 0;
}

```

// Init_var: Intialise variables for cost of reproduction and population size

```

void init_var(int *female, int *male, int *inter, int *popsize)
{
    printf("\nPlease enter the COST OF REPRODUCTION");
    printf("\nFirst for FEMALES:");
    scanf("%d", female);
    printf("\nAnd now for MALES:");
    scanf("%d", male);
    printf("\nHow many INTERACTIONS (rounds) per game?:");
    scanf("%d", inter);
    printf("\nWhat is the POPULATION SIZE?(max 1000):");
    scanf("%d", popsize);
}

```

// Init_score: Enter the scores for the different interaction types

```

void init_score(float *ff, float *mm, float *fm, float *mf)
{
    printf("\n\nPlease enter the scores....");
    printf("\n1) For female:female interactions:"); // equal to 3.00
    scanf("%f", ff);
    printf("\n2) For male:male interactions:"); // 1.00
    scanf("%f", mm);
    printf("\n3) For a female playing a male (FM):"); // 4.00
    scanf("%f", fm);
    printf("\n4) For a male playing a female (MF):"); // 1.50
    scanf("%f", mf);
}

```

// init_pop: Give players a score, sex, and a 'type' - defector, reciprocal altruist or NRA. This 'type' will only be applied to males playing females

```

void init_pop(int sex[], int score[], int popno, int type[], float props[])
{
    int i;
    int x;

    for (i=0; i < popno; i++)
    {
        sex[i] = rand()%2; // 0 is male, 1 is female
        score[i] = 0;
        x = rand()%1000;

        if (x < (props[0]*10))
        {
            type[i] = 0;
        }
    }
}

```

```

    if ((x >= (props[0]*10) ) && (x < (10*(props[0]+props[1])))
    {
        type[i] = 1;
    }
    if (x >= (10*(props[0]+props[1])))
    {
        type[i] = 2;
    }
}
}

// Scores gained from the Prisoner's Dilemma. Poptype is male-type (defector, RA or
// NRA. l = number of games (usually 100).
void interact(int sex[], int score[], int p1, int p2, int l, float ff, float mm, float fm, float mf, int
    poptype[])
{
    if (sex[p1] == 0) // male-male interaction
    {
        if (sex[p2] == 0)
        {
            score[p1] += l*mm;
            score[p2] += l*mm;
        }
        else
        {
            if (poptype[p1] == 0) // male-fem interaction
            // defector male
            {
                score[p1] += l*1;
                score[p2] += l*1;
            }
            if (poptype[p1] == 1) // reciprocal altruism
            {
                score[p1] += l*3;
                score[p2] += l*3;
            }
            if (poptype[p1] == 2) // NRA
            {
                score[p1] += l*mf; // mf = 1.5
                score[p2] += l*fm; // fm = 4.0
            }
        }
    }
    else
    {
        if (sex[p2] == 1) // female-female interactions
        {
            score[p1] += l*ff;
            score[p2] += l*ff;
        }
        else // fem-male interactions
        {
            if (poptype[p2] == 0)
            {
                score[p1] += l*1;
                score[p2] += l*1;
            }
            if (poptype[p2] == 1)
            {
                score[p1] += l*3;
            }
        }
    }
}

```

```

        score[p2] += l*3;
    }
    if (poptype[p2] == 2)
    {
        score[p1] += l*fm;
        score[p2] += l*mf;
    }
}
}
}

```

// Repro-test: Are the players of opposite sex? Do they have enough points to pay MRC or FRC? If answers to both questions are yes, then they can reproduce

```
int repro_test(int sex[], int score[], int p1, int p2, int malecost, int femcost)
```

```

{
    int flag = 0;

    if ((sex[p1] == 0) && (sex[p2] == 1))
    {
        if ((score[p1] >= malecost) && (score[p2] >= femcost))
        {
            flag = 1;
            score[p1] -= malecost;
            score[p2] -= femcost;
        }
    }

    if ((sex[p2] == 0) && (sex[p1] == 1))
    {
        if ((score[p2] >= malecost) && (score[p1] >= femcost))
        {
            flag = 1;
            score[p2] -= malecost;
            score[p1] -= femcost;
        }
    }
    return flag;
}

```

// Init_maletype: Set proportions of each male-type, usually 1/3 of each

```
void init_maletype(float prop[3])
```

```

{
    do{
        printf("\n Enter initial number of defecting males:");
        scanf("%f", &prop[0]);
        printf("\n Enter initial number of cooperating males:");
        scanf("%f", &prop[1]);
        printf("\n Enter initial number of super-cooperating males:");
        scanf("%f", &prop[2]);
    } while((prop[0] + prop[1] + prop[2]) != 100);
}

```

```

// count-type: records results
void count_type(int poptype[], int popsize, Results *result, int runno)
{
    int i;
    float tally[3] = {0};

    for(i=0; i < popsize; i++)
    {
        if (poptype[i] == 0)
            tally[0] ++;
        if (poptype[i] == 1)
            {tally[1] ++;}
        if (poptype[i] == 2)
            {tally[2] ++;}
    }
    for(i=0; i < 3; i++)
    {
        tally[i] = (float)tally[i]/popsize*100;
        result[runno].prop[i] = tally[i];
    }
}

// Create_child
void create_child(int childtype[], int parenttype[], int dad, int child)
{
    childtype[child] = parenttype[dad];
}

// new_pop: Reset for new population
void newpop(int sex[], int score[], int oldtype[], int newtype[], int popsize)
{
    int i;

    for (i=0; i < popsize; i++)
    {
        sex[i] = rand()%2;
        score[i] = 0;
        oldtype[i] = newtype[i];
    }
}

int another(void)
{
    int again = 0;
    printf("\nWould you like to repeat this experiment? (0=NO, 1=YES)");
    scanf("%d",&again);
    return(again);
}

void print_results(Results *result, int end)
{
    FILE *suckerptr;
    int i,j;

    if((suckerptr = fopen("suckers.dat","w")) == NULL)

```

```
    printf("\nThe suckers file cannot be opened, sucker");
else
for(i=1; i <= end; i++)
{
    for(j=0; j <3; j++)
    {
        fprintf(suckerptr, "%.2f, ", result[i].prop[j]);
    }
    fprintf(suckerptr, "%.2f\n", result[i].time);
}

fclose(suckerptr);
}
```

Appendix 4: Seasonality and Resource Quality

A4.1. Basic Outline

start

user sets cost of reproduction for males (MRC) and females (FRC)

set *run counter* = 0

set environment quality (poor, medium or high) for each of the 12 months
(Note: in a stable experiment, resource quality remains constant)

While *run counter* < 30 do this:

{

Generate 650 agents at random, where each agent has:

- sex (M/F)

- 12 strategy strings for each interaction type and environment quality

- score = 0

- a memory of it's games with all other players for the last two months

set *generation counter* = 0

set *offspring counter* = 0

set *generation time counter* = 0

While *generation counter* < 20,000 do this:

{

set *month* = 1, i.e. it is the first month

while *offspring counter* < 50 do this:

{

1. Every member of the population plays 1 round of the Prisoner's Dilemma with every other member. Play is based on the interactions between players in the last two months, their sexes and the environment quality for that month. Players gain pay-offs according to fig. 5.1.

2. Every agent that has enough points to reproduce (MRC or FRC, according to gender) is put in to a 'fertile male' or 'fertile female' array. Pairs are chosen at random, from the 2 arrays, to reproduce by crossover and mutation of strategy strings. 2 new offspring are created each time. Reproduction continues until either the male or female fertile array is empty. Agents may reproduce more than once, if they have enough points.

3. When reproduction is complete, the offspring counter is updated.

4. *Month* is increased by 1. If *month* = 13, then reset to *Month* = 1.

}

Replace adult population with offspring

Set *offspring counter* = 0

Set all scores = 0

}

Collate and print results (average scores)

run counter is increased by +1

}

End

A4.2. Main program

/* This program is designed to look at how the quality and seasonality of environmental affects the evolution of cooperative strategies. The Prisoner's Dilemma pay-off matrix is adjusted for the season and the quality of the environment. Three qualities are possible, where 1 is the poorest quality. Each individual has a strategy based on environment quality. Environments may be stable or seasonal. See chapter 5. */

/* Please note: I have not included the funtion files (seasdef.h, seascall.h etc) in this appendix. This is because these files are very long, and are extremely similar to those used in previous programs. */

```

#include <stdio.h>
#include <stdlib.h>
#include <time.h>
#include "seasdef.h"
#include "seascall.h"
#include "prisoner.h"
#include "repro.h"
#include "results.h"

main()
{
    Agents *adults = (Agents *) calloc(SIZE, sizeof(Agents));
    Strategy *s1 = (Strategy *) calloc(SIZE, sizeof(Strategy));
    Strategy *s2 = (Strategy *) calloc(SIZE, sizeof(Strategy));
    Strategy *s3 = (Strategy *) calloc(SIZE, sizeof(Strategy));
    Memory *mem = (Memory *) calloc(SIZE, sizeof(Memory));
    Strategy *s1off = (Strategy *) calloc(SIZE, sizeof(Strategy));
    Strategy *s2off = (Strategy *) calloc(SIZE, sizeof(Strategy));
    Strategy *s3off = (Strategy *) calloc(SIZE, sizeof(Strategy));
    check_arrays(adults, s1, s2, s3, mem);           // check memory
    check_arrays(adults, s1off, s2off, s3off, mem);

    Data results;
    int rcmale, rcfemale;           // cost of reproduction, set by user
    int end;                       // total no. generations to run
    int i,j;
    int run = 0;                   // run number
    int gen = 1;                   // generation no.
    int offno = 0;
    int environ[12];              // Set environement quality for 12 months
    int month = 0;
    int t = 0;                     // measures generation time

    float rescount[MONTHS] = {0}; // to record results
    float monthavg[MONTHS];
    float s1avg;                  // results in poor quality habitats
    float s2avg;                  // results in medium quality
    float s3avg;                  // results in high quality

    srand(time(NULL));           /* seed random number generator*/

    user(&rcmale, &rcfemale, &end); // set parameters */
    set_environ(environ);        // set environment quality
    init_files();                // clear results files

    while (run < RUN)
    {
        // start of new run
        // start a new set of results
        cleanresults(&results);
    }
}

```

```

init_adults(adults); // create a new adult population
init_strategies(s1,s2,s3); // initialise strategies

while (gen <= end) // start of new generation
{
    while (offno < SIZE)
    {
        if((t <24) && (gen%100 == 0) ) // record results
        {
            recordresults(adults, &results, s1, s2, s3, environ[month], t,mem);
            rescount[t] ++;
        }
        switch (environ[month]) // What is the env. type?
        {
            case(1): // poor?
                prisdilem(adults, s1, environ[month], t, mem); // play PD
                break;
            case(2): // medium?
                prisdilem(adults, s2, environ[month], t, mem); // play PD
                break;
            case(3): // high? play PD
                prisdilem(adults, s3, environ[month], t, mem);
                break;
        }

        // Reproduction
        offno = repromanager(adults, s1, s2, s3, rcmale, rcfemale, s1off, s2off, s3off, offno);
        t++;
        month +=1;
        if (month >= 12)
            month = 0;
    }
    if(gen%100 == 0)
    {
        printf(" .... GEN%d ",gen);
    }
    gen ++;
    swap(s1, s1off); // offspring become new gen.
    swap(s2, s2off);
    swap(s3, s3off);
    init_adults(adults); // reset variables
    offno = 0;
    month = 0;
    t = 0;
}
updateresults(&results, rescount);
run++;
printf("\n\nNew Run %d",run);
gen = 1;
}
return 0;
}

```

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