THE EFFECTS OF SPATIAL HETEROGENEITY ON EXPERIMENTAL POPULATIONS

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ABSTRACT

The effect of spatial heterogeneity on a number of population interactions was investigated. Populations consisting of 2 artificial prey species differing in colour were presented to wild birds in two spatial arrangements (random or aggregated). Although the overall prey frequencies and densities were the same in both arrangements, rare prey suffered significantly less predation when randomly mixed among a more common prey species than when aggregated with conspecifics. Spatial patterning as well as frequency may be an important component of apostatic selection. This may have an important effect on competition between prey species at the local (i.e., within-patch) spatial scale.

Spatial heterogeneity in light conditions had a significant effect on interspecific and intraspecific interactions in Drosophila. The more photopositive D. simulans dispersed to brighter areas than D. melanogaster both in the field and in the laboratory, where in heterogeneously lit "RW" population cages, species overlap was less than in the homogeneously lit cages. This reduced interspecific competition but did not lead to long-term coexistence. Light preferences of samples from the RW cages changed during the experiment and were more divergent than samples from the homogeneously lit cages. Light intensity is not an arbitrary factor because in homogeneously lit bright white light ("WW") cages there was coexistence between D. simulans and white-eye D. melanogaster (which is effectively blinded in bright light).

Light preferences in Drosophila are modifiable by experience. Flies had a significantly greater preference for the light conditions to which they had already been exposed. This learned component increases the flexibility of D. melanogaster to exploit its cosmopolitan (i.e., unpredictable) niche. D. simulans, although it has a more restricted and photopositive niche, also has this flexibility. The adaptiveness of this is discussed.
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1.1 Introduction

Although adaptation to the physical environment ultimately limits a species distribution and abundance – a species may not be able to survive in certain habitats irrespective of potential interactions with other species – the proximate limits to a species range are often set by interactions with other species (Hutchinson, 1959; Fretwell, 1972; Andrewartha and Birch, 1984; Roughgarden and Diamond, 1986). Spatial heterogeneity is important because, although many models assume that these interactions occur in homogeneous environments, the real world is anything but uniform. Spatial heterogeneity can affect population interactions such as competition and predation so that species unable to coexist in a homogeneous environment may be able to if there is appropriate heterogeneity which competing species can exploit. This is particularly important for populations (including many insects) which exploit patchy and ephemeral resources and must disperse to new patches or else face extinction.

Spatial heterogeneity usually involves some sort of patchiness and, in the last 20 years, has attracted many (often theoretical) studies on topics such as its effects on the maintenance of genetic variation (Hedrick et al, 1976; Hedrick, 1986), speciation (Maynard
Smith, 1966; Rausher, 1984; Bush and Howard, 1986), on coexistence and the limits to similarity among coexisting competitors (Horn and MacArthur, 1972; Levin, 1974; Slatkin, 1974; Atkinson and Shorrocks, 1981; Kareiva, 1986; Lawton, 1986; May and Seeger, 1986), and on species diversity and community structure (May, 1973; Casewell, 1978; Menge et al., 1985; Sih et al., 1985).

In these studies, some form of active dispersal (including habitat selection) or habitat segregation often plays an important role (Levins, 1968; Fretwell, 1972; Casewell, 1978; Jones, 1980; Ives and May, 1985; Kareiva, 1986; May and Seeger, 1986). If, for example, competing species respond differently to spatial heterogeneity, then differences in dispersal (including habitat selection) and hence species distributions can occur so that species may be able to coexist in heterogeneous environments simply because of the way they react to the spatial heterogeneity. Indeed, in a patchy environment, relative mobility (or dispersal) between patches can be more important than competitive ability within patches: coexistence may be possible if, for example, competitively weaker species have greater powers of dispersal (Skellam, 1951; Caswell, 1978; Kareiva, 1986). Competition can also be reduced by aggregation: if a competitively dominant species has a sufficiently clumped distribution (in its pattern of resource use or oviposition site choice, for example) refugia in a patchy environment may arise with inferior, fugitive competitors surviving in vacant patches even without any compensating advantages in superior mobility (Lloyd and White, 1980; Atkinson and Shorrocks, 1981; Ives and May, 1985).
Patchiness can also have a significant effect on predation and parasitoid-host interactions (Wiens, 1976; Hassell et al., 1977; Casewell, 1978; Heads and Lawton, 1983; Holt, 1984; Menge et al., 1985; Schmitt, 1985; Sih et al., 1985; Walde and Murdoch, 1988) which, like competition, can play a major role in population interactions (both affect the growth, survival or reproductive output of interacting species: Table 1.). Predation and competition are, in fact, two of the three basic classes in which interspecific interactions can be divided (the other being mutualism: Pianka, 1983; Begon et al., 1986).

Although dispersal, habitat selection, competition and predation can be intricately linked (Roughgarden and Diamond, 1986; Werner, 1986) it is often helpful to consider these interactions separately and, in this thesis, I will investigate three ways that spatial heterogeneity can have a significant effect on experimental population interactions where there is no resource heterogeneity. First, in Chapter Two, I will show how, on a uniform background, the spatial patterning of prey can produce spatial heterogeneity which affects frequency-dependent (apostatic) predation by visually hunting birds and hence relative prey survival. Chapters Three and Four will investigate how patchiness in an environmental factor (light) can affect microhabitat selection and hence intraspecific and interspecific interactions in D. melanogaster and D. simulans.
1.2 Spatial Heterogeneity: Definitions and Scale

Almost all environments have some form of spatial heterogeneity produced by the physical environment and organisms themselves. Aggregation, limited or nonrandom dispersal, local chance occurrences such as fires or windthrows in forests as well as the nonuniform depletion of resources, can all generate spatial variation even when the environment is, at first, homogeneous (Levin, 1974; Segel, 1976). In order to minimise any misunderstanding, here I use spatial heterogeneity as some form of spatial variation or non-uniformity which can have a significant effect on population interactions. This is best thought of in terms of an environment subdivided into discontinuous subsections or patches which differ in some way (for example, patch quality, environmental factors or selection pressure).

Obviously, this patchiness can occur over different spatial scales and this has led to some difficulty with definitions (Wiens, 1976). Menge and Sutherland (1976), for example, think of spatial heterogeneity as the number of habitats in a given locality whereas many consider it at a more local scale, namely patchiness within a habitat (Southwood, 1976; Wiens, 1976; Pianka, 1983; Price, 1984). As the scale investigated changes, the degree of spatial heterogeneity may also change: small scale random patterns may become patchy at larger scales, and so on. This in itself can have an important effect on population interactions (Wiens, 1976; Holt, 1984; Kareiva, 1986; Wiens et al., 1986) and one must be aware of the possible importance of scale on population interactions. For example, small
scale investigations may only examine single environmental patches and lead to the conclusion that one species excludes another whereas larger scale studies on more than one patch may show that coexistence is possible because, at the larger scale, competitors exploit different patches (Casewell, 1978). Furthermore, significant differences in local population interactions may not be important at the larger community scale where, overall, individual effects balance out. Alternatively, by looking at the wrong spatial scale, significant interactions may be overlooked (Chesson and Case, 1986; Wiens et al., 1986; Ricklefs, 1987; Wade and Murdoch, 1988).

The question of scale has led to such prefixes as macro- and micro- spatial or habitat (Lomnicki, 1988) and there is some difficulty in arriving at a precise definition (Wiens, 1976). However, the range of an animal's movement largely determines what scale is important: the micro-prefix, for example, is generally used when the different patches are within the dispersal range of a species. This again emphasizes that any definition of patchiness must be organism-defined (Wiens, 1976). This is similar to the concept of environmental grain (which is best interpreted as a behavioural response to the environmental mosaic [Wiens, 1976]) where patch size and dispersal is also emphasized. It is best described by the two extremes: if patches are small compared to an animal's dispersal, the animal may move about and encounter patches as they are distributed so that the environment is perceived in a fine-grained manner. An environment will be perceived as coarse-grained if patches are large compared to an animal's mobility.
so that an animal remains within a single large patch even if alternatives are available (Levins, 1968).

As well as dispersal, how animals perceive and react to the patchiness must also be considered: the same environment may be patchy to some but not other species (Holt, 1984). This, in itself, can be important (MacArthur and Levins, 1964; Levins, 1968; Wiens, 1976; Caswell, 1978; Holt, 1984; Kareiva, 1986). Body size can also have an effect — environmental microspatial heterogeneity often increases as the size of an organism decreases (Lomnicki, 1988) so that, for example, the microclimate around individual plant leaves often has a significant effect on small insects (Willmer, 1986).

Spatial heterogeneity can be subdivided into two distinct but interlinked components: there can be resource or environmental patchiness (or both). It should also be noted that resource heterogeneity can have two very different meanings. First, that there is more than one resource and, second, that a single resource has a discrete and subdivided distribution. For example, Shorrocks et al (1979) use both resource subdivision and resource heterogeneity in their classification of how different degrees of spatial heterogeneity can affect coexistence between two competing species (Figure 1.1) and coexistence may occur if there is either resource heterogeneity (leading to niche segregation or resource partitioning, case bi) or a single but subdivided resource (case aii). Shorrocks et al, (1979) use the term environmental heterogeneity to include both resource heterogeneity and heterogeneity in
extrinsic, abiotic factors such as light and temperature. However, by environmental patchiness I mean spatial heterogeneity in an extrinsic environmental factor. This can be in addition to, or instead of, the other types of spatial heterogeneity already described and it should be noted that, strictly speaking, environmental factors also include biological interactions such as predation and competition.

The question of scale can also blur definitions (such as the difference between resource and habitat segregation) so that the same interaction can be defined differently depending on the scale investigated. Schoener (1974a) in his classification of resource dimensions important in interspecific competition overcomes this by taking the somewhat extreme view that both micro- and macro- habitat segregation are essentially forms of resource partitioning (see below).
1.3 Competition and Spatial Heterogeneity

1.3.1 Competition and Species Interactions

A common assumption in competition theory is that population interactions occur in uniform or homogeneous environments where results such as competitive exclusion can occur (Chesson and Case, 1986). In heterogeneous environments, however, competitors unable to coexist in homogeneous environments may be able to because of the differences in the way they exploit the environment (thus reducing competition). This is important because, outside of simple laboratory environments found in the laboratory, most species interact in a complex world: an observation which has led to numerous attempts to find the limiting ecological factors which make coexistence possible in nature. In addition, the effect of spatial heterogeneity may be dependent on whether intraspecific or interspecific competition is more important. The former can lead a population or species becoming more of a generalist (with a broader niche) while the latter can often lead to greater specialisation and a narrower niche (Levins, 1969; Pianka, 1983).

Competition, by definition, adversely affects the growth, survival or population size of all the species involved and, symbolically, it is usually portrayed as a "--" interaction (see Table 1.1) which can occur between individuals of the same or different species. Essentially, competition occurs when some necessary resource is in limited supply (Ayala, 1970) and this resource may be in the form of nutrients, light, space or pollinators (for competing plants), or food, breeding sites, space or mates (for animals).
Although competition has been classified in a number of ways (Birch, 1957; Schoener, 1983), the simplest classification is that of two contrasting types, namely, exploitation (or resource) and interference competition (Birch, 1957; Krebs, 1978; Begon and Mortimer, 1986).

Resource or exploitation competition occurs when individuals of the same or different species utilize common resources that are in short supply. Such interactions are generally indirect: the competitors may never meet. Interference competition, on the other hand, can be quite direct: a competitor may harm another in the process of seeking or utilizing a resource even if the resource is not in short supply. As Pianka (1983) makes clear, interference competition involves such direct interactions as the production of toxins or aggressive encounters and territoriality which deny access to the resource by the loser of any contest. Exploitation competition involves the depletion of a resource by a more efficient species or individuals to a level that it fails to support other competitors (Diamond, 1978; Begon and Mortimer, 1986).

Usually this dichotomy is sufficient to categorise the types of competition but there can be difficulties, such as competition over space, where competitive effects do not easily fall into either class (Schoener, 1983). However, whatever the nature of the interaction, interspecific competition results in the reduction in fitness of all the competitors involved and, depending on the conditions, there are a number of possible outcomes ranging from
competitive exclusion to stable coexistence (Arthur, 1982; Barker, 1983; Roughgarden, 1983).

Classical competition theory is built upon the Lotka-Volterra competition equations and from these somewhat simple and biologically unrealistic equations (see Ayala, 1970, for example) together with the experimental work of Gause (Gause, 1934; Gause and Witt, 1935) developed the so called competitive exclusion principle. Sometimes called Gause's principle (Hardin, 1960), competitive exclusion has played an extremely important, if not vital, role in the development of competition and niche theory (Hardin, 1960; DeBach, 1966; Diamond, 1978; May and Seger, 1986). Indeed, when Hutchinson (1957) proposed the modern form of the niche, he emphasized the role of interspecific competition in delineating a species realised niche, visualising the niche as an abstract n-dimensional hypervolume with each dimension being a separate, independent required resource so that the resulting set space encloses the complete range of conditions under which a species can reproduce successfully and indefinitely. The fundamental niche is reduced by factors such as other competitors which can lower the reproductive increase of a species in certain parts of its potential or fundamental niche so that these parts are absent from the species actual or realised niche which — to eliminate any doubt about his belief on the importance of interspecific competition — Hutchinson called the post-competitive niche.
Species competing for the same limiting resources cannot coexist indefinitely in a homogeneous environment, competitive exclusion will lead to the local extinction or displacement of the competitively weaker species (Pianka, 1983). This been found in a number of biological control studies where the outcome of the experimental introduction of species ecologically very similar to pest species (including insect herbivores) has been competitive displacement (Claridge, 1987). In order to coexist, competing species must differ in their ecologies in some significant way and, of importance here, is that there must be sufficient environmental heterogeneity for these differences to be manifested. Spatial heterogeneity is hence important because, in homogeneous environments, adaptations which reduce interspecific encounters (such as resource partitioning, niche or habitat segregation) and, therefore, promote coexistence cannot be manifested. Furthermore, experiments show that, as more ecological niche dimensions are studied (that is, greater complexity or spatial heterogeneity), the less likely it is that intense competition will occur between species which are sympatric in nature (Price, 1984).

Hutchinson's view now seems a somewhat extreme one since it ignores other processes such as predation and disease which can restrict a species fundamental niche and may be of equal if not greater importance than competition. Nevertheless, Hutchinson's formulation enabled the niches of coexisting competing species to be visualised as having different niche dimensions which made the testing of the limits to similarity between competing species more
tractable (Hutchinson, 1957; MacArthur, 1972; Diamond, 1978). If today its primacy as the major process in the structure and evolution of communities is no longer acceptable, the ideas behind competitive exclusion are still of value (see Diamond, 1978; Schoener, 1982, 1983; Strong et al., 1984; Andrewartha and Birch, 1984; Diamond and Case, 1986; May and Seeger, 1986; den Boer, 1986 and replies of Abrams et al., 1986; for recent views and reviews).

Coexistence between competing species may thus be possible when the environment provides sufficient heterogeneity for competing species to exhibit differences in their realized niches (Chesson and Case, 1986). For example, Crombie (1947) found that unless the complexity of the laboratory environment was increased, Tribolium confusum invariably eliminated another beetle, Oryzaephilus surinamensis in mixed cultures. The addition of small glass tubes provided a refuge for O. surinamensis against pre-adult predation by the larger T. confusum (which find the tubes inaccessible) and coexistence was now possible. Although the distributions of two sibling species of blowfly virtually coincide in parts of Australia, environmental heterogeneity has permitted specialised larval niches with Lucilia cuprina larvae exploiting living sheep and L. sericata, carrion. In a homogeneous environment, however, only one species can survive: in the absence of carrion, only L. cuprina survives, and without living sheep, only L. sericata can survive because L. cuprina larvae are outcompeted in carcases and, conversely, L. cuprina outcompeted L. sericata in living sheep (90% of infected
sheep gave rise to *L. cuprina*, the remaining 10% gave mostly *L. cuprina* and a few *L. sericata*, Waterhouse, 1947).

Competition theory has stimulated many experiments on the limiting similarity between coexisting competing species, the results of which give qualified support to the competitive exclusion principle. However, the mere detection of ecological differences between species is certainly not a verification of the competitive exclusion principle (see Den Boer, 1986; for a recent criticism). One must always be aware that some other factor involved may give the same result. For example, the extinction of the caribou in Nova Scotia and New Brunswick following the introduction of the white-tailed deer was found to be due to a nematode parasite passed from deer to caribou and not due to competition (Anderson, 1965; Embree, 1979).

Another criticism of many studies of character displacement (and niche segregation, see below) is the lack of evidence for competition acting during the investigation. This may be due to a number of possibilities: the first, obviously, is that competition is not important; alternatively, past interactions have led to the avoidance of competition by the evolution of niche displacements so that interspecific competition may not now be apparent. Further possibilities are that the critical resource has not been identified or that competition, although not always present, has a significant effect when acting (see Lawton and Strong, 1981; Pontin, 1982; Price, 1984; Strong et al., 1984; Diamond and Case, 1986 for
references on this and the debate on the "ghost of competition past" in general). This problem at least shows that a thorough knowledge of the ecology of the species in question is essential before attempting to reach any worthwhile conclusions about the processes which may or may not be involved.

A good example is that of Morse's work, reported by Diamond (1978). Morse (1971) noted that the breeding territories of three bird species in Maine were mutually exclusive. Furthermore, each spring when the birds returned to their Maine breeding grounds from their southern wintering grounds, Morse observed wood thrushes fighting the other two species. These fights occurred during the first week after their arrival but not thereafter; the territories set out during the first week were then maintained without further fighting. As Diamond (1978) points out, an observer absent during the first week would be unaware that the territories were due to competitive exclusion caused by interspecific competition.

Obviously, the importance of competition as a major factor in community structure would be severely downgraded if competing species were, in fact, able to coexist on the same resource in a homogeneous environment. However, although apparent examples have been found, in most cases, coexistence was due to some other factor such as predation (see below) or, on further investigation, previously unknown ecological differences were uncovered. Another possibility is that, although the competing species share the same habitat and certain resources, the limiting resources may not have
been correctly identified and further examination may find previous­ly overlooked differences (Broadhead and Wapshere, 1966; Mitchell, 1968; Tahvanainen, 1972; Davidson, 1980, 1985; Andrewartha and Birch, 1984; Price, 1984; Begon and Mortimer, 1986; for example).

Often closer examination reveal microhabitat differences between species found in the same habitat with competing species, in fact, exploiting different niches. Even in seemingly homogeneous environments there can be micro-spatial separation in species overlap. Moore (1952) found differences in oviposition preferences in mixed *D. melanogaster* and *D. simulans* populations with the centre of old food cups acting as a refuge oviposition site for *D. simulans*. Arthur (1986) found that coexist, between *D. melanogaster* and *D. hydei* was possible if the medium depth was sufficient for interspecific differences in larval foraging depth to occur. Mitchell (1968) found that two parasitic mites were colonizing different areas of their shared host's body (the damselfly *Cercion hierglyphicum*), with one species on the thorax and the other on the abdomen. Similarly, two flea beetles (*Phyllotreta cruciferae* and *P. striolata*) occupy different surfaces of the same *Brassica oleracea* leaves (Tahvanainen, 1972).

There may be one or more additional extrinsic factors, such as predation or environmental processes including temperature and rainfall, which reduce the population densities to such an extent that competition is not important (Chesson and Case, 1986). Other factors, such as fluctuating environments, can act on the direction
of competition so that its effects are reversed before competitive
exclusion can occur (Hutchinson, 1957). Alternatively, limiting
resources may be renewed so fast that a competitively inferior
species can find the resource in sufficient quantity before it is
completely consumed by a superior competitor (Underwood, 1978,
1979). This suggests that other factors can be more important than
competition and that community structure is not always controlled by
competition so that the argument is not whether competition occurs
in the wild but, rather, when is it of more importance than other
processes (Connell, 1979; Strong et al., 1984; Case and Diamond,
1986). Nonetheless, spatial heterogeneity plays an important part in
competitive interactions enabling species to evolve and exhibit
adaptive mechanisms such as resource partitioning and habitat
segregation which promote coexistence.
1.3.2 Resource Partitioning

As Darwin (1859) pointed out, the evolutionary significance of competition is that, where possible, competitors will respond to natural selection so as to reduce or minimize the adverse effects of competition. In other words, coevolution between competing species can occur (Roughgarden, 1983), the two most commonly observed processes being resource partitioning and habitat segregation (Diamond, 1978; Pontin, 1982). Interspecific competition is often reduced by resource partitioning (Schoener, 1974a) where competitors have sufficient non-overlap along the resource utilization axes which delineate their respective realized niche spaces for coexistence to be possible (Hutchinson, 1957; MacArthur and Levins, 1964). Schoener (1974a), in his review of the literature, found evidence for resource partitioning in more than 80 natural communities, and, in a later survey, he found that competition had occurred in some 90% of the 164 field-experimental studies on interspecific competition then published (Schoener, 1983).

Schoener (1974a) also identified and ranked five resource dimensions by their degree of importance in niche segregation; namely, macrohabitat, microhabitat, food type, time of day and seasonality of activity. In other words, habitat segregation can be thought of as a form of resource partitioning, although often at a larger scale. Scale is important because Schoener (1983) found that when the niche dimensions investigated were food type or microhabitat use, a greater degree of ecological overlap implied a
greater tendency to compete whereas the opposite was true at the macrohabitat scale.

Associated with resource partitioning is the concept of character displacement, which simply proposes that there will be divergence in some character in areas of sympatry and that this divergence is an evolutionary response to interspecific competition (Brown and Wilson, 1956; Arthur, 1982). The evolution of character displacement can be thought of as competing species becoming more specialized, and Darwin (1959) and Brown and Wilson (1956), among others, have argued that, as a result of competition, generalists will tend to evolve into divergent specialists, and, as shown by Lawlor and Maynard Smith (1976), the main advantage is the increased efficiency in the exploitation of the same total range of resources when two generalist species are replaced by two specialists. Furthermore, this may involve divergence into new resources if limiting resources are not as equally well utilised by competitors (MacArthur and Levins, 1964, 1967; Pontin, 1982).

Usually, character displacement studies involve morphological characters which are believed to have a direct bearing on resource use and, although there have been a number of cases where character displacement may have been found (Fenchel, 1975; Diamond, 1978; Pontin, 1982; Roughgarden, 1983; Diamond, 1987), these can all be criticised for not being conclusive (Arthur, 1982; Diamond, 1987). However, there does now appear to be at least one clear-cut example (Fjeldså, 1983, 1986 [as reported by Diamond, 1987]). The character
in question, however, need not necessarily be morphological, it can be physiological or behavioural (including reproductive character displacement), so that the consequent temporal or spatial differences in the zone of contact may reduce the number of interspecific contacts to a level that allows coexistence even if the species still share the same food resources (Pontin, 1982). In such cases, this behavioural form of character displacement can, perhaps, be thought of as microhabitat selection (see below) which reduces the overlap in resource use of the competing species and leads on to the more general phenomenon of habitat segregation (sometimes called niche shifts or segregation) which can also promote coexistence (MacArthur and Levins, 1964). As is often the case with such classifications, the difference between the terms resource partitioning and habitat segregation can be somewhat arbitrary and hence interchangeable.

The advantage of using Hutchinson's definition of the niche when investigating resource partitioning is that it is a quantifiable one so that, at least in theory, the degree of resource partitioning (and, hence, niche overlap) can be measured (Ayala, 1970). In practice, a single niche dimension is usually considered (Pianka, 1976) and involves morphological characters closely correlated with the limiting resource being exploited: feeding structures (bill or jaw size, for example) or body size, which are often correlated with mean food size (Schoener, 1974b).
The effect of interspecific competition is, therefore, to reduce species overlap which is often by a decrease in niche width, in other words, increased specialization in resource or habitat use, (Pianka, 1983; Schoener, 1983; Price, 1984; Diamond and Case, 1986). On the other hand, with similar reasoning it can be seen that intraspecific competition between various genotypes may increase niche width by increasing the spectrum of resource use, and so on, so that if intraspecific interactions are, for some reason, more important than interspecific ones then a species may become more of a generalist. There is, therefore, often a balance between interspecific competition which tends to promote specialization and intraspecific competition which tends to promote generalisation (Pianka, 1983), a topic which will be returned to later.

1.3.3 Resource Subdivision or Patchiness

Although resource partitioning involves some form of resource heterogeneity (more than one limiting resource), coexistence is still possible on a single limiting resource if there is some other form of spatial heterogeneity present. Mathematical models show that, while unable to coexist on a single, undivided (that is, a continuous or homogeneous) limiting resource, competing species (even of unequal competitive ability) may be able to if the resource is subdivided into patches. In these models, resource partitioning or habitat segregation in the usual sense is not necessary. Instead, the two important parameters are the degree of resource patchiness and how the competing species disperse among the patches. The general conclusion is that coexistence is possible if the species
have clumped distributions among the patches (Skellam, 1951; Horn and MacArthur, 1972; Levin, 1974; Lloyd and White, 1980; Atkinson and Shorrocks, 1981; Shorrocks and Rosewell, 1984; Hassell and May, 1985). For example, if each species has a negative binomial distribution a superior competitor will colonize only some of the patches, leaving other patches vacant for the other species to colonize.

Two of the assumptions of classical Lotka-Volterra based competition theory - that migration is unimportant and that the environment is spatially homogeneous (Chesson and Case, 1986) - do not, therefore, hold in such models. In effect, the aggregation of the superior competitor leads to vacant breeding sites or refugia being available for the weaker competitor, thus facilitating coexistence. In such cases, interspecific competitive ability is of less importance than the degree of intraspecific aggregation among the patches so that the number of interspecific interactions in any one patch is reduced and interspecific competition is largely avoided even if a single limiting resource is being exploited (Atkinson and Shorrocks, 1981).

Skellam (1951) put forward a related model where coexistence between two annual plant species was due to the random dispersal of seeds over potential sites. The competitively weaker (but with the higher reproductive potential) survives by colonizing and surviving in sites not colonized by the competitively superior (but with the lower reproductive potential) species. This is similar to
Hutchinson's idea of fugitive species which can only become established in randomly vacated sites (Hutchinson, 1951, 1953; also see Brian, 1956). In other words, a competitively weaker species may be able to coexist with a stronger species because new, vacant sites (or patches) arise each generation and the competing species colonize these sites by random dispersal so that the weaker species becomes established in suitable vacant sites or microrefuges free from the superior species (Hutchinson, 1957).

Horn and MacArthur (1972) and others (see Casewell, 1978) have also based their models on random colonization of patches and show that coexistence is a balance between local extinctions and recolonisations in a patchy environment of two similar habitat types. Spatial uniformity, however, leads to the extinction of the fugitive species (Levin, 1974). Furthermore, Levin (1974) shows that in Horn and MacArthur's (1972) model, coexistence is possible with only one type of habitat patch so long as the patch is highly subdivided. Levin's (1974) own model examines the effect of migration rates between one or more patches where each species establishes itself in a patch in sufficient numbers to be able to withstand invasion from the other species. The success of a species as a competitor within a patch is hence dependent on initial numbers so that each species has a refuge in patches where it is numerically dominant (Shorrocks et al., 1979). Again, as Levin points out, these patches do not have to consist of different resources: the patchiness itself provides the spatial heterogeneity which, together with the migration rates, promotes coexistence. If the migration
rate between patches is too high, there is effectively only a single patch, and coexistence may no longer be possible (Levin, 1974). Patchiness together with dispersal can also reduce the chances of competitive exclusion occurring by extending the persistence time (the time for competitive exclusion to occur) so that there is effectively coexistence (Casewell, 1978).

In models of competition among a patchy ephemeral resource, competitive ability is, therefore, of less importance than resource subdivision (patchiness) and the degree of independent aggregation of the competing species over the patches. (The resource is ephemeral because, although renewable, each patch can only support a single generation.) There can be coexistence on a single resource if it is patchy and ephemeral and each of the competing species has an independent aggregated distributions thus reducing the overlap in distributions. The degree of aggregation of the species is important because, in these models, an inferior competitor will be excluded if the species are randomly distributed among the patches, whereas coexistence is possible if they both have negative binomial distributions with no covariance between the species (Atkinson and Shorrocks, 1981; Ives and May, 1985).

Shorrocks and his coworkers (Shorrocks et al., 1979; Atkinson and Shorrocks, 1981) have developed a particularly interesting model because it aims to represent the nature of breeding and feeding sites of many insect communities which exploit discrete, ephemeral resources such as dung, carrion, fruit, fungi and dead wood.
In this model, coexistence is possible between unequal competitors because of the patchiness of the resource and the degree of intraspecific aggregation (clumping) of eggs laid among the patches. A negative binomial distribution of individuals (and, therefore, eggs laid) over the patches leads to a significant reduction in the overlap (and, therefore, interspecific competition) of the two species and thus promotes coexistence (Shorrocks et al., 1979). Analytical studies have extended the model and show it to be robust giving similar results whether competition within a patch is either scramble or contest (Ives and May, 1985).

The model, which has been extended to multispecies communities (Shorrocks and Rosewell, 1986), shows that interspecific competition, though possible, need not be an important organising force in such insect communities (Shorrocks et al., 1984; Shorrocks and Rosewell, 1986) and that coexistence between two species can be extended by dividing the resource into more and smaller breeding sites (Atkinson and Shorrocks, 1981).

Interestingly, the model is more powerful when both resource subdivision and independent aggregation is incorporated (Atkinson and Shorrocks, 1981) and experiments have found that increased patchiness can, indeed, increase aggregation and hence reduce interspecific competition in dipteran communities. Kneidel (1985) found that the overlap in species distributions decreased when two Dipteran species oviposited among more subdivided (patchy) breeding sites. The two species of flies (Fannia howardi and Megaselia scalaris) which breed on carrion (dead snails, arthropods, mice and...
similar carrion) oviposited for a day in population cages which varied only in the degree of patchiness of a single resource. There was a significant reduction in the overlap in distribution of the two competing species in the cages with high patchiness (twelve 0.5g sections of pork kidney) compared to cages with low patchiness (three 2g sections of pork kidney). However, the increased patchiness in breeding sites also led to a decrease in percentage survival in both species because of severe intraspecific larval competition in the small pieces of food and, as the experiments were carried out for only one generation, the results can only give qualified support that increased patchiness of breeding sites can decrease species overlap on the same resource and hence prolong coexistence as proposed by Atkinson and Shorrocks' model.
1.3.4 Competition and Habitat Segregation

Habitat segregation, where competing species exploit different parts of their shared environment, can also promote coexistence. Like resource partitioning, some form of spatial heterogeneity is necessary but here environmental heterogeneity is of greater importance because the competing species are exploiting environmental rather than resource heterogeneity. The main difference between resource partitioning and habitat segregation is that the former involves the exploitation of resource heterogeneity at the same place whereas the latter involves spatial variation of resources and the differential use of one or more spatially separated resources. Habitat segregation can, therefore, lead to coexistence even without resource partitioning because it involves responses to one or more axes of environmental heterogeneity. The competing species use cues provided by the environmental heterogeneity for active dispersal to different areas, the adaptive value of which is that interspecific competition is reduced. For example, using a theory of optimal habitat selection, Rosenzweig (1979a and b, 1981) suggests that habitat selection (see below) by sympatric competing species may lead to coexistence by the coevolution of nonoverlapping habitat use. An important practical consequence of this is that present day competition may no longer be detectable between such coexisting competing species.

Habitat segregation can occur from large scale habitat differences to very small scale or microhabitat differences (Pontin, 1982); the latter differences are often called niche segregation,
shifts or differences (Diamond, 1978). This variety of terms, particularly at the local level, is not necessarily helpful because, strictly speaking, niche differences can involve both resource and habitat differences. Indeed, at the very local scale the distinction between resource partitioning and microhabitat differences is largely arbitrary.

There are many examples of habitat segregation (Diamond, 1978; Pianka, 1983; Diamond and Case, 1986; Werner, 1986), often between species of fish or birds. Lack, for example, believed that the habitat differences he found between closely related species of birds had arisen because of past competition (Lack, 1945; Mayr, 1970; Krebs, 1978). MacArthur (1958) in his study of 5 warbler species of the genus *Dendroica* (all of which are insect eaters, about the same size and are found on the same trees in New England forests) found that coexistence was at the microhabitat level and involved differences in searching for the same food in the same habitat rather than by resource partitioning: each of these species of birds had its own unique pattern of exploiting the forest including feeding at different tree heights or on branches of different diameters.

Habitat selection can be the proximate cause of species distributions (Fretwell, 1972) and the type of habitat selection which can reduce interspecific competition by habitat segregation is well illustrated by Shapiro and Cardé's (1970) work on sibling species of Satyrid butterflies and Schroder and Rosenzweig's (1975) on Kangaroo
rats *Dipodomys*. Shapiro and Cardé found that *Lethe eurydice* and *L. appalachia* displayed strong mutually exclusive habitat selection when in sympathy. Interspecific competition was, therefore, minimised by adult behaviour rather than by any difference in larval food. (Interestingly, although a third congeneric species *L. portlandia anthodon* overlaps *L. appalachia* in adult habitat preference, it has a different larval food plant.) However, as Shapiro and Cardé point out, this habitat selection, which does indeed minimise interspecific interactions, may be due either to evolutionary responses to interspecific competition or in response to different selective regimes while in allopatry and that the subsequent differences in habitat preferences which also promote habitat segregation and coexistence when in sympathy had not evolved in response to interspecific competition. Schroder and Rosenzweig (1975), however, believe that the interspecific differences in habitat differences between *Dipodomys ordii* and *D. merriami* were indeed maintained by present competition but could not conclusively show that the habitat selection observed had evolved in response to past competition.

Further evidence comes from Wiens (1986) who reports that habitat selection in some birds is in response to interspecific competition with natural selection acting on the patterns of habitat selection so that they are optimally adjusted to the habitat preferences of other potentially competing species, thus reducing niche overlap and, therefore, interspecific competition as has been proposed earlier (MacArthur and Levins, 1964).
However, like the controversy about the importance of competition in general, the problem is to show that the present day species distributions are indeed due to competition (whether acting now or in the past) rather than in response to some other process (Connell, 1980). The observation of habitat differences is not enough. As Howard and Harrison (1984) point out, although the observed association of one species with a particular habitat and of a closely related species with another habitat may be due to habitat preferences, this need not be a response to competition between the two. The distributions may be due to other interspecific interactions such as predation and parasitism or that each species survives better in some habitats irrespective of the presence of the other species. In field studies, it is possible to show that present day species distributions are due to competition by the removal of one or more species in an experimental area (Diamond, 1986). Recent studies including detailed work on a number of species and communities (Diamond, 1978; Inouye, 1978; Pianka, 1983 and Diamond and Case, 1986), answer many of these criticisms and the work of Moulton and Pimm (1986) and Diamond (1986) on a number of bird communities appear to answer most, if not all, of the criticisms including the critical evidence that the observed differences are indeed a consequence of competition (Connell, 1980).

Another problem is being present while habitat selection is evolving as a response to interspecific competition (in the sense of Rosenzweig, 1981) occurs. This has been rarely observed; but one possible case where allopatric taxa have met and then developed
spatial separation by habitat, apparently because of interspecific competition (Diamond and Case, 1986), is that of the expansion and subsequent retreat of the Azure tit's (*Parus cyanos*) range. Pleske (1912; Vaurie, 1957) who observed these changes over several decades, believes that this retreat was due to contact and competition with its close relative, the Blue tit (*Parus caeruleus*).

The important point to be emphasised here is that even ecologically closely related species which show little or no resource partitioning may still be able to coexist by behavioural differences which lead to habitat selection (if there is the appropriate environmental heterogeneity). Furthermore, the environmental cues used need not necessarily be the selective agents acting directly on the species because the adaptive value of such habitat selection is that the overlap between species is reduced and interspecific competition minimised.
1.4 Spatial Heterogeneity and Predation

1.4.1 Predation and Diversity

Predation, which in its widest sense includes herbivore-plant, parasite- and parasitoid-host interactions, can be visualized as a -+ interaction (see Table 1.1): the predator benefits directly from the interaction while the prey is adversely affected in that it is consumed by the predator! Predation is frequently claimed to be an important organising force which promotes and maintains species diversity in at least some communities (see Menge and Sutherland, 1976; Schoener, 1983; Pianka, 1983; Sih et al, 1985; for recent reviews) by reducing the intensity of competition between competing prey species so that competitive exclusion is unlikely (Clarke, 1962; Paine, 1966; Roughgarden and Feldman, 1975; Pontin, 1982; Giller, 1985; Chesson and Case, 1986).

Clarke (1962) put forward the idea that predators may be able to stabilize prey populations by feeding disproportionately on the most common prey, coining the term "apostatic selection" for this type of frequency-dependent predation. Concentration on common prey means that apostatic selection can promote coexistence because rarer prey, simply by virtue of their rarity, are at a selective advantage. Furthermore, predators which respond to prey in this way will cause prey species abundances to become more even which in itself may increase species diversity (Glasser, 1979).

Murdoch (1969) called the concentration on the common prey (so that there is a non-linear relationship between the proportions of
different prey present in a population and the proportion consumed) "switching" (Figure 1.2). For switching to occur, preferences have to be able to change as prey frequencies change, (Curio, 1976) and this has been found in many predators from protozoa to birds (Murdoch and Oaten, 1975). Moreover, it is an adaptive optimization strategy which combines the advantages of general feeding with the efficiency of specialization (Cornell, 1976). In other words, because of the constraints imposed on predators (see Chapter 2), optimal foraging can be thought of as an adaptive optimizing strategy and apostatic selection (which can be caused by switching) as the causal mechanism employed by predators (Hubbard et al., 1982; Greenwood, 1984b).

Most of the experimental evidence for apostatic selection comes from either semi-natural experiments with predators (usually wild passerine birds) being presented with artificial prey (Allen and Clarke, 1968; Allen, 1974, 1976; Bantock and Harvey, 1974; Bantock et al., 1975) or laboratory experiments with captive predators feeding on a variety of prey (Popham, 1941, 1942; Murdoch, 1969; Manly et al., 1972; Cook and Miller, 1977; Fullick and Greenwood, 1979; Willis et al., 1980). The prey are usually polymorphic for body colour but there have been experiments on body shape, size, and colour patterning as well as for smell (Shelton, 1987; Raymond, 1984; Soane and Clarke, 1973). Other experiments include the elegant work of Cahn and Harper (1976a and b) who found that sheep could forage and select for clover leaves apostatically and thus maintain
the observed leaf marking polymorphism (see also Ayala and Campbell, 1974; Murdoch and Oaten, 1975; Greenwood, 1985).

Evidence from nature is somewhat limited, most has come from observations on polymorphic snails such as *Cepaea* (Clarke, 1962a, b; 1969) and the African land snail *Limicolaria martensiana* (Owen, 1965a, b) which are particularly useful because shell remains are left after predation (see also Owen and Weigert, 1962; Clarke, 1962, 1969; Ayala and Campbell, 1974 and Edmunds, 1974). Moment (1962) proposed a form of apostatic selection (independently to Clarke (1962)) which he called reflexive selection to explain the very high degree of visual polymorphism in brittle stars and other animals (see also Owen and Whiteley, 1986). Most of the evidence, however, has been criticised and hence the generality of apostatic selection in the wild (Murdoch and Oaten, 1975; Jones et al., 1977, Krebs, 1978; Endler, 1986; Goodhart, 1987). There is, however, more indirect evidence where the effect of predation has been inferred by observing the consequences on the prey. Indeed, apostatic selection was first put forward as a mechanism that could explain the high degree of visual polymorphism observed in many invertebrate prey, with some of the morphs being non-cryptic (Clarke, 1962; Moment, 1962).

1.4.2 Spatial Heterogeneity and Predation

A consequence of predator pressure and hunting strategies is the evolution of antipredator defences such as distastefulness, mimicry, warning colours and camouflage or crypsis (Wickler, 1968; Robinson,
1969; Edmunds, 1974; Harvey and Greenwood, 1978; Pianka, 1983): a topic largely outside the scope of this thesis. However, the effects of spatial heterogeneity on predation and hence on prey interactions are of importance here. There is considerable evidence, both theoretical and experimental, that the impact of predation is affected by spatial heterogeneity, and that predation itself affects the spatial distribution and abundances of prey species (including parasitoid-host and herbivore-plant interactions as well as more conventional predator-prey interactions).

Spatial heterogeneity can affect predator-prey interactions in a number of ways. One form is environmental or structural heterogeneity where the complexity makes prey harder to find: in simple environments predators often have less difficulty in searching for prey (Hassell, 1976; Hassell et al., 1977). The experimental increase of structural complexity can also reduce the impact of predation (Ware, 1973; Russ, 1980; Thompson, 1982; Crowder and Cooper, 1982; Gilinsky, 1984; Cook and Streams, 1984), the stability of communities of species associations (including predator-prey and competition studies) is higher in heterogeneous model environments (Gause, 1934; Smith, 1972; May, 1973; Caswell, 1978; Vance, 1978; Hastings, 1980). Furthermore, in experimental studies the persistence of prey is dependent on the availability of refuges (Crombie, 1947; Huffaker, 1958; Connell, 1961a,b; Paine, 1966, 1974; Salt, 1967; Neill, 1975; Menge et al., 1985).
Refuges are areas where predation risks are reduced thereby degrading predator efficiency (at least locally) and generally reducing the overall effect of predators on prey. Refuges can be total (physical shelters, for example) where prey are safe from predators (Wiens, 1976; Menge et al., 1985) or transient (or partial) caused by predator foraging behaviour which is frequently nonrandom or aggregative (Curio, 1976). This behaviour can lead to some prey escaping predation so that the prey population is partially buffered from the negative effects of predator, thus stabilizing the interaction (Hassell and May, 1985; Sih et al., 1985; Begon and Mortimer, 1986): a response found in many classes of predators, both invertebrates and vertebrates (Curio, 1976). Aggregated foraging behaviour is often seen in response to prey patches because predators can forage optimally by concentrating on patches of higher than average quality so that some patches of prey may escape predation (Krebs, and McCleery, 1984; Begon and Mortimer, 1986; Stephens and Krebs, 1986; Krebs, 1987).

It should also be noted that, although these responses can stabilize predator-prey interactions, they are manifested because, in these cases, they are of selective advantage to the predators (Begon and Mortimer, 1986). Indeed, not all predators show this response: the true fruitfly Dacus tryoni oviposits more evenly than would be expected with a random distribution with the result that few host fruit remain uninfected and intraspecific larval competition is reduced to a minimum because few fruit become overcrowded (Monro, 1967).

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Another form of spatial heterogeneity which can alter predator behaviour, including preferences, is that of patchiness in prey distributions. This can occur at different spatial scales: prey may, for example, be found in separate areas or subhabitats so that predators are faced with a coarse-grained environment. Here, switching occurs between areas or subhabitats (Ware, 1971; Murdoch and Oaten, 1975; Werner and Hall, 1979; Werner et al., 1981; Zach and Smith, 1981) rather than where switching occurs in response to changes in the relative frequencies of prey within an area or patch. This tendency to forage in particular areas is strengthened by the ability of many predators to associate specific areas with either particular prey types or with prey quality (Croze, 1970; Krebs, 1973; Curio, 1976). Similarly, Werner et al., (1981) found that different preferences were formed by spatial variation in prey abundances.

The response of predators to patchiness is of interest here because the subdivision of the environment into patches, together with limited dispersal between patches, can promote coexistence (Huffaker, 1958; Hassell, 1978). In Caswell's (1978) model of predator mediated coexistence, two competing species suffer predation from a third species. Coexistence between the prey species was possible if the model consisted of an open, nonequilibrium system with the environment subdivided into patches with limited, stochastic dispersal between these patches. However, in a closed system, where, in effect, the environment is a single homogeneous habitat patch with no dispersal possible, coexistence was not found.
Under the strict conditions of this model (total competitive exclusion between the two prey species, no frequency-dependent predation within a patch) predation was unable to promote coexist coexistence within a patch.

In other words, although a species became extinct quite often in a patch, the discrete microhabitats (patches) found in the spatially heterogeneous environment enabled the species to persist by repeated colonization of vacant patches. Indeed, this appears to be the situation found in rocky intertidal communities (Menge et al., 1985). Furthermore, the outcome of Casewell's predator mediated model of coexistence has a similar outcome to that of Atkinson and Shorrocks model of competition in a patchy environment, thus showing the potential of spatial heterogeneity in promoting coexistence (Atkinson and Shorrocks, 1981).

Holt (1984) has also examined predation and spatial heterogeneity, emphasizing the importance of the spatial scale perceived by both predator and prey. The scale experienced by the prey may be coarse-grained whereas a predator may perceive it as fine-grained so that the prey patches become effectively a single, homogeneous patch to a predator with high mobility. In this case, there is shared predation between prey in different patches which leads to stable segregation of the prey species between patches. Holt (1984) calls this "apparent competition" because, although competition has not played a part in the model, the result is as
though there had been habitat segregation due to exploitation competition.

There are a number of mechanisms by which prey can reduce the impact of predation within patches as well (warning colouration, mimicry and distastefulness, for example) but one way is by altering their spatial distribution so that they are spaced out. At low population densities, the encounter rate of a predator can be reduced to such a level that its preference for that prey may decay through too low a reward rate. Indeed, the efficacy of spacing-out by prey can be inferred by the observation that many cryptically coloured animals are solitary (de Ruiter, 1952; Edmunds, 1974) and this has been corroborated by the experiments of Tinbergen et al., (1967) and Croze (1970) who found that spaced-out artificial cryptic prey suffer less predation (see also Chapter 2).

The effects of spacing-out on predation can also be used by non-cryptic prey especially parasite-host and plant-herbivorous insect interactions, with more dispersed host plants generally suffering less predation (see Hassell, 1982; Root and Kareiva, 1984; Kareiva, 1986). Prey spacing-out behaviour will also counteract predators' habit of area-restricted (or concentrated) searching (Smith, 1971, 1974a,b; Krebs, 1973; Curio, 1976) which is often an efficient foraging behaviour because most animals tend to have non-random clumped distributions (Taylor, 1961). Spacing-out behaviour can also reduce the risk of predation in general, Krebs (1971) found that the nearer a great tit Parus major nest was to another's nest in his
study area in Wytham Woods the greater the chance of predation by weasels, which are a major predator of great tit nestlings (Dunn, 1977). However, the effect of spatial distribution of polymorphic prey within a patch on frequency-dependent predation has been overlooked and little is known on how predator behaviour may be altered (and hence prey survival) when faced with prey with contrasting patterns of prey spatial distributions. This will be investigated in Chapter 2.
1.5 Conclusions

Although there is considerable evidence that both predation and interspecific competition are important in the structure of communities, the key controversy is the relative roles of predation and competition (Giller, 1984; Sih et al., 1985); a controversy that has yet to be resolved (Connell, 1979; Strong et al., 1984; Diamond and Case, 1986; Rickleffs, 1987). Only a limited number of field experiments have involved both predators and competitors and most of these have involved rocky intertidal communities. The results suggest that predation and interspecific competition are generally (and roughly equally) as important (Sih et al., 1985). However, Giller (1984) believes that the evidence does not support the hypothesis that predation is the primary process in the structure and evolution of communities. Indeed, the main criticism is not whether competition can occur but how prevalent is it; other environmental factors may prevent resources from becoming limiting by keeping populations below carrying capacity so that processes such as variable environments and disturbances may prevent competitive exclusion (Connell, 1979; Wiens, 1976, 1986).

Predation can reduce competition by keeping prey populations below the carrying capacity of the environment so that resources are not limiting. Predation can, therefore, influence the limits to similarity between competing prey species. Roughgarden and Feldman (1975), for example, found broader limits to similarity in resource use when a predator was added to classical competition equations. In such cases, predation can be thought of as an extrinsic factor that
acts as an additional resource axis (Levin, 1970). The predator represents one or more of the limiting factors leading to the suggestion that predator pressure may be how assemblages of potentially competing species can show high degrees of resource use overlap without any differential partitioning of resources (Chesson and Case, 1986).

The effect of predation on species diversity is enhanced if predators concentrate on the dominant (and usually most common) competitor in a community (Ayala and Campbell, 1974; Roughgarden and Feldman, 1975; Connell, 1978) thereby preventing any one prey species from monopolizing a potentially limiting resource (Connell, 1970; Sih et al., 1985). Paine (1966), for example, found that the starfish, Pisaster, was acting as a keystone predator which promoted species diversity in the intertidal community by keeping many of the prey populations below carrying capacity and hence reduced the chances of competitive exclusion. Other experiments have also shown the importance of predation in increasing species diversity (Connell, 1970; Lubchenco and Gaines, 1981; and see Menge and Sutherland, 1976; Sih et al., 1985 for further references). Frequency-dependent predation can also increase diversity by preventing competitive exclusion and permitting greater niche overlap, thus increasing the number of coexisting species (Connell, 1978). Hassell (1979), for example, found that switching (concentrating on the most common prey: see Chapter 2) by a predator stabilized one predator n-prey systems. Furthermore, this compensatory mortality was the only mechanism that could stabilize
interactions where there was complete niche overlap between prey species.

Predation can, therefore, have an important role in the structure and evolution of communities. However, most of the evidence for predator-mediated coexistence involves lower trophic levels (zooplankton and intertidal communities) and the number of examples of predation being the important factor in field experiments is fewer than those for competitive interactions (Giller, 1984; Sih et al., 1985). Furthermore, predation can also decrease species diversity especially when predators lack preferences and there is high predation pressure (Addicott, 1974; Casewell, 1978; Moss, 1980; Hunter and Russel-Hunter, 1983). Scale is important: predation is most likely to reduce diversity at the local scale (Menge and Sutherland, 1976; Anderson, 1979; Whittacker, 1979; Holt, 1984). Predation generally decreases diversity within patches but increases or maintains diversity among patches (Menge et al., 1985; Schmitt, 1985). In other words, the conditions necessary for predation to promote or maintain diversity appear to be somewhat restrictive. However, since the late 1970's there has been a shift to the view that predator-prey interactions are of greater importance in the structure and evolution of communities than competitive ones (Paine, 1966; Harper, 1969; Connel, 1975; Sih et al., 1985).

These two processes can directly affect each other: for example, predation can increase competition by forcing prey species to compete for limited number of refuges available in an area (Buss,
1986) so that the risk of predation can compel prey species to feed together (Werner, 1986). Conversely, competition can increase the risk of predation (Kareiva, 1986); a major consequence of competition among fish is that growth rates are reduced and smaller fish are at a greater risk from predators than are larger fish (Werner, 1986). Theoretical studies also show that predation and competition can interact in the maintenance of species diversity so that, overall, predation and competition are complementary hypotheses which should not be considered as if in a vacuum. Instead, they should be considered as mechanisms whose effects and relative importance are largely determined by the abiotic environment in which they occur.

These interactions are further complicated by variable environments, the frequency and degree of ecological crunches including disturbances, and the time lags involved in population responses which keep populations below levels at which resources become limiting (Connell, 1979; Wiens, 1986). An example of this can be seen in the combination of factors involved in the explanation of the high diversity observed in herbivorous insect guilds. As well as competition (Claridge, 1987), these include predation, parasitism, plant distribution and quality, the difficulty in finding hosts and dispersal in general, plant chemistry and variable weather! (Lawton and Strong, 1981; Giller, 1984; Kareiva, 1986). Furthermore, interactions may be mutualistic at low densities and competitive at high densities (Kareiva, 1986).
The role of spatial heterogeneity in population interactions is not, however, questioned; in some communities such as insect herbivores it is paramount (Karieva, 1986; Lawton, 1986). Patchiness can reduce the effect of both predation and competition so that, in a patchy environment, how species disperse among patches may determine coexistence (Caswell, 1978; Hassell, 1978; Ives and May, 1985; Chesson and Case, 1986; Shorrocks and Rosewell, 1986). For example, in an experimental predatory:prey mite system, Huffaker (1958) found that increased spatial heterogeneity produced greater stability. In a patchy environment, therefore, species interactions can be a combination of dispersal, predation and competition (Hassell, 1978; Kareiva, 1986). In Caswell's (1978) model, coexistence is also possible in a patchy environment but not in a homogeneous one where differential dispersal can not occur.

Dispersal can also be important at the intraspecific level: animals which exploit patchy and ephemeral resources must move to new vacant patches or else die out. For many insects (including Drosophila) whose populations are mosaics of extinctions and recolonizations, this form of dispersal is a key mechanism by which they can respond to the spatial and temporal unpredictabilities often present in their environment (Southwood, 1977). Furthermore, the larval stage is generally sedentary so that adult dispersal provides the source of recolonists (Andrewartha and Birch, 1954; Ehlrich, 1983). Local populations can be highly divided and unstable (Stalker, 1976; Taylor and Powell, 1983; Hoffman and Nielsen, 1985) because the sites exploited are often small in size, discrete and
ephemeral. In orchards, for example, the usual number of *D. melanogaster* females ovipositing in any one site (such as a fallen apple) is less than five (Hoffman and Nielson, 1985). The ephemeral nature of breeding sites can also lead to great variation in population numbers during the year, often on a cyclical basis (Spencer, 1968; Shorrocks, 1974, 1982; Parsons, 1983; Speith and Ringo, 1983).

One form of active dispersal which may be particularly important for animals confronted by a complex, heterogeneous environment is habitat selection (Jones, 1980). Habitat selection (sometimes called habitat fidelity) is difficult to define satisfactorily. (Indeed, the term "habitat selection" has been critised as it implies that the organism weighs up the alternatives available — a behaviour not always important or available (Miller and Strickler, 1984; Hoffman and Turelli, 1985; Parsons and Hoffman, 1986).) Taylor and Powell (1978) define habitat selection as a tendency to return to areas similar to those in which the animals were originally captured. They also propose that such habitat choice is an adaptive response to a heterogeneous environment. A consequence of this tendency to remain in areas in which individuals have optimum fitness is that gene flow between sub-populations is restricted and, in theory at least (the evidence for habitat selection is somewhat equivocal [Hedrick *et al*., 1986]), this can maintain genetic variation and cause speciation (Felsenstein, 1981; Rausher, 1984; Rice, 1984; Futuyama and Peterson, 1985; Hedrick *et al*., 1986; Taylor, 1986; Diehl and Bush, 1989).
Habitat selection - which is probably best thought of as a behavioural mechanism by which an organism locates and accepts a habitat or area - can involve environmental cues as well as the internal state of the organism (Hoffman and Parsons, 1986). It may be a predetermined, genetical trait, or may involve some degree of learning, or a mixture of the two. An advantage in having a modifiable or learned component to habitat selection is that the animals in a population are able to change their behaviour and can, therefore, rapidly exploit new or vacant niches that generation without having to wait for genetic (ie, between-generation or evolutionary) changes. This within-generation change permits resource tracking and the exploitation of suboptimal habitats so that an area which has become more favourable (because, for example, of overcrowding in a previously optimal area or an area which is usually suboptimal is now vacant of competitors or predators) can be rapidly colonized and efficiently exploited.

Another advantage in having flexibility in habitat preferences is that individuals in a population can respond more rapidly to changes in the balance between intra- and inter-specific competition than by solely genetic means. This means that individuals can exploit all of the range of resources available and the cost of individual specialization within a population is thus avoided (Jaenike, 1986a). This is often the case for parasitoid-host interactions where female parasitoids often emerge into environments with few hosts and so have to disperse to new areas (Vinson, 1981, 1984). Intraspecific competition will tend to increase niche width thus making a species
more of a generalist whereas interspecific competition tends to reduce niche width and make a species (or population) more specialised (Pianka, 1983). If this can occur behaviourally (that is, by non-evolutionary or within-generation change), a species or population can rapidly respond to the changes. Habitat selection, therefore, can have more than one effect (and with more than one selective agent acting) so that it may be difficult to ascertain how it may have arisen in the first place.

In a spatially heterogeneous environment, habitat selection which affect species distributions (Fretwell, 1972) may also be important at the interspecific level because it reduces interspecific competition while, at the intraspecific level, it may be important in mate finding. There may be, therefore, positive feedback between habitat selection, the effective finding of mates and the reduction of competition (Colwell, 1986). Colwell (1985a and 1985b) found that habitat selection (in the form of host fidelity) is important for short-lived, mobile animals such as insects and mites where, in a patchy environment with ephemeral breeding sites, mating ability is optimised by host fidelity which brings conspecifics together onto the same host plant (see Andrewartha and Birch, 1984; for further examples).

Whatever the controversy about the importance and relative role of competition and predation, there is little doubt about the importance of heterogeneity in general, and spatial heterogeneity in particular, on these two interactions. Spatial heterogeneity struct-
ures species distributions and interactions (Feisinger et al., 1988) so that coexistence, species diversity, the structure of communities, and even the genetic diversity of individual species in a community may all be influenced by a patchy environment. In this thesis I examine some of the effect of spatial heterogeneity on competition and predation.

In Chapter 2, I investigate the effect of frequency-dependent ("apostatic") predation and prey spatial patterning within patches and whether such predation can promote coexistence by favouring the mixing of prey types in the same patch so that, although living on a homogeneous background, the spatial distribution of the prey themselves provides the spatial heterogeneity.

Chapter 3 and 4 will examine how microenvironmental patchiness can affect population interactions of Drosophila melanogaster and D. simulans in the wild and the laboratory. The environmental factor examined here is light and these two Drosophila species are ideal for such studies because, apart from light preferences, there are few significant differences in their ecologies. In Chapter 3, I investigate the effect of environmental patchiness on intraspecific interactions in D. melanogaster and whether such environmental patchiness in light conditions can affect light preferences so that populations become subdivided by microhabitat selection and whether this change is a solely behavioural (non-evolutionary) one or do the subdivided populations become genetically differentiated?
In Chapter Four, I examine if the interspecific differences in light preferences are adaptations which lead to interspecific differences in microhabitat selection and hence reduce competition between these two very similar sympatric species so that, in a patchy light environment, species overlap is reduced and coexistence promoted when exploiting the same resources.
FACTORS

Resource
ie, Breeding sites

Environmental
ie, temperature, light

DEGREE OF PATCHINESS

a) One Factor
i) Undivided
ie, a single resource

b) 2+ Factors
i) Undivided
ie, 2+ resources

ii) Divided

Figure 1.1
A simple Classification of Spatial Heterogeneity.
Figure 1.2
Switching occurs when a predator concentrates on common prey so that there is a non-linear relationship between the proportions of different prey present in a population and the proportions consumed.
<table>
<thead>
<tr>
<th>Type of Interaction</th>
<th>A</th>
<th>B</th>
<th>Nature of the interaction</th>
</tr>
</thead>
<tbody>
<tr>
<td>Competition</td>
<td>-</td>
<td>-</td>
<td>Each population inhibits the other</td>
</tr>
<tr>
<td>Predation</td>
<td>+</td>
<td>-</td>
<td>A, the predator, kills and consumes members of B</td>
</tr>
<tr>
<td>Parasitism</td>
<td>+</td>
<td>-</td>
<td>A, the parasite, exploits members of B, the host, which is affected adversely</td>
</tr>
<tr>
<td>Mutualism</td>
<td>+</td>
<td>+</td>
<td>Interaction is favourable to both but is obligatory</td>
</tr>
<tr>
<td>Protocooperation</td>
<td>+</td>
<td>+</td>
<td>Interaction is favourable to both but is not obligatory</td>
</tr>
<tr>
<td>Commensalism</td>
<td>+</td>
<td>0</td>
<td>A, the commensal, benefits whereas B, the host, is not affected</td>
</tr>
<tr>
<td>Amensalism</td>
<td>-</td>
<td>0</td>
<td>A is inhibited, but B is unaffected</td>
</tr>
</tbody>
</table>
2.1 Introduction

Predation can have a significant effect on prey populations (see Chapter 1) and the impact of predation is often reduced by antipredator mechanisms such as mimicry, warning colouration, distastefulness and crypsis (Wickler, 1968; Robinson, 1969; Edmunds, 1974; Harvey and Greenwood, 1978; Endler, 1978, 1986). Another possible antipredator mechanism exploits the fact that, for whatever underlying biological reasons, predators often take more of common prey (Curio, 1976) so that, in mixed populations, prey that are rare and different may have a selective advantage. Moment (1962), for example, suggested that the massive polymorphism in colour and pattern of some prey species evolved in response to pressure from visually hunting predators.

This variation is adaptive in that it may reduce the overall predation rate because visually hunting predators such as birds are unable to form preferences for all of the variety of distinct morphs available (Croze, 1970; Pietrewicz and Kamil, 1979, 1981; Owen and Whiteley, 1986) so that some escape predation. Moment (1962) called this "reflexive selection" because it is the variation per se which is adaptive with the fitness of a phenotype being related to its frequency in a population. A possible example is that of Croze's (1970) experiments on painted baited mussel shells where, overall,
trimorphic artificial prey populations suffered less overall predation from foraging crows than did monomorphic populations.

A similar form of frequency-dependent predation proposed independently by Clarke (1962a) is "apostatic selection" where, in mixed populations, prey which are different from the norm are at a selective advantage. This is also due to the tendency of predators to concentrate on the more common prey and, because predators take disproportionately more of common prey species, rare species will be at a selective advantage simply by virtue of their low frequency in the population (Clarke, 1962a and b; Clarke and O'Donald, 1964; Clarke, 1969; Murray, 1972; Murdoch and Oaten, 1975). This extends Moment's idea of reflexive selection because, not only will apostatic selection promote polymorphism within prey species (as can reflexive selection), it may also promote coexistence between competing species and hence increase local diversity.

This foraging behaviour is due to predators often having only a limited time available for foraging (for example, blue tits, *Parus caeruleus* have to find a prey item every 2.5 seconds of the available daylight in order to survive the British winter nights (Gibb, 1962)) so that natural selection will act so as to maximize energy gain and reduce the costs of hunting (MacArthur and Pianka, 1966; Pulliam, 1974; Charnov, 1976; Oaten, 1977; Krebs, 1978; Lucas, 1983; Greenwood, 1984a; Krebs and Mc Cleery, 1984; Pyke, 1984; Stephens and Krebs, 1986). When confronted with a diversity of resources, optimal foraging often leads to predators concentrating
on larger or the most common prey items. This is especially true when predators are unable to accurately assess prey abundance and distribution (Murdoch and Oaten, 1975; Lucas, 1983; Greenwood, 1984a).

To forage optimally, predators must also be able to react rapidly to changes in prey abundances so that predator preferences change as prey frequencies vary. This can occur by a number of mechanisms (Curio, 1976; Stephens and Krebs, 1986). Murdoch (1969) called this series of behaviours of concentrating on the common prey "switching", defining it as the absence of a linear relationship between the proportions of different prey present in a population and the proportion consumed by predators (see below).

Spatial heterogeneity can also have a significant effect on predation and hence population interactions (see Chapter 1) because predator behaviour, including preferences, can be altered by spatial heterogeneity — which may be caused by the environment or the spatial distribution of the prey themselves, or both. There are two main ways in which prey distributions can be heterogeneous: prey density may vary between patches, or prey are in separate patches or subhabitats so that predators are faced with a coarse-grained environment leading to predators being unable to forage in all of the available patches. Here, switching occurs between patches, areas or subhabitats (Ware, 1971; Murdoch and Oaten, 1975; Werner and Hall, 1979; Werner et al., 1981; Zach and Smith, 1981) rather than between prey types whose relative frequencies change within a patch.
This tendency to forage in particular areas is strengthened by the ability of many predators to associate specific areas with either particular prey types or with prey quality (Croze, 1970; Krebs, 1973; Curio, 1976). Furthermore, predators often show area-restricted (or concentrated) searching behaviour where predators tend to remain in the vicinity of where the last prey was captured (Curio, 1976; Krebs, 1973; Stephens and Krebs, 1986), an often efficient foraging behaviour because most animals tend to have non-random clumped distributions (Taylor, 1961).

A consequence of this area-restricted searching is that the impact of predation may be reduced by prey spacing-out behaviour where the nearest neighbour distance between prey is greater than the predator searching radius. Tinbergen et al., (1967) found that in a series of experiments with painted chicken eggs, carrion crows took significantly more eggs when the "inter-egg distance" was 50cm (24 out of 27 eggs, 89% of the total) than when the distance was 800cm (5 out of 27, or 15%). Using artificial flour and lard prey, Croze (1970) also found that as prey density increased the number of prey surviving decreased. He also showed that with the crowded populations, the crows took less time to find the prey than with the scattered populations and that this was due to the birds using area-restricted searching behaviour.

Spacing-out behaviour is particularly important for prey which use crypsis (where prey are camouflaged to resemble part of their background [Edmunds, 1974; Endler, 1978]) as their primary anti-
predator defence. To gain maximum protection individuals have to be widely dispersed so that prey are at a low population density and hence reduce the predator-prey encounter rate to such a low level that a predator's preference (or possibly searching image) for that particular prey is lost through too low a reward rate (see below). Indeed, many camouflaged prey are solitary (De Ruiter, 1952; Edmunds, 1974). Widely dispersed prey (even if not cryptic) can also be at an advantage: Krebs (1971) found that the nearer a great tit *Parus major* nest was to another's nest in his study area in Wytham Woods the greater the chance of predation by weasels, which are a major predator of great tit nestlings (Dunn, 1977). As predators find it harder to search for them, more dispersed hosts generally suffer less predation in, for example, parasitoid-host and plant-herbivorous insect interactions, (Hassell, 1982; Kareiva, 1986; Root and Kareiva, 1984).

This is not to say that all prey are dispersed, many prey are not cryptic so that being close together in groups or flocks can be an effective anti-predator mechanism. For example, flocks of starlings *Sturnus vulgaris* bunch up and fly close to each other when they are threatened by peregrine falcons—a behaviour which deters the predator from attacking (Tinbergen, 1951 in Edmunds, 1974). It is also interesting to note that prey that are very similar are often found in groups, herds or schools (Edmunds, 1974; Bertram, 1978). Such prey behaviour may actually swamp predators in an area so that some of the prey survive by the sheer number of prey available at the same time. Wallace (1889) called this type of behaviour
arithmetic mimicry after he had observed that many species of butterflies which suffered high levels of predation had synchronised emergence of adults.

Polymorphism is another way where prey density can be kept low with each prey morph at a low density which effectively increases inter-morph distance so that the overall population can be higher than in a similar monomorphic population. This is also a consequence of apostatic selection and Croze (1970) found that trimorphic prey populations do indeed suffer less predation than monomorphic populations with the same overall densities.

Although prey spatial distribution can have a significant effect on predation and hence prey survival, most experiments on apostatic selection have ignored any spatial component to frequency-dependent predation often using random prey distributions while most experiments on the effects of spatial heterogeneity have ignored frequency-dependent predation (for example, Hassell, 1978, 1982; Kareiva, 1986). Where spatial heterogeneity has been examined it has been in terms of variation in patch quality (the number or quality of prey in a patch), clumped versus dispersed distributions or interpatch distances of the same prey type (Krebs, 1978; Kamil and Sargent, 1981; Hassell, 1982; Pianka, 1983; Greenwood, 1984a; Krebs and McCleery, 1984), or, if more than one prey is available, the different types are found in separate areas (Murdoch and Oaten, 1975).
In this chapter I will present a series of experiments on how the spatial distribution of polymorphic prey affects relative prey survival using the simplest case of populations of two morphs (or species) differing in colour which are presented to predators on a uniform, simple background so that the spatial heterogeneity experienced by the predators is provided by the spatial arrangement of the prey themselves.
2.2 Materials and Methods

In these experiments I use a design related to that of Allen and Clarke (1968) who presented coloured pastry baits to wild passerine birds in their normal surroundings. The baits consisted of uncooked pastry (one part lard to three parts of flour by weight) made into cylinders 7mm long and about 3.5mm wide, dyed with food colouring either green (Pointing apple green K 6027) or brown (Pointing brown K 6024), two colours that are commonly found among prey (Allen, 1973). The experiments were first undertaken simultaneously at two sites at Bedford College, London (eight experiments). However, as it was not possible to adequately monitor the two sites, the experiments were transferred to a single site in a secluded house garden in Oxford where one experiment was performed each day over two years (43 experiments).

The baits were laid out in a ten by ten metre square grid on a closely cut lawn at a density of 2 baits per square metre giving a total of 200 baits per experiment. Three series of experiments were undertaken: the first involved 9 times as many green to brown baits; the second used the reversed frequency and the third equal numbers of the two colours. To examine the spatial component of frequency-dependent predation the baits were presented in one of two specific spatial arrays for each of the frequencies. The first distribution used a randomly distributed prey arrangement similar to that found in the standard apostatic selection experiments. The second, which I will call an "aggregated" distribution, had the prey types aggregated in different parts of the grid (Figure 2.1). Only the
arrangement of the prey was altered, the overall densities and frequencies in the two distributions were the same.

In each of the series the baits were presented in both of the arrangements described above so that there were, in all, three sets of frequencies and two spatial arrangements. When the baits were to have a random distribution the colour of the baits in any one meter square was determined by a random numbers table, and for the aggregated distribution the colours were assigned to separate parts of the grid which for the rare colour meant the 10 squares of one edge of the grid. Colours at equal frequencies were assigned to the left, right, top or bottom sectors of the grid, alternated at random. Each experiment was continued until approximately 100 baits had been taken, the position and number of baits eaten was then recorded and the remaining baits removed.

As baits were not replaced during an experiment, the results were analysed using the coefficient of selection, $B$, developed by Manly (Manly et al., 1972; see also Cock, 1978) and transformed by arcsine transformation giving $B_t$ values from 0 to 90 degrees and calculated so that the relative preference for green baits increases as the value of $B_t$ increases, with a value of 45° signifying no preference. $B_t$ is best seen as the relative risk of predation for the two types of baits, with the values indicating the probability that a green will be the next bait taken if there were an equal number of the two colours available.
2.3 Results

The main predators were common garden birds: a pair of blackbirds (*Turdus merula*) and small groups of 3 to 4 starlings (*Sturnus vulgaris*). A few baits were also taken by solitary song thrushes (*Turdus philomelus*), chaffinches (*Fringilla coelebs*), robins (*Erithacus rubecula*) and house sparrows (*Passer domesticus*). The birds were not seen to search for other prey while in the area but hunted only for the baits. Furthermore, the birds—especially the small groups of starlings—rushed around the area trying to get to the baits first indicating that searching speed was at a premium. The requisite 100 baits were usually taken within four or five hours from the set up and baits near the centre of the grid were more likely to be taken than those at the edge. Overall, in ten of the experiments involving random prey distributions, baits in the central squares were significantly more likely to be taken than those at the edge (in only one were prey taken significantly more often from the edge and in five there was no significant differences between central and peripheral squares (Table 2.1)).

Table 2.2 and Figure 2.2 show that although there was frequency-independent preference for brown with relatively fewer green baits taken (indicated by all the $\beta_t$ values being lower than 45°), there were marked differences in prey survival between the two spatial distributions. In experiments in which baits were distributed at random, frequency had a significant effect on the probability of predation with the preference for brown increasing as the frequency of brown increased. This is potentially pro-apostatic selection.
(where there is frequency-independent preference for a particular prey in addition to a frequency-dependent preference [Greenwood, 1984b]) and this frequency-dependent advantage of rare morphs scattered among individuals of a more common phenotype is familiar to that found by Allen and by others (Allen, 1988).

In the aggregated distribution, baits suffered the reverse: there was a significant increase in the chances of a rare prey being eaten so that it was positively disadvantageous for the rare colour to be aggregated together. This effect did not arise because of the rare prey were at the edges of the grid but in spite of it, since the birds concentrated their foraging towards the centre of the array.

In both the 9:1 and 1:9 green to brown experiments, therefore, the rare colour suffered significantly less predation when in the randomly distributed arrangement. The average $B_t$ value at the Bedford College site (where brown when rare) was $21.98\pm5.63$ when in the aggregated arrangement and $35.07\pm6.58$ when random ($t$-test=$3.99$, $p<0.01$). At the Oxford site, the average $B_t$ values were $27.24\pm4.12$ and $39.26\pm6.67$ respectively ($t$-test=$3.69$, $p<0.002$). When green was rare, $B_t$ was $35.02\pm6.16$ when aggregated and $22.71\pm8.05$ when randomly distributed ($t$-test=$2.98$, $p<0.01$). There was no significant difference, however, between treatments for experiments with equal frequencies: $B_t$ was $30.60\pm9.41$ for the aggregated distribution and $31.89\pm4.72$ for the random distribution ($t$-test=$0.34$, not significant).
2.4 Discussion

In these experiments, there is a significant spatial component to frequency-dependent predation with the frequency-dependent advantage of rare prey being lost in the aggregated distribution. Rare prey, therefore, have a greater chance of escaping predation when distributed among other more common prey types. This has a greater effect on rare prey because the loss of a single bait represents a much greater loss to the rare prey population in an experiment (1 out of the 20 rare coloured baits).

The effect of spatial patterning on prey survival probably results from predator searching behaviour. The constraints on optimal foraging (which are a balance between the cost of obtaining an item and the benefits gained from eating it) often lead to predators concentrating on common items in polymorphic prey populations so that the proportion of a particular prey eaten does not reflect its abundance in the population (Murdoch and Oaten, 1975). In other words, optimal foraging is an adaptive optimization strategy and apostatic selection or switching the causal mechanism (Hubbard et al., 1982; Greenwood, 1984b). Predators often do this by assessing prey abundance by encounter rates and preferences are formed for prey which are encountered above a threshold rate. This is most likely to be for common prey and, in polymorphic populations, will lead to frequency-dependent predation (Murdoch and Oaten, 1975; Curio, 1976; Kamil and Sargent, 1981; Stephens and Krebs, 1986).
One mechanism frequently suggested is "search image formation", a form of optimal foraging for cryptic prey which can be thought of as a perceptual change in the ability of a predator to detect familiar cryptic prey (Lawrence and Allen, 1983). As crypsis is one of the commonest ways antipredator mechanism, this could be an important predator behaviour (Poulton, 1884; Edmunds, 1974; Endler, 1978, 1981). The modern form of search image was proposed by Tinbergen (1960) to account for the foraging behaviour of Great tits suggesting that the birds were concentrating on the more common prey by forming search images (or "learnt to see" [Von Uexküll, 1934; Dawkins, 1971a; Dawkins, 1969]) for the common prey species of caterpillars. The adaptive significance is that, although the predator decreases its ability to detect rare prey, the increased probability of detecting an individual of the abundant prey within the predator's visual field more than compensates for this. As Matthews (1977) points out, searching images involve selective attention or discrimination learning with predators filtering out important cues from the totality of stimuli.

Switching will, therefore, occur when a preferred prey becomes rare because the rate of reinforcement of the existing searching image declines below a certain threshold and is, therefore, lost whereas encounters with a more common prey will lead to a searching image for that prey being formed. Pigeons, for example, having to forage on mixed grain populations presented on a complex background concentrated on the more common prey types and, as the rate of discovery (and hence the reward rate) of the more common grain type
fell below a threshold value, the birds switched. However, when the prey were easy to find by being presented on simple backgrounds (and thus not cryptic) or at equal frequencies, this did not happen (Bond, 1983).

There is, however, not only considerable confusion over what is meant by search images but, also, on how to test for it without confusing it with other mechanisms predators may employ (Krebs, 1973; Murdoch and Oaten, 1975; Curio, 1976; Lawrence and Allen, 1983; Guilford and Dawkins, 1987). Indeed, after careful examination of previous experiments, Guilford and Dawkins (1987) conclude that none of the previously accepted examples are conclusive evidence for searching images and suggest that, rather than any perceptual change, the predators were simply decreasing their search rate. Predator preferences may well be the result of becoming more familiar with a prey type (see Krebs, 1973; Murdoch and Oaten, 1975; Curio, 1976; Kamil and Sargent, 1981 for reviews on the formation and maintenance of preferences) and many of the examples which been put forward as evidence for search image formation can be equally (if not better) explained by such predator behaviour. Unlike searching images, such preferences can also occur when foraging for noncryptic prey: an important point because, like most bait experiments (Allen, 1988), the baits used in my experiments were not cryptic so that, by definition, the birds could not have been using searching images.

Nevertheless, for whatever underlying behavioural mechanism, apostatic selection can still occur when predators are confronted
with polymorphic prey populations because foraging predators are more likely to encounter the more common types of prey and, therefore, form preferences for these prey with which they have become familiar. When, for example, naive passerine birds were presented with mixed populations of artificial prey at frequencies of 9:1, the birds tended to become trained to the common prey colour (Allen and Clarke, 1968; Allen, 1972).

Indeed, most of the evidence for predator preferences involve training experiments where naive predators are presented with a single prey type and then presented with mixed prey populations containing familiar and unfamiliar prey types (Murdoch and Oaten, 1975). If training has occurred, the predators will take more of the prey with which they are more familiar. Furthermore, preferences can be changed or reversed by a second period of training for another prey type (Allen, 1974, 1984; Murdoch and Oaten, 1975; Greenwood, 1986). This is equivalent to the situations where a prey type becomes rare so that the rate of encounters with that prey decrease to a level that the predators lose any preference and, if other more common prey are available, this may lead to switching (Murdoch and Oaten, 1975). Murdoch (1969) reports that switching was only possible if there was an initial period of training where patches of the abundant prey were first presented to the predators so that preferences were formed before mixed prey populations were presented (see also Murdoch and Oaten, 1975).
This means that predators will be most likely to form preferences after a period of training on populations with a single prey type. This is not necessarily biologically unrealistic as many prey species have patchy distributions: the predatory snails used by Murdoch (1969) normally hunt on sea shores where such patches of prey are often found. In their review of the experimental evidence, Murdoch and Oaten (1975) concluded that environmental heterogeneity (and its affect on prey spatial distribution) increased the likelihood that switching will occur. Similarly, Werner et al. (1981) found that different preferences were formed by spatial variation in prey abundances.

Although alternate prey are generally assumed to be effectively mixed together, there is a spatial component implicit in Murdoch's switching model (Murdoch, 1969; Murdoch and Oaten, 1975) because predator preference "c" can be divided into two constants (Murdoch, 1969).

i) e: predator preference.

ii) k: the relative availability of the prey and denotes the ratio:

\[
\frac{\text{fraction of species 1 contacted}}{\text{fraction of species 2 contacted}}
\]

In most experiments—including Murdoch's (1969) — k and e can not be distinguished while k is assumed to be constant so that the relative availability of the two prey types is linearly related to their frequencies in the population. A consequence of this is that relative rather than absolute prey densities are important. In my
experiments, however, it is relative prey densities that change. The increased predation on the aggregated rare prey may thus be due to the higher relative bait densities in the aggregated distribution because, although the absolute densities remain constant between the two bait arrangements, the relative density of the rare aggregated prey is effectively the same as that of the common prey (2m$^{-2}$), whereas in the random arrangement the relative density of the rare prey is 0.2m$^{-2}$ and 1.8m$^{-2}$ for common prey. In these circumstances, the tendency of individual predators to sample "runs" of particular prey items (Royama, 1970) may lead to rare aggregated prey with the same appearance being at such a disadvantage that the frequency-dependent advantage which arises when they are scattered among contrasting baits is lost. With the 1:1 populations, however, the two prey types are effectively as easy to find in both of the two spatial arrangements as the difference in relative densities between the two distributions is very small (Table 2.3). In other words, the prey encounter rate is sufficiently high in either spatial arrangement for existing predator preferences for both colours to be maintained.

Although only three frequencies were used, the effect of the prey relative distributions on predator behaviour can also be seen by the observation that switching appears to have occurred in the randomly distributed experiments but not in the aggregated ones. As will be recalled, switching is said to have occurred if, when at a low frequency, a prey suffers less predation than expected while at a high frequency, it is over-predated (Figure 2.3). The expected
values for my experiments were calculated from Murdoch's (1969) equation where:

\[
c = \frac{cF}{1-F+cF},
\]

\(c\) the predator preference is estimated from \(F\), of 0.5 (frequency of Green baits) and then used to generate values of \(c\) at frequencies (\(cF,\)) at 0.9 and 0.1. There is evidence for switching in the randomly distributed arrangement but not in the aggregated results (Table 2.4). This suggests that the difference was, indeed, due to the rare prey being easier to find in the aggregated distribution so that, unlike in the randomly distributed population, a prey was at a disadvantage in being rare.

As most of the birds concentrated on the more common coloured baits in the 9:1 populations, the difference in rare prey survival was due to a few birds with a rare colour preference and their ability to find the rare baits. Minority preferences within a predator population are not unusual (Brown, 1969; Murton, 1971; Allen, 1972; Bryan and Larkin, 1972; Bryan, 1973): Allen and Clarke (1968), for example, found that although most of the birds concentrated on the common colour when presented with bait populations with 9:1 frequencies, one or more birds preferred the rare colour and ignored the more common baits. In my experiments, therefore, the results are most likely to be caused by predators with a preference for the rare colour and they being more likely to find the rare coloured baits in the aggregated arrangement. Minority colour preferences could have been formed while the birds were
foraging away from the experimental sites. However, as the birds were wild and not ringed, it was not possible to observe their feeding habits away from the study area but the point to be emphasised here is that, as discussed above, such a preference for the rare coloured baits is more likely to maintained when predators are presented with the aggregated prey distribution because of the effect of relative densities and encounter rates.

Interestingly, I was able to observe birds taking both colours in foraging bouts when feeding on 1:1 populations leading to what Murdoch (1969) would call an overall weak preference (c<sub>1</sub>) whereas birds feeding on the 9:1 populations would generally only take a single colour, including, occasionally, rare baits. Unfortunately, it was not possible to keep track of individual birds during the experiments and it would be worthwhile examining whether individual birds are indeed more likely to take runs of rare prey when the baits are in the aggregated arrangement.

In some circumstances, aggregation may be an advantage for potential prey. Warningly coloured and distasteful insects are often found living in groups which has the advantage that a predator's initial experience is less likely to be forgotten before another prey item is encountered and hence reduce the overall prey loss (Gittleman and Harvey, 1980; Harvey, 1983). There is further supporting evidence from prey species which want to be more easily found or noticed by foraging predators. In these cases, the prey are often found in groups or patches. Flowers, for example, that
exploit visually searching pollinators are usually all the same colour in an area so that the pollinators (hummingbirds, for example) can easily learn the single colour (Grant, 1966); while plant-pollinator and floral mimicry evolution is believed to be dependent on the plant spatial distribution (Feinsinger, 1983; Dafni, 1984; 1986) and by reducing the distances which have to be travelled, aggregation by plants can also increase the efficiency of the exploitation of pollinators (Real, 1983). Levin and Anderson (1970) have shown that if two sympatric and simultaneously flowering species compete for pollinators which forage and develop frequency-dependent preferences the reproductive success of a species increases with its relative frequency. In their model, a rarer species is soon excluded unless there are large single species patches so that a pollinator, which normally visit neighbouring plants, is more likely to find and pollinate flowers of the same species.

My results suggest that there is a spatial component to frequency-dependent predation which can have a significant effect at a very local scale (here within a 10 by 10 metre experimental area). This spatial component extends the effects of apostatic selection on population interactions by promoting the mixing of prey species or morphs at the local population scale. Rare prey types (or species) which are dispersed among more common prey will suffer relatively less predation at the local scale than when aggregated and apostatic selection by visually hunting predators, for example, could lead to
the mixing of neighbouring populations and hence promote coexistence.

This effect is probably most important in the zone of contact between populations competing for space where both habitats are similar and fairly homogeneous so that both prey species would be able to live in either area in the absence of the other species. Frequency-dependent predation will favour rare migrants moving into the other species range, promote the mixing of species within populations at a very local scale and coexistence, which in the absence of such predation may not be possible due to interspecific competition. It would be interesting to obtain data on neighbouring mixed populations of the land snail *Cepaea nemoralis* and *C. hortensis* where it has been suggested that interspecific competition may lead to spatial displacement (Tilling, 1985). Migration between pure species populations could lead to the introduction of rare migrants which are less vulnerable to predation than the more common residents. There is often migration between snail populations so that ill-camouflaged (non-cryptic) morphs can be found in neighbouring polymorphic populations such as *Hygromia striolata* (Jones et al., 1974) or the mixed populations of *Theba pisana* and *Xeropicta vestalis* on the border between areas of sand (where *Theba pisana* is dominant and very abundant) and areas of more heavy soil (where *X. vestalis* is found) where there is visual predation on the snails which closely resemble each other (Heller and Gadot, 1987).
Although it is generally thought that predation acts at a larger spatial scale than does competitive interactions (Menge et al. 1985; Schmitt, 1985), this is not necessarily so: my results show that the spatial component to frequency-dependent predation can occur within an area of only 10 by 10 metres. This is most likely to be important for population interactions between relatively immobile or sessile animals such as on the rocky intertidal shore where competition for space is paramount. There has been considerable interest on how in such communities, frequency-dependent predation can prevent a prey species from outcompeting other prey species (Paine, 1966; Menge et al., 1985; Sih et al., 1985) or promote polymorphism within species (Berry and Crothers, 1974; for example). My results suggest that the local effect of the spatial component of frequency-dependent predation may prevent competitively superior prey species from forming large single species patches within multispecies communities and, therefore, promote coexistence at the local (within community) scale. Rarer species will suffer less predation when their neighbours are individuals of more common prey species and this may reduce interspecific competition and hence promote the mixing of species at a very local scale (see Figure 2.4). Similarly, this spatial effect may be important in post-dispersal seed interactions where, recently, there has been considerable interest in how frequency-dependent predation can affect post-dispersal seed predation (Greenwood, 1985).

The frequency-dependent advantage of rare palatable prey may depend upon their spatial patterning and, if the pattern is
inappropriate, this advantage can be lost or reversed. In all the experiments, however, there was an overall preference for brown baits so that none of the experimental frequencies or patterns would lead to coexistence (or stable polymorphism). However, these results show that the persistence of a prey species (or the fitness of a morph) may depend on its position in relation to others as much as on its relative abundance.
2.5 Summary

Experiments on artificial prey in aggregated or randomly distributed arrangements show that the relative survival of a rare prey species in a 2 species population with different colours (Brown and Green) is dependent not only on its frequency but also on the colour of its neighbours. A rare prey species aggregated with conspecifics of the same colour suffer greater predation than when randomly distributed among the more common prey species. As the overall prey densities and frequencies remained the same, the differences in prey spatial patterning provided the spatial heterogeneity over which the predators (wild birds) must forage and this altered the birds' preferences and hence prey survival. Spatial patterning as well as frequency may, therefore, be an important component of apostatic selection.
Note: In both arrangements, the position of the 2 baits within each of the metre squares was random.

1. 9:1 Aggregated bait distribution

```
   oo oo oo oo oo oo oo oo oo
   oo oo oo oo oo oo oo oo oo
   oo oo oo oo oo oo oo oo oo
   oo oo oo oo oo oo oo oo oo
   oo oo oo oo oo oo oo oo oo
   oo oo oo oo oo oo oo oo oo
   oo oo oo oo oo oo oo oo oo
   oo oo oo oo oo oo oo oo oo
```

2. 9:1 Random bait distribution

```
  oo  oo  oo  oo  oo  oo  oo  oo
  oo  oo  oo  oo  oo  oo  oo  oo  oo  oo
  oo  oo  oo  oo  oo  oo  oo  oo  oo  oo
  oo  oo  oo  oo  oo  oo  oo  oo  oo  oo
  oo  oo  oo  oo  oo  oo  oo  oo  oo  oo
  oo  oo  oo  oo  oo  oo  oo  oo  oo  oo
  oo  oo  oo  oo  oo  oo  oo  oo  oo  oo
  oo  oo  oo  oo  oo  oo  oo  oo  oo  oo
```

Figure 2.1

Prey spatial arrangements: aggregated and random
Figure 2.2
The effect of frequency and spatial distribution on the relative predation of green baits. Preference for green increases with increasing value of $\beta_i$. 

- 88 -
Figure 2.3
Switching occurs when a predator concentrates on common prey so that there is a non-linear relationship between the proportions of different prey present in a population and the proportions consumed.
1. Between patches spatial components

Rare prey suffer less predation in mixed species populations so that migration of prey into patches containing more common prey species will be promoted.

2. Within patch spatial component

Individuals of the rarer species will be favoured when neighbours are from other, more common prey species thus promoting mixing and coexistence at the local, within patch level:

Figure 2.4

Spatial component of apostatic selection and the promotion of coexistence at the local (within-patch) level
Table 2.1

Relative predation of baits in central versus edge squares in the 1:1 randomly distributed experiments:

i) Overall:

Proportion of baits eaten:

<table>
<thead>
<tr>
<th></th>
<th>Green Baits</th>
<th>Brown Baits</th>
<th>$\chi^2$</th>
<th>$\chi^2$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Edge</td>
<td>0.32</td>
<td>0.45</td>
<td>13.114</td>
<td>5.491</td>
</tr>
<tr>
<td>Centre</td>
<td>0.49</td>
<td>0.57</td>
<td>***</td>
<td>*</td>
</tr>
</tbody>
</table>

ii) Individual 1:1 Randomly distributed experiments:

Proportion of baits eaten:

<table>
<thead>
<tr>
<th></th>
<th>Green Baits</th>
<th>Brown Baits</th>
<th>$\chi^2$</th>
<th>$\chi^2$</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. Edge</td>
<td>0.51</td>
<td>0.37</td>
<td>7.220</td>
<td>n.s.</td>
</tr>
<tr>
<td>Centre</td>
<td>0.80</td>
<td>0.49</td>
<td>**</td>
<td></td>
</tr>
<tr>
<td>2. Edge</td>
<td>0.43</td>
<td>0.23</td>
<td>n.s.</td>
<td>n.s.</td>
</tr>
<tr>
<td>Centre</td>
<td>0.51</td>
<td>0.22</td>
<td></td>
<td></td>
</tr>
<tr>
<td>3. Edge</td>
<td>0.53</td>
<td>0.76</td>
<td>n.s.</td>
<td>13.138</td>
</tr>
<tr>
<td>Centre</td>
<td>0.40</td>
<td>0.40</td>
<td>***</td>
<td></td>
</tr>
<tr>
<td>4. Edge</td>
<td>0.38</td>
<td>0.11</td>
<td>n.s.</td>
<td>7.535</td>
</tr>
<tr>
<td>Centre</td>
<td>0.35</td>
<td>0.40</td>
<td>**</td>
<td></td>
</tr>
<tr>
<td>5. Edge</td>
<td>0.47</td>
<td>0.06</td>
<td>9.778</td>
<td>10.727</td>
</tr>
<tr>
<td>Centre</td>
<td>0.80</td>
<td>0.37</td>
<td>***</td>
<td>***</td>
</tr>
</tbody>
</table>

*p<0.05; **p<0.01; ***p<0.005.

Note: each 100 m² grid consisted of 36 peripheral or "edge" squares and 64 inner or "central" squares.
Table 2.2

Mean arcsine-transformed $\beta_e$ values (with 95% confidence limits), measuring preference for green baits.

i) Bedford College London.

<table>
<thead>
<tr>
<th>DATES</th>
<th>FREQUENCIES</th>
<th>DISTRIBUTION</th>
<th>AGGREGATED</th>
<th>RANDOM</th>
<th>t-test</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>(GREEN)</td>
<td>AGGREGATED</td>
<td>RANDOM</td>
<td></td>
<td></td>
</tr>
<tr>
<td>25/11/81-3/12/81</td>
<td>0.9</td>
<td>21.98±5.63</td>
<td>35.07±6.58</td>
<td>3.99 **</td>
<td></td>
</tr>
<tr>
<td></td>
<td>(N=3)</td>
<td>(N=5)</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

ii) Lovelace Road, Oxford:

<table>
<thead>
<tr>
<th>DATES</th>
<th>FREQUENCIES</th>
<th>DISTRIBUTION</th>
<th>AGGREGATED</th>
<th>RANDOM</th>
<th>t-test</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>(GREEN)</td>
<td>AGGREGATED</td>
<td>RANDOM</td>
<td></td>
<td></td>
</tr>
<tr>
<td>24/7/82-20/1/83</td>
<td>0.9</td>
<td>27.24±4.12</td>
<td>39.26±6.67</td>
<td>3.69 ***</td>
<td></td>
</tr>
<tr>
<td></td>
<td>(N=8)</td>
<td>(N=8)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>30/1/84-23/2/84</td>
<td>0.5</td>
<td>30.60±9.41</td>
<td>31.89±4.72</td>
<td>0.34 ns</td>
<td></td>
</tr>
<tr>
<td></td>
<td>(N=5)</td>
<td>(N=5)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>27/6/83-26/11/83</td>
<td>0.1</td>
<td>35.02±6.16</td>
<td>22.71±8.05</td>
<td>2.98 **</td>
<td></td>
</tr>
<tr>
<td></td>
<td>(N=9)</td>
<td>(N=8)</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

| t-test | 2.40 * | 3.89 *** |

(***p<0.002, **p<0.01, *p<0.05)
Table 2.3
Relative bait densities in the aggregated and randomly distributed arrangements.

<table>
<thead>
<tr>
<th>Frequency (G:B)</th>
<th>Random</th>
<th>Aggregated</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Green</td>
<td>Brown</td>
</tr>
<tr>
<td>1:1</td>
<td>1.0m$^{-2}$</td>
<td>1.0m$^{-2}$</td>
</tr>
<tr>
<td>9:1</td>
<td>1.8m$^{-2}$</td>
<td>0.2m$^{-2}$</td>
</tr>
<tr>
<td>1:9</td>
<td>0.2m$^{-2}$</td>
<td>1.8m$^{-2}$</td>
</tr>
</tbody>
</table>
Table 2.4
Test for switching: random versus aggregated distributions (Lovelace Rd. site only):

i) Random distribution.

<table>
<thead>
<tr>
<th>Observed</th>
<th>Expected</th>
<th>Obs-Exp.</th>
</tr>
</thead>
<tbody>
<tr>
<td>F,(Green) 0.9</td>
<td>0.90</td>
<td>0.82</td>
</tr>
<tr>
<td></td>
<td>0.91</td>
<td>0.82</td>
</tr>
<tr>
<td></td>
<td>0.77</td>
<td>0.82</td>
</tr>
<tr>
<td></td>
<td>0.86</td>
<td>0.82</td>
</tr>
<tr>
<td></td>
<td>0.89</td>
<td>0.82</td>
</tr>
<tr>
<td></td>
<td>0.91</td>
<td>0.82</td>
</tr>
<tr>
<td></td>
<td>0.89</td>
<td>0.82</td>
</tr>
</tbody>
</table>

p<0.035; Sign Test.

<table>
<thead>
<tr>
<th>Observed</th>
<th>Expected</th>
<th>Obs-Exp.</th>
</tr>
</thead>
<tbody>
<tr>
<td>F,(Green) 0.1</td>
<td>0.03</td>
<td>0.05</td>
</tr>
<tr>
<td></td>
<td>0.01</td>
<td>0.05</td>
</tr>
<tr>
<td></td>
<td>0.02</td>
<td>0.05</td>
</tr>
<tr>
<td></td>
<td>0.00</td>
<td>0.05</td>
</tr>
<tr>
<td></td>
<td>0.10</td>
<td>0.05</td>
</tr>
<tr>
<td></td>
<td>0.08</td>
<td>0.05</td>
</tr>
<tr>
<td></td>
<td>0.06</td>
<td>0.05</td>
</tr>
</tbody>
</table>

n.s. p=0.254; Sign Test.

Overall, p<0.025; Sign Test.

Cont.,
Table 2.4 cont.

Test for switching: random versus aggregated distributions (Lovelace Rd. site only):

ii) Aggregated distribution.

<table>
<thead>
<tr>
<th></th>
<th>Observed</th>
<th>Expected</th>
<th>Obs-Exp.</th>
</tr>
</thead>
<tbody>
<tr>
<td>$F_r(Green)$ 0.9</td>
<td>0.86</td>
<td>0.83</td>
<td>+0.03</td>
</tr>
<tr>
<td></td>
<td>0.69</td>
<td>0.83</td>
<td>-0.14</td>
</tr>
<tr>
<td></td>
<td>0.84</td>
<td>0.83</td>
<td>+0.01</td>
</tr>
<tr>
<td></td>
<td>0.83</td>
<td>0.83</td>
<td>-----</td>
</tr>
<tr>
<td></td>
<td>0.75</td>
<td>0.83</td>
<td>-0.08</td>
</tr>
<tr>
<td></td>
<td>0.80</td>
<td>0.83</td>
<td>-0.03</td>
</tr>
<tr>
<td></td>
<td>0.81</td>
<td>0.83</td>
<td>-0.02</td>
</tr>
<tr>
<td></td>
<td>0.82</td>
<td>0.83</td>
<td>-0.01</td>
</tr>
</tbody>
</table>

n.s. $p=0.145$; Sign Test.

<table>
<thead>
<tr>
<th></th>
<th>Observed</th>
<th>Expected</th>
<th>Obs-Exp.</th>
</tr>
</thead>
<tbody>
<tr>
<td>$F_r(Green)$ 0.1</td>
<td>0.08</td>
<td>0.06</td>
<td>+0.02</td>
</tr>
<tr>
<td></td>
<td>0.07</td>
<td>0.06</td>
<td>+0.01</td>
</tr>
<tr>
<td></td>
<td>0.02</td>
<td>0.06</td>
<td>-0.04</td>
</tr>
<tr>
<td></td>
<td>0.08</td>
<td>0.06</td>
<td>+0.02</td>
</tr>
<tr>
<td></td>
<td>0.06</td>
<td>0.06</td>
<td>-----</td>
</tr>
<tr>
<td></td>
<td>0.10</td>
<td>0.06</td>
<td>+0.04</td>
</tr>
<tr>
<td></td>
<td>0.09</td>
<td>0.06</td>
<td>+0.03</td>
</tr>
<tr>
<td></td>
<td>0.09</td>
<td>0.06</td>
<td>+0.03</td>
</tr>
<tr>
<td></td>
<td>0.04</td>
<td>0.06</td>
<td>-0.02</td>
</tr>
<tr>
<td></td>
<td>0.05</td>
<td>0.06</td>
<td>-0.01</td>
</tr>
</tbody>
</table>

n.s. $p=0.172$; Sign Test.

Overall, n.s. $p=0.952$; Sign Test.
CHAPTER THREE

THE ROLE OF EXPERIENCE AND SPATIAL HETEROGENEITY
ON HABITAT SELECTION IN DROSOPHILA MELANOGASTER

3.1 Introduction

In heterogeneous environments, habitat selection, which involves the dispersal of genotypes to those areas where their fitness is highest, can maintain genetic polymorphism (Levins, 1968; Taylor, 1976; Clarke, 1979; Hedrick, 1986). It can also restrict gene flow and act as a form of nonrandom dispersal so that a population may become subdivided genetically which can lead to the formation of host races and even new species (Maynard Smith, 1966; Parsons, 1980; Felsenstein, 1981; Futuyma and Peterson, 1985; Hedrick, 1986; Diehl and Bush, 1989; Tauber and Tauber, 1989). A number of studies have indeed found both genetic differentiation between microhabitats and genetic variation in habitat preference (Stalker, 1976; Taylor and Powell, 1977; Partridge, 1978; Jones, 1980; Hedrick, 1986). There can also be genetic variation in resource and oviposition site choice in insects (Futuyma and Peterson, 1985; Jaenike and Grimaldi, 1983; Jaenike, 1986a and b; Hedrick, 1986; Klaczko et al., 1986) and this has similar evolutionary consequences to that of habitat selection (Jaenike, 1986b).

Habitat selection has been found in a number of mark-recapture studies where animals tended to return to habitats or micro-climates similar to that in which they were initially captured (Partridge, 1978; Taylor and Powell, 1978; Kekić et al., 1980; Shorrocks and
Nigro, 1981; Hedrick, 1986). However, there are negative and conflicting results and it may be that some positive results are artefacts due to stressful conditions (Atkinson and Miller, 1980; Turelli et al., 1984; Hoffman and Turelli, 1985).

Experience can affect most insect behaviour patterns, including both resource and habitat selection (Matthews and Matthews, 1978; Partridge, 1978; Morse, 1980; Futuyma and Peterson, 1985; Jaenike, 1986a). Exposure during the larval or early adult stage to substrate or environmental cues can modify subsequent preferences (Thorpe, 1938, 1939; Hershberger and Smith, 1967; Manning, 1967; Jaisson, 1980; Jaenike, 1982, 1983, 1986a; van Alphen and Vet, 1986) so that polymorphism may be promoted by learning and conditioning as well as by genetic variation in habitat preference. This might be particularly important in broad-niched species such as *D. melanogaster* which exploit a wide variety of unpredictable resources. Behavioural flexibility due to such rapid associative learning may, therefore, lead to faster tracking of changes in resource abundance than can purely genetic changes (Colwell, 1986a).

Habitat selection in insects involves a complex set of behaviours which involves sequential sampling of the environment using various cues (Grossfield, 1978). Selection of oviposition sites also involves a number of different steps using different sensory modalities and environmental cues within a searching area already chosen (Miller and Stickle, 1984) so that both short range cues and habitat selection during an active dispersal phase are involved (see
Grossfield, 1978; Vinson, 1984; van Alphen and Vet, 1986; Papaj, 1986). This initial dispersal is often the most important stage in habitat selection and, particularly in the initial stages, need not involve resource based cues. Many insects, including many parasitoids and phytophagous species, use light as such a cue before other shorter ranged cues such as olfaction are utilized (van Alphen and Vet, 1986). Light is particularly important for many species of Drosophila (see Chapter 4) and intraspecific variation in light preferences might also lead to nonrandom dispersal, and hence to habitat selection in heterogeneous light environments.

However, for there to be differences in habitat selection within a species, there must be within-population variation in light preferences. Light preferences in Drosophila have a polygenetic inheritance (Grossfield, 1978) and there is indeed variation within populations. Kekić et al., (1980) found that D. subobscura flies from dark areas were more photonegative than flies from neighbouring, brighter areas. This is largely a genetical difference because such preferences were also found in the F, offspring which had been reared under the same laboratory conditions. Kekić and Marinković (1978) found that in D. melanogaster eye size was correlated with photopreferences so that within a population, photonegative flies had significantly larger eyes than more photopositive ones; while Kekić and Valvajter (1978) found that selection for photopreferences in D. subobscura led to photonegative flies having significantly larger eyes than flies from photopositive selected line. There are also between-population differences in light preferences
(Grossfield, 1978; David et al., 1983; Kekić and Marinković, 1979; Marinković et al., 1980). For example, positive phototaxis in *D. melanogaster* increased with distance from the equator (Medioni, 1962).

The extent for genetic variation in light preferences is also manifest in the speed by which directional selection leads to photopositive or photonegative lines (see Rockwell and Seiger, 1973; Grossfield, 1978, Parsons, 1982). In addition, many mutants, especially eye mutants, respond differently to light (Waddington et al., 1954; Medioni, 1962; Grossfield, 1978). Indeed, one of the best examples of habitat selection maintaining a polymorphism is that involving light preferences in heterogeneous light environments (Jones and Probert, 1980; Mueller, 1985; Hedrick, 1986). In addition, light conditions have been implicated in some field experiments on intraspecific habitat selection as Taylor and Powell (1978) did not observe habitat fidelity on overcast days.

There has been very little work, however, on how prior experience of light may affect light preferences and consequently dispersal and habitat selection. Taylor did find that laboratory-raised flies did not show habitat fidelity in the field (Hedrick, 1986) and that the lighting conditions in which *Drosophila* flies were reared affected subsequent dispersal (Taylor, 1986). Nevertheless, the important question on how environmental variation and conditioning affects light preferences and, therefore, intraspecific habitat selection has been neglected.
In this chapter I investigate whether previous experience of light can indeed affect subsequent light preferences and habitat selection in *Drosophila melanogaster*. I also examine whether this habitat selection can occur in environments where the light conditions provide the only spatial heterogeneity and if, over generations, such behavioural differences can lead to any detectable genetic differentiation in light preferences occurring in the subdivided population.
3.2 Materials and Methods

3.2.1 Stocks

An outbred wildtype stock of *Drosophila melanogaster* was tested (this stock was also used to set up an outbred white-eye *D. melanogaster* stock with which interspecific comparisons with *D. simulans* were undertaken: see Chapter 4) and had been kept in bottles in the laboratory under room temperature and light conditions. Random samples were taken to test normal light preferences and other randomly chosen samples were used to form the experimental populations for a series of conditioning experiments.

3.2.2 Light Preference Testing Apparatus

Because the larval stage is largely sedentary, the most important component affecting dispersal in *Drosophila* is adult preferences. I used a specially designed apparatus for testing dispersal in adult flies which consisted of clean, unused WHO mosquito insecticide testing kits. These consist of two transparent cylinders connected by a central joint with a moveable partition (Figure 3.1). One of the cylinders was left transparent while the other was covered with the same SASCO red light filter as used in the dim red light regime (see below). Samples to be tested were divided into two equal groups by the cold-counting method and a group was put into each of the cylinders, the apparatus was levelled and, once the flies had settled down, the partition was carefully opened so that the small hole was opened and movement by walking and flying between the two cylinders was possible. The apparatus was illuminated by three 40 watt fluorescent lights so that the two cylinders had approximately
the same light intensities as used in the experimental light regimes. After two hours the partition was closed and the flies counted so that the light preference of the flies could be measured by their relative distribution.

The testing apparatus measures relative light preferences and hence phototaxis. Phototaxis and light preferences are a relative rather than an absolute characteristic and are best defined in population terms (Rockwell and Seiger, 1973; Grossfield, 1978). As phototaxis is operationally defined and is further complicated by the fact that it is affected by environmental (time of day, temperature) and other variables including escape response (Lewontin, 1959; Rockwell and Seiger, 1973; Grossfield, 1978; Markow, 1979 for critical reviews), one can only safely compare preferences and say that, for example, under a certain set of experimental conditions a population is more or less photopositive than another.

I attempt to reduce these problems by keeping the lines under the same conditions (apart from light) and by testing samples at the same time, in the same type of testing apparatus and under the same conditions. Each of the samples was tested in a separate testing kit with six samples tested at the same time. The kits were cleaned before use and randomly assigned to each sample to be tested. There was no food in (or near) the testing apparatus.
This testing procedure gives the relative preferences between samples tested under the same conditions so that although the absolute preference values may change, the relative differences - which is the characteristic which produces relative dispersal and hence habitat selection - are still measurable and can be compared directly by matched-paired statistics. Exposure can be inferred to have had an effect on light preferences if a greater proportion of adults from a line which had experienced dim red light disperse to the dim red light cylinder of the test apparatus than do adults from a line which had experienced bright white light. Although both sexes were tested together, the results were analysed separately and, unless otherwise indicated, there is no difference between the relative preferences of the two sexes. For simplicity, a tendency to disperse to the dim red light cylinder will be defined as a photonegative preference and a tendency to disperse to bright white light as a photopositive light preference.

3.2.3 Experimental Populations

Two populations were set up (Figure 3.2): "No-choice" lines where the flies experienced one of the light conditions and "RW choice" cages where the flies could disperse between the light conditions. Both populations were maintained under constant light (three 40 watt flourescent tubes) and temperature (25°C) conditions. Two light regimes were used, dim red light (which had a light intensity of 0.7 lux) and bright white light (170 lux). Dim red light was provided by fixing 10 layers of ROSCO CINELUX 621 RED LIGHT FILTER onto the glass tops of the cages, while the bright white light sectors had
just bare glass (Figure 3.3). The walls and floors of the red light sectors were painted matt black and the white light sectors were painted white.

Standard Drosophila maize meal medium seeded with active yeast was used giving 5.65g of fresh food per vial and each population cage sector had 12 vials. A third of each sector's vials were changed each week so that there was a continuous adult cage population with overlapping generations. The No-choice lines were each kept in 25 food vials with the next generation being set up every 3 weeks from emerging offspring. To reduce the effects of environmental parameters other than light, all the experiments used the same food and were maintained at the same temperature (there was less than a 0.4°C difference in temperature between the two light regimes).

3.2.3.1 No-choice Experiments
The No-choice lines were kept in vials, two randomly chosen pairs in each with 25 tubes in dim red light and 25 in bright white light. Subsequent generations of each line were started by setting up 25 fresh vials with 50 randomly chosen pairs using the cold-counting method under normal laboratory lighting. This means that both the larvae and adults were kept in the same light regime throughout their life cycle (Figure 3.2). The advantage of this is that the time spent in the various light conditions was known so that the time taken for the formation of light preferences could be measured.
3.2.3.2 RW Choice Cages

Other lines were put in heterogeneously lit population cages with one sector illuminated by dim red light and the other with bright white light from three 40 watt fluorescent tubes. The two cage sectors were connected by a small hole in the internal partitioning wall so that the flies are able to disperse between light conditions. 12 food tubes were maintained in each sector with one third being changed weekly. To prevent the escape response which can occur when the food tubes are changed (see Chapter 4), the hole in the partition wall was closed with cotton wool during the changing of food tubes. Each cage was initiated by putting equal numbers of a stock (25 pairs) on each sector of a cage (Figure 3.2). At intervals, sample tubes were placed in the cages, stoppered and subsequent offspring were collected.
3.3 Results

3.3.1 No-choice Lines: Initial Adult Exposure

50 pairs of the stock (with two pairs of flies per food vial) were randomly assigned to each light regime. In the first experiment, the flies were able to feed, mate, and oviposit in the light regimes for 5 days after which the adults were removed and their light preferences tested. Although flies from the dim red light line were more photonegative with 42% dispersing to the dim red light compared to 31% for flies from the bright white light line, the difference was not significant (Table 3.1).

In experiment 2, samples from the same stock was tested after 10 days in the light regime. This time there was a significant difference ($p<0.005$, $\chi^2$ test) with the dim red light line being more photonegative (Table 3.1). The two experiments show that experience of light conditions can significantly alter adult light preferences.

3.3.2 No-choice Lines: Subsequent Generations

Offspring from experiment 1 (50 pairs) were used to found long-term "No-choice" lines. Subsequent generations were also initiated by 50 pairs of offspring randomly chosen from the previous generation so that there was no selection on my part for more photopositive or negative light preferences. In the 9 tests for light preferences, there was an overall and highly significant difference between the two lines with adults from the dim red light regime being more photonegative ($p<0.005$, $n=9$, Wilcoxon matched-pairs signed rank test; Table 3.1).
3.3.3 The Effect of Light Intensity on Light Preference Tests

A number of tests were performed to investigate whether as well as being able to distinguish between dim red light and bright white light, the flies can distinguish between red light of different intensities. The light preference test apparatus was modified by covering the bright white light test cylinder with a single layer of red light filter thus giving the flies a choice between red light of different intensities. Light intensity in the dim red light test cylinder ("R_0") cylinder) remained 1.2 lux, and 20 lux in the one layer of red filter ("R,") cylinder. Each sample was divided so that one half was tested in the usual test apparatus with dim red light (1.2 lux) and bright white light ("W" cylinder) with a light intensity of 125 lux, and the other in the modified test apparatus.

In the four pairs of tests using adult flies from the No-choice Lines, there was no significant difference between the proportion choosing dim red light in the two test apparatus with flies from the bright white light line choosing either bright white light or the brighter of the two red light conditions (Table 3.2).

3.3.4 The Effect of Preadult Experience on Preferences

To test whether preadult experience can affect adult light preferences, after offspring were removed to found the F₆ generation, the F₅ tubes (which still contained developing pupae and larvae) were put into constant darkness. Subsequently emerging adults were collected on two separate days (Figure 3.4). There was a significant difference between the two No-choice lines adults
collected after 3 days of constant darkness, the dim red light exposed line was significantly more photonegative ($\chi^2 = 7.9685$, p<0.005). No such difference, however, was found between adults which had emerged after 4 days (Table 3.3).

The pupal stage in wildtype *D. melanogaster* takes about 4 days at 25°C (Shorrocks, 1972) and eye-pigmentation occurs in the pupa during the 3 days before eclosion (Bodenstein, 1950). Adult flies which emerged during the first three days in the dark were, therefore, exposed to the light regimes as late pupae whereas adults which emerged a day later (on day 4) had pupated (and emerged) in constant darkness so that their eyes had at no time experienced the light regimes (Figure 3.4). This provides some evidence that adult light preferences can be formed as early as in the late pupal stage by which time the adult head and eyes are clearly visible.

### 3.3.5 Reversal of Light Preferences and Effect of Darkness

#### 3.3.5.1 The Effect of Reversing Light Regimes on Light Preferences

To investigate whether preferences can be modified or even reversed by further experience, adults were kept in the opposite light regime to that in which they had formed preferences. The adults were periodically tested to determine how long preferences, once formed, can be maintained during exposure to the opposite light regime.

*F*$_{3}$ generation of the No-choice line adults (which had also been used to set up the *F*$_{4}$ generation) were placed in the opposite light regime. After 7 days of being in the reverse regime there was no
reversal in light preferences (Table 3.4). Repeated experiments using offspring from the F_1 No-choice lines and F_2 offspring showed a limited reversal of light preferences. There was a significant change in adults from the dim red light line whose preference changed from 42.2% to 81.8% choosing bright white light after 3 days in the reverse regime (p<0.001, $\chi^2$ test). There was also a significant change in the F_2 dim red light to bright white light regime ("R = W") flies and, again, no significant change in the bright white light to dim red light regime ("W = R") flies (Table 3.4).

3.3.5.2 Darkness and the Reversal of Light Preferences

Attempts to reverse light preferences were more successful if the flies were kept in darkness for a period before exposure to the opposite light regime. Adults from the No-choice lines were put in either darkness or the appropriate light regimes and tested after 1 day. The white light line was significantly more photopositive than the dim red light line (Table 3.5). No difference, however, existed between flies kept in constant darkness. After testing, the group which had been kept in darkness was put in the opposite regime (Figure 3.5) so that, after the period in darkness, the flies from the bright white light line were then put into dim red light (and the opposite for the dim red light line). When retested after 5 days, preferences had reversed with a highly significant difference between the lines ($\chi^2$ test p<0.005, Table 3.5).
When flies from the No-choice lines emerged over 3 days in the light:dark cycle of normal laboratory conditions instead of in the appropriate light regime, there was no difference between the lines (Table 3.5). However, there was a significant difference in light preferences between adults which had been kept in the appropriate light regimes (and used to found the next No-choice line generation). Once tested, the flies which had emerged in laboratory conditions were put in the opposite light regime. After 4 days, there was a significant and reversed difference in light preferences between the two lines (Table 3.5).

3.3.6 Long Term Effects of Light Conditions on Preferences

Long term, genetical changes in the light preferences of the No-choice *D. melanogaster* lines were investigated on week 118 (some 82 generations since the lines were set up) by randomly taking adults from each line to form two more lines each with 25 tubes and two pairs of flies per tube. These new "L:D" lines were put into an incubator with a 12 hour light:dark cycle (Figure 3.6). After 11 days, the adult flies had retained their preferences: adults originally from the bright white light line were significantly more photopositive than adults originally from the dim red light line ($\chi^2=11.812, p<0.001$; Table 3.6). As expected, there was also a significant difference between the original No-choice lines kept in the usual light regimes with adults from the bright white light line being more photopositive ($\chi^2=7.507, p<0.01$).
F, offspring from the L:D lines were used to found the next generation and 14 days later the adults were tested. There was no significant difference between the two lines, which were both highly photopositive (Table 3.6). This shows that light preferences are formed anew every generation (even after being kept in the light regimes for 82 generations). The adults were then put in the opposite light regime to that their parents had been exposed (see Figure 4.5) and after 6 days retested. There was a significant difference between the two lines with the adults kept in bright white light being more photopositive ($\chi^2 = 26.9$, p<0.001). Furthermore, adults from the No-choice lines of the same age showed very similar preferences (Table 3.6). Light preferences can hence be easily reversed even in flies kept in the light regimes for some 80 generations.

3.3.7 RW Choice Cage-lines

3.3.7.1 Light Preferences from Cage Samples

Two RW cages (see 3.2.3.2) were set-up each with 25 pairs of D. melanogaster to a sector. In the spatially heterogeneously lit RW cages, flies can disperse to either of the two light regimes so that there is the potential for the cage population to become subdivided by individual differences. To test for differences in light preferences between the two sectors, sample tubes were put in the cages. After 24 hours, any adults were removed, and the tubes were stoppered and left in the cages. Any offspring were collected and their light preferences tested.
Samples from dim red light cage sectors were significantly more photonegative (Wilcoxon matched-pairs signed rank test, \( p<0.025 \), \( n=6 \); (Table 3.7) which demonstrates that spatial heterogeneity can lead to a population becoming behaviourally subdivided. However, as found with the No-choice lines, there was no significant difference in light preferences between adults from RW cage samples which had emerged in constant darkness (Table 3.7).

3.3.7.2 Light Preferences of Cage Adults

Light preferences of adult flies living in the cages were also tested. Adults were caught by putting fresh food vials in the cages and, after 24 hours, gently stoppering up the vials without letting the adult flies escape. Caught flies were then collected, cold-counted and, after recovery, tested.

Adults caught in the two cage sectors had significant different light preferences and had, therefore, become divided into two behaviourally differing subpopulations. In the three tests, flies caught in the dim red light cage sectors were consistently more photonegative than adults caught in the bright white light sectors (Table 3.8).
3.4 Discussion

These experiments involved a simple choice between two light conditions and hence investigated relative rather than absolute preferences. This lack of absolute preferences has led to difficulties in the interpretation of the results of many choice experiments (Jaenike, 1986a). However, the problems of using only relative preferences were overcome in my experiments by the testing of flies from the different light regimes at the same time so that any effect of the light regimes will be manifest in a consistent relative difference between trials conducted. In my experiments, there was a consistent difference in the relative preferences of flies kept in the two light regimes. This shows that there is a significant learned component to variation in light preferences so that, in response to a heterogeneously lit environment, a *Drosophila* population can rapidly become behaviourally subdivided. Furthermore, this microhabitat selection appeared even in the absence of any resource heterogeneity and did not, therefore, involve substrate-based cues.

Habitat selection often involves both learned and innate components (Wiens, 1976; Partridge, 1978) with the former involving early experience. For example, Wiens (1970, 1972) found that when reared under the same conditions, red-legged tadpoles (*Rana aurora*) prefer striped backgrounds (which presumably corresponds to the submerged sticks and grasses found in their normal habitat) whereas cascade tadpoles (*R. cascadae*) prefer backgrounds composed of squares (which is similar to the gravelly substrates in which they...
However, when reared on the inappropriate substrate, the tadpoles did not show the preference for the background on which they are normally reared.

Although *Drosophila* males are attracted to the residual odours of females from the same geographical area (Hoffman and Parsons, 1984; Parsons and Hoffman, 1986), it is unlikely that olfactory cues were involved in my experiments. All the lines were set up from the same stocks and the testing procedure ensured that any olfactory cues were cancelled out. It was also possible to reverse light preferences between offspring emerging from the same vials by changing the light regime for flies emerging later.

Mimura (1986) found that dewinged *Boettcherisca peregrina* flies could be conditioned to various backgrounds so that flies which had been exposed to horizontal bars preferred this background to vertical bars. Similarly, flies exposed to the vertical bars preferred the vertical bar background to the horizontal bar background and flies exposed to right-down oblique stripes had a significant preference for that background. The flies (which had pupated in darkness) were simply exposed to the backgrounds every 5 hours for 5 days after emergence and then tested by measuring their walking rate of arrival at either end of an arena which had a choice of backgrounds.

Mimura believes that his results are due to neurological changes caused by synapse change through disuse. This seems unlikely here.
because light preferences could be changed in adults of differing age. Physiological changes in eye pigmentation does not seem to play a role either because white-eye *D. melanogaster* can also show differences in light preferences (see Chapter 4). It is unlikely that other temporary changes in eye structure could affect light preferences (Mazokhin-Porshnyakov, 1969; Frazier, 1985) because, once formed, the preferences could be maintained for several days even when kept in different light regimes. Cold counting of flies in normal light before the light preference tests were carried out had no effect on the difference between lines.

The advantage of these light preferences in *Drosophila* is that *D. melanogaster* is a colonizing species exploiting patchy, ephemeral and unpredictable resources where habitat selection is particularly important (Fretwell, 1972; Wiens, 1976; Parsons, 1982; Vinson, 1981, 1984; van Alphen and Vet, 1986). There are two components in habitat and resource choice: learned and genetic variation, the balance between the two depends on the organism. As insects such as *Drosophila* are small and short-lived with little time for learning, most insect behaviour is often thought to be innate, hard-wired or closed programmed, with their behaviour patterns being "fixed" (Mayr, 1974; Parsons, 1977, 1982; Papaj, 1986) and hence largely genetical. There are many examples of such innate variation (Parsons, 1977, 1982; Futuyma and Peterson, 1985; Hay, 1985; Jaenike, 1985; Jaenike and Grimaldi, 1983; Hedrick, 1986). However, even fixed action patterns can be modified by experience. A cockroach avoids its normal dark habitats if fed in the light and given
a mild electric shock whenever it approaches dark areas (Matthews and Matthews, 1978). There are many examples of learning in insects (Dudai and Quinn, 1980; Hay, 1985) and *D. melanogaster* and other *Drosophila* are affected by experience (Hay, 1985) so that learning is also probably responsible for the differences in light preferences found in my experiments.

Variation in resource use or habitat selection may also be influenced by experience such as larval or adult conditioning including associated learning or conditioning (Thorpe, 1938, 1939; Grossfield, 1978; Jaisson, 1980; Papaj, 1986). Jaenike (1982), however, found no evidence for larval conditioning in resource or oviposition choice in *Drosophila* but did suggest that early adult experience of the larval environment affects oviposition behaviour (Jaenike, 1982). This will have a similar effect to that of larval conditioning because, if newly emerged adults tend to linger in their larval environment (as is the case for *D. melanogaster*), then females will become conditioned to the larval environment or resource type.

This may be an efficient way of coping with seasonal variation in resource abundance. For example, if hard selection occurs (where the number of adults emerging from a resource type is a function of the fitness of various genotypes), then new and rare alleles can increase in frequency by environmentally induced preferences to a new resource if the rare allele has greater egg to adult viability in the new larval resource. Females can respond to hard selection in
the preadult stage by altering their oviposition behaviour which can also lead to a shift in resource use so that a population can adapt to a secondary resource without any genetic variation in preferences. Such a strategy may also be important in determining population structure and the evolution of host-races and speciation (Jaenike, 1982; Futuyma and Peterson, 1985; Hedrick, 1986).

This may also be a useful strategy for cosmopolitan species where learned resource and habitat choices can increase the flexibility of broad niched species in exploiting unpredictable resources by enabling individuals to rapidly track the changing availability of resources. All individuals may also be able to exploit all the resources available and the population can hence avoid the cost of individual specialization (Jaenike, 1986a). *D. melanogaster* is such a species and must exploit a variety of fermenting resources in heterogeneous environments. Females frequently have to exploit resources unlike the one in which they emerged so that resource-based genetic variation may be of limited use. The same is true of many parasitoid-host relationships in which habitat selection is important because females often emerge into environments with few hosts and have to disperse to new areas (Vinson, 1981, 1984). Here, associative learning (where oviposition sites are found and selected by an associated rather than a direct cue) may be important (Lewis and Tumlinson, 1988).

Jaenike (1982, 1983, 1985, 1986a&b) did not consider the importance of associated learning or conditioning on resource choice in
Drosophila. However, I have shown the importance of light in dispersal and how light conditions can alter light preferences and habitat selection in D. melanogaster so that light acts as an associated cue not directly related to oviposition sites. Microhabitat selection occurred without any resource heterogeneity: the food was the same in all the light conditions. Although the changes in light preferences lasted much longer than many examples of learning in Drosophila, the preferences had a large learned component because subsequent experience can change preferences very quickly.

My experiments also suggest that Jaenike's (1982) emphasis on the effects of early adult experience is correct. However, for D. melanogaster at least, light conditions as well as resource type in which the flies emerge have to be included. Possibly other cosmopolitan and generalist species have a greater learned component than do more resource specialised species where oviposition site variation may be resource based. In other words, the more predictable the environment the more the genetic basis for the variation.

Although D. melanogaster feed and oviposit in the same resources, adults and larvae do not have identical nutritional requirements so that resource choice is affected by the trade off between a female's own food needs and the survival of larvae in a particular resource (Jaenike, 1986c). Another advantage in having a learned and flexible component to light preferences is that the same females can change
light preferences and hence resource choice. This may explain why Jaenike (1986a) found that food choice in wild by lab-reared *D. melanogaster* was affected by the type of food on which they had been kept before release. This effect diminished after a few hours and was generally extinguished after a day.

*Drosophila* live in patchy, discontinuous habitats where habitat selection may be important in enabling flies to pass through unfavourable areas and to disperse to favourable ones. The oviposition sites within areas are also patchily distributed and this is similar to parasitoid-host relations where individuals have to assess which areas are worth searching in detail for the resources (Grossfield, 1978; Miller and Strickler, 1984; Van Alphen and Vet, 1986; Jaenike, 1986b). The advantage of *D. melanogaster* in using light preferences as habitat selection is that *D. melanogaster* are found in a wide range of light intensities even in the same microhabitat (see Chapter 4) so that light conditions can act as longer ranged cues and reduce the time wasted in searching for sites in resource poor areas. Once within an area, shorter ranged resource based cues such as olfaction can used be to find specific sites. Even insect species which rely heavily on other senses (such as chemoreceptors) often use light during the first dispersal phase of habitat selection (Grossfield, 1978; Vinson, 1984; Miller and Strickler, 1984; van Alphen and Vet, 1986).

The effectiveness of light preferences in *D. melanogaster* is increased because both dispersal and oviposition behaviour are
affected by light. It is very unlikely that resource and habitat selection are under the control of the same set of genes: there must be tight linkage or very strong selection for the two traits to respond to the same selection pressures (Futuyma and Peterson, 1985). Jaenike (1986b) found independent genetic control of ovipos-ition behaviour and habitat choice in *D. tripunctata* which will limit this species flexibility in exploiting a cosmopolitan niche. However, learned light preferences (such as those in *D. melanogaster*) can act in the same way on all life stages: niche choice and fitness can become associated through learning rather than linkage.
3.5 Summary

The effect of light conditions on variation in microhabitat selection in *D. melanogaster* in spatially heterogeneous light environments was investigated. Flies had significantly greater preferences for light conditions which they had already been exposed to. These light preferences represent a form of habitat selection as they lead to nonrandom dispersal. Once formed, preferences can be maintained for several days after exposure to the light regime while exposure to another light regime can change preferences. The learned component of this behaviour may be adaptive for species such as *D. melanogaster* which are often faced with a heterogeneous environment because learned preferences can increase a population's flexibility in resource use without incurring the cost of individual specialisation.
Light preference testing apparatus

Figure 3.1

Moveable partition (open)

110mm

45mm

15mm Hole

Bright white light cylinder

Dim red light cylinder
1) No-choice Lines:

![Diagram of No-choice Lines]

- Base Laboratory Stock Population
- Dim Red Light Regime: $F_0$: 50 pairs
  - $F_1$ and subsequent generations: 50 randomly chosen pairs found next generation
- Bright White Light Regime: $F_0$: 50 pairs
  - $F_1$ and subsequent generations: 50 randomly chosen pairs found next generation

ii) RW "Choice" Cages

![Diagram of RW Choice Cages]

- Base Laboratory Stock Population
- RW Cage
  - Dim Red Light Sector $\leftrightarrow$ Bright White Light Sector
  - Note: Subsequent generations can mate and move freely between cage sectors.

Figure 3.2

No-choice and RW Population Cage Lines
Glass tops

- Covered holes for changing of food tubes
  - Food tubes
  - Hole in partition wall

Figure 3.3

RW "Choice" population cage design
No-choice Lines: $F_6$ Generation Offspring

Dim Red Light Line | Bright White light Line

---|---

Darkness
- tubes containing larvae and pupae put into the dark

Light preferences tested after adults emerged in either:

---

1) 1 day of darkness. i.e., adults had been exposed to light conditions during pupation but had emerged in darkness.

ii) 6 days of darkness. i.e., adults had pupated and emerged in the dark.

Figure 3.4
Preadult experience experiment.
Dim Red Light Line  Bright White light Line

Adults Light Preferences Tested

Constant Darkness for 1 Day

Adults Light Preferences Retested

Light Regimes Reversed for 5 Days

Adults Light Preferences Retested

Figure 3.5

Darkness and light preference reversal experiment on No-choice Lines
Figure 3.6
Experiment on the long term effects of the light regimes on light preferences.
Table 3.1
No-choice Lines: Light preferences (%W) for the initial exposure experiments (28/10/85 and 11/12/85).

i) 5 day exposure:

<table>
<thead>
<tr>
<th>Light Regime</th>
<th>White light (n)</th>
<th>Dim red light (n)</th>
<th>W-R</th>
<th>χ²</th>
</tr>
</thead>
<tbody>
<tr>
<td>D. melanogaster</td>
<td>71.1 (80)</td>
<td>58.0 (70)</td>
<td>+13.1 n.s.</td>
<td></td>
</tr>
</tbody>
</table>

ii) 10 day exposure:

| D. melanogaster      | 85.0 (78)      | 59.0 (61)        | +26.0 ** |

** p<0.005, where %W is the percentage of flies found in the bright white light tube of the test apparatus.

iii) No-choice Line: Light preferences (%W) of F₁, and following generations of D. melanogaster (28/10/85 - 24/5/86).

<table>
<thead>
<tr>
<th>Light Regime</th>
<th>White light</th>
<th>Dim red light</th>
<th>W-R</th>
<th>χ²</th>
</tr>
</thead>
<tbody>
<tr>
<td>(F₀)</td>
<td>71.1</td>
<td>58.0</td>
<td>+13.1 n.s.</td>
<td></td>
</tr>
<tr>
<td>F₁</td>
<td>85.5</td>
<td>28.8</td>
<td>+56.2 ***</td>
<td></td>
</tr>
<tr>
<td>F₂</td>
<td>92.0</td>
<td>57.0</td>
<td>+56.2 ***</td>
<td></td>
</tr>
<tr>
<td>F₂</td>
<td>86.7</td>
<td>81.1</td>
<td>+5.6 ns</td>
<td></td>
</tr>
<tr>
<td>F₃</td>
<td>83.3</td>
<td>63.7</td>
<td>+19.6 ***</td>
<td></td>
</tr>
<tr>
<td>F₄</td>
<td>85.2</td>
<td>70.5</td>
<td>+14.4 *</td>
<td></td>
</tr>
<tr>
<td>F₅</td>
<td>62.2</td>
<td>42.2</td>
<td>+20.0 *</td>
<td></td>
</tr>
<tr>
<td>F₆</td>
<td>78.5</td>
<td>47.5</td>
<td>+31.0 ***</td>
<td></td>
</tr>
<tr>
<td>F₇</td>
<td>88.2</td>
<td>70.1</td>
<td>+18.1 *</td>
<td></td>
</tr>
</tbody>
</table>

Overall, p<0.005; (N=9; Wilcoxon match-paired signed-rank test).

* p<0.05, ** p<0.005, *** p<0.001, where %W is the percentage of flies found in the bright white light tube of the test apparatus.
Table 3.2
The Effect of Light Intensity on Preferences

Light preferences of No-choice *D. melanogaster* lines when tested in dim red light (R₁₀) and brighter red light (R₁) rather than in the usual dim red light (R₁₀) and bright white light (W).

<table>
<thead>
<tr>
<th>No-choice Line:</th>
<th>Bright White Light</th>
<th>Dim Red Light</th>
<th>W-R</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. 6/3/86</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>i) R₁₀ vs R₁</td>
<td>30.8</td>
<td>53.8</td>
<td>-23.0</td>
</tr>
<tr>
<td>ii) R₁₀ vs W</td>
<td>26.8</td>
<td>32.1</td>
<td>-5.3</td>
</tr>
<tr>
<td>2. 26/3/86</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>i) R₁₀ vs R₁</td>
<td>22.2</td>
<td>45.6</td>
<td>-23.4</td>
</tr>
<tr>
<td>ii) R₁₀ vs W</td>
<td>32.9</td>
<td>48.1</td>
<td>-15.2</td>
</tr>
<tr>
<td>3. 9/5/86</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>i) R₁₀ vs R₁</td>
<td>34.5</td>
<td>46.3</td>
<td>-11.8</td>
</tr>
<tr>
<td>ii) R₁₀ vs W</td>
<td>52.5</td>
<td>59.4</td>
<td>-6.9</td>
</tr>
<tr>
<td>4. 19/5/86</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>i) R₁₀ vs R₁</td>
<td>24.3</td>
<td>30.9</td>
<td>-6.5</td>
</tr>
<tr>
<td>ii) R₁₀ vs W</td>
<td>25.9</td>
<td>47.7</td>
<td>-11.8</td>
</tr>
</tbody>
</table>

Overall, p<0.005 (n=8; Wilcoxon matched-paired signed-rank test).
Table 3.3
Preadult Experience and Light Preferences.
No-choice Lines: Light Preferences (%W) of *D. melanogaster* lines exposed to the light regimes during either late pupal and larval stage or only the larval stage (7/2/86 - 13/2/86).

<table>
<thead>
<tr>
<th>No-choice Line:</th>
<th>White light</th>
<th>Red light</th>
<th>$\chi^2$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Length of exposure to light regimes</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1. Late pupal; adults emerged in darkness:</td>
<td>44.1</td>
<td>24.2</td>
<td>***</td>
</tr>
<tr>
<td>2. Larval; pupated and adults emerged in darkness:</td>
<td>36.5</td>
<td>42.7</td>
<td>ns</td>
</tr>
</tbody>
</table>

*** p<0.005, where %W is the percentage of flies found in the bright white light tube of the test apparatus.
Table 3.4
Light regime reversal in *D. melanogaster* No-choice lines.

i) Effect of Light reversal on F₃ generation adult light preferences (%W).

<table>
<thead>
<tr>
<th>Date</th>
<th>W Light Regime</th>
<th>R Light Regime</th>
<th>χ²</th>
</tr>
</thead>
<tbody>
<tr>
<td>9/1/86</td>
<td>85.2</td>
<td>70.8</td>
<td>n.s.</td>
</tr>
<tr>
<td>16/1/86</td>
<td>W&gt;R</td>
<td>R&gt;W</td>
<td></td>
</tr>
<tr>
<td>χ²</td>
<td>*</td>
<td>n.s.</td>
<td></td>
</tr>
</tbody>
</table>

ii) Effect of 3 days of reversed light regimes on F₄ generation adults light preferences (%W).

<table>
<thead>
<tr>
<th>Date</th>
<th>W Light Regime</th>
<th>R Light Regime</th>
<th>χ²</th>
</tr>
</thead>
<tbody>
<tr>
<td>17/1/86</td>
<td>62.2</td>
<td>42.2</td>
<td>n.s.</td>
</tr>
<tr>
<td>20/1/86</td>
<td>W&gt;R</td>
<td>R&gt;W</td>
<td></td>
</tr>
<tr>
<td>χ²</td>
<td>**</td>
<td>n.s.</td>
<td></td>
</tr>
</tbody>
</table>

iii) Effect of 7 days of reversed light regimes on the light preferences (%W) of F₅ generation adults.

<table>
<thead>
<tr>
<th>Date</th>
<th>W Light Regime</th>
<th>R Light Regime</th>
<th>χ²</th>
</tr>
</thead>
<tbody>
<tr>
<td>30/1/86</td>
<td>78.5</td>
<td>47.4</td>
<td></td>
</tr>
<tr>
<td>31/1/</td>
<td>W&gt;R</td>
<td>R&gt;W</td>
<td></td>
</tr>
<tr>
<td>1/2</td>
<td>82.8</td>
<td>64.7*</td>
<td></td>
</tr>
<tr>
<td>7/2</td>
<td>92.3²</td>
<td>70.0¹</td>
<td></td>
</tr>
<tr>
<td>χ²</td>
<td>***</td>
<td>*</td>
<td>n.s.</td>
</tr>
</tbody>
</table>

1) *** p<0.001, ** p<0.005, * p<0.05; χ² test on difference in light preferences between light regimes where %W is the percentage of flies found in the bright white light tube of the test apparatus.

2) χ² test on change in light preferences of light reversed lines: 

   i) ** p<0.005, p<0.05; χ² test on difference in light preferences between light regimes where %W is the percentage of flies found in the bright white light tube of the test apparatus.

Note: %W is the percentage of flies found in the bright white light tube of the test apparatus.
Table 3.5
Darkness and Light Preference Reversal.
The effect of darkness on subsequent light preferences (\%W) in light
regime reversal experiments in \textit{D. melanogaster} No-choice lines:
i) The effect of darkness.

<table>
<thead>
<tr>
<th>Light Regime</th>
<th>White light</th>
<th>Red light</th>
<th>$\chi^2$</th>
</tr>
</thead>
<tbody>
<tr>
<td>a) 21/1/86 Kept in light regimes</td>
<td>70.2</td>
<td>52.0</td>
<td>**</td>
</tr>
<tr>
<td>b) 21/1/86 1 day of darkness</td>
<td>64.9</td>
<td>63.6</td>
<td>ns</td>
</tr>
<tr>
<td>c) 26/1/86 b) flies put in reverse light regimes</td>
<td>36.7</td>
<td>61.6</td>
<td>***</td>
</tr>
</tbody>
</table>

ii) The effect of a light:dark (L:D) cycle on light preferences (\%W)
of \textit{D. melanogaster} No-choice lines.

<table>
<thead>
<tr>
<th>Line emerged in the light regimes (25/4/86):</th>
<th>%W</th>
<th>$\chi^2$</th>
</tr>
</thead>
<tbody>
<tr>
<td>W light line</td>
<td>88.2</td>
<td>**</td>
</tr>
<tr>
<td>R light line</td>
<td>68.7</td>
<td>**</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Line emerged and kept in L:D cycle (25/4/86):</th>
<th>%W</th>
<th>$\chi^2$</th>
</tr>
</thead>
<tbody>
<tr>
<td>W Light line</td>
<td>55.0</td>
<td>ns</td>
</tr>
<tr>
<td>R Light line</td>
<td>58.7</td>
<td>ns</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Adults from L:D lines which were put in the reverse light regimes for 4 days:</th>
<th>%W</th>
<th>$\chi^2$</th>
</tr>
</thead>
<tbody>
<tr>
<td>W+L:D+R</td>
<td>51.8</td>
<td>**</td>
</tr>
<tr>
<td>R+L:D+W</td>
<td>74.7</td>
<td>**</td>
</tr>
</tbody>
</table>

*** p<0.005, ** p<0.01.
Table 3.6
Long term effects of the light regimes on light preferences (%W) of the *D. melanogaster* No-choice lines.

<table>
<thead>
<tr>
<th></th>
<th>%W</th>
<th>χ²</th>
</tr>
</thead>
<tbody>
<tr>
<td>i) Samples kept in light regimes, 16/2/88:</td>
<td></td>
<td></td>
</tr>
<tr>
<td>W light line</td>
<td>94.0</td>
<td></td>
</tr>
<tr>
<td>R light line</td>
<td>79.0</td>
<td>**</td>
</tr>
<tr>
<td>ii) Samples from No-choice lines which had developed in light:</td>
<td></td>
<td></td>
</tr>
<tr>
<td>(W)L:D line</td>
<td>90.0</td>
<td></td>
</tr>
<tr>
<td>(R)L:D line</td>
<td>69.0</td>
<td>***</td>
</tr>
<tr>
<td>iii) F, adults from L:D line adults from (i) also kept in L:D conditions, 18/3/88:</td>
<td></td>
<td></td>
</tr>
<tr>
<td>(W)L:D line</td>
<td>89.4</td>
<td></td>
</tr>
<tr>
<td>(R)L:D line</td>
<td>91.5</td>
<td>ns</td>
</tr>
<tr>
<td>iv) Testing of adults from iii) which had been kept in the reverse light regime since 18/3/88, 24/3/88:</td>
<td></td>
<td></td>
</tr>
<tr>
<td>(W)L:D→R line</td>
<td>56.1</td>
<td></td>
</tr>
<tr>
<td>(R)L:D→W line</td>
<td>83.1</td>
<td>***</td>
</tr>
<tr>
<td>v) Light preferences of F, adults kept in the No-choice lines:</td>
<td></td>
<td></td>
</tr>
<tr>
<td>W light line</td>
<td>85.9</td>
<td></td>
</tr>
<tr>
<td>R light line</td>
<td>51.2</td>
<td>***</td>
</tr>
</tbody>
</table>

** p<0.01, *** p<0.001.
Table 3.7
RW Cage Sample Light Preferences

A. Light preferences (%W) of cage samples (17/12/85 - 6/3/86).

<table>
<thead>
<tr>
<th>Cage Sector</th>
<th>White light</th>
<th>Red light</th>
<th>W-R</th>
<th>( \chi^2 )</th>
</tr>
</thead>
<tbody>
<tr>
<td>i</td>
<td>39.1</td>
<td>20.0</td>
<td>+19.1</td>
<td>ns</td>
</tr>
<tr>
<td>ii</td>
<td>46.2</td>
<td>12.5</td>
<td>+33.7</td>
<td>*</td>
</tr>
<tr>
<td>iii</td>
<td>52.9</td>
<td>32.7</td>
<td>+20.2</td>
<td>*</td>
</tr>
<tr>
<td>iv</td>
<td>82.7</td>
<td>59.7</td>
<td>+23.0</td>
<td>***</td>
</tr>
<tr>
<td>v</td>
<td>80.0</td>
<td>56.5</td>
<td>+23.5</td>
<td>ns</td>
</tr>
<tr>
<td>vi</td>
<td>88.9</td>
<td>77.3</td>
<td>+11.6</td>
<td>ns</td>
</tr>
</tbody>
</table>

Overall, \( p<0.025 \) (N=6; Wilcoxon match-paired signed-rank test).

\* \( p<0.05 \), \*** \( p<0.001 \); where %W is the percentage of flies found in the bright white light tube of the test apparatus.

B. Adults from cage samples which emerged in darkness (20/2/86).

<table>
<thead>
<tr>
<th>Cage 1.3 <em>D. melanogaster</em></th>
<th>W+D</th>
<th>R+D</th>
<th>( \chi^2 )</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cage 1.3 <em>D. melanogaster</em></td>
<td>35.3</td>
<td>43.7</td>
<td>ns</td>
</tr>
<tr>
<td>Cage 2.3 <em>D. melanogaster</em></td>
<td>26.7</td>
<td>33.3</td>
<td>ns</td>
</tr>
</tbody>
</table>

\*** \( p<0.005 \), \** \( p<0.025 \).
Table 3.8
RW Cage Adults Preferences.
Light preferences (%W) of adult flies caught in the cage sectors (2/1/86 - 30/4/86).

<table>
<thead>
<tr>
<th>Cage Sector</th>
<th>White light</th>
<th>Red light</th>
<th>(\chi^2)</th>
</tr>
</thead>
<tbody>
<tr>
<td>i)</td>
<td>86.2</td>
<td>59.0</td>
<td>***</td>
</tr>
<tr>
<td>ii)</td>
<td>78.9</td>
<td>63.3</td>
<td>**</td>
</tr>
<tr>
<td>iii)</td>
<td>82.1</td>
<td>72.3</td>
<td>ns</td>
</tr>
</tbody>
</table>

*** \(p<0.001\), ** \(p<0.025\), where %W is the percentage of flies found in the bright white light tube of the test apparatus.
CHAPTER FOUR

SPATIAL HETEROGENEITY, MICROHABITAT PREFERENCES AND COMPETITION

BETWEEN DROSOPHILA MELANOGASTER AND D. SIMULANS

4.1 Introduction

Competitive exclusion need not occur if there is spatial heterogeneity: various models (Skellam, 1951; Horn and MacArthur, 1972; Levin, 1974; Lloyd and White, 1980; Atkinson and Shorrocks, 1981; Shorrocks and Rosewell, 1984; Hassell and May, 1985) suggest that species of unequal competitive ability, although unable to coexist on a single, undivided resource, can coexist on a single resource if it is subdivided into patches. The degree of resource patchiness and how the competing species disperse among the patches are both important and, as discussed in Chapter One, coexistence is possible if the species have clumped distributions. If, for example, each species has a negative binomial distribution, then the superior competitor will colonize only some of the patches and leave others vacant for other species. The reduction in interspecific interactions in each patch decreases interspecific competition so that intraspecific aggregation is more important than interspecific competitive ability and species can coexist on the same resource (Atkinson and Shorrocks, 1981).

In insect communities, exploited resources are often discrete, highly subdivided and ephemeral. Many such communities are mosaics of extinction and recolonisation by dispersal (Kareiva, 1986) and, as the larval stage of most insects is relatively immobile, the
aggregation of the eggs laid by mobile, winged adults is particularly important. Interspecific larval competition can be avoided if adults lay their eggs among the patches in such a way that larvae of different species are not likely to be found together.

Habitat selection can also be important in interspecific interactions. If habitat selection is mediated by an extrinsic, environmental factor such as light, coexistence may be possible even when species compete for a single resource. This environmental (abiotic) spatial heterogeneity can be superimposed on resource patchiness and, if competing species react differently to the environmental factor, such heterogeneity can lead to nonrandom species distributions and hence acts as an additional, extrinsic niche dimension or axis along which partitioning is possible. Coexistence in a two patch model environment can occur if there are differences in relative dispersal (microhabitat selection) so that the two species occupy different patches (Levin, 1974). Interspecific competition will be reduced even if the competing species do not show resource partitioning because the differences in patch choice means that each species can establish itself in a patch and withstand subsequent invasion from the other.

The sibling species Drosophila melanogaster and D. simulans are often sympatric (as assessed by adult collections) and can coexist with little or no significant resource partitioning, often emerging from the same type of resources (Carson, 1965; Atkinson, 1979a;
Atkinson and Shorrocks, 1977; Bos and Boerema, 1981; David et al., 1983; Parsons, 1973, 1975; Parsons and Stanley, 1981; Capy et al., 1987). As there is interspecific competition in both field and laboratory (Barker, 1983; Parsons, 1975, 1983) and competitive exclusion is a possibility at the microhabitat scale (Barker, 1983), there has been much interest on by what mechanisms these two very similar species can coexist at the microhabitat level.

4.2 Competition Between *D. melanogaster* and *D. simulans*

*D. melanogaster* and *D. simulans* are the only cosmopolitan species in the 8 species *melanogaster* subgroup (Patterson and Stone, 1952; Parsons and Stanley, 1981; Leumeunier and Ashburner, 1984; Leumeunier et al., 1986). Their success is due to their ability to exploit fermenting resources such as fallen fruit and rotting vegetables and this enables them to colonize disturbed or man-made habitats (Throckmorton, 1975; Parsons, 1978, 1983). Their dispersal has been greatly helped by their close association with man (David, 1979) and are not normally found far from human dwellings – an observation that led Dobzhansky (1965) to call them animal weeds.

Although *Drosophila melanogaster* and *D. simulans* are morphologically virtually identical (Sturtevant, 1920), there is strong sexual isolation so that hybrids (which are sterile) are rare (Barker, 1962; Mourad et al., 1972). The two species are also ecologically so similar that similar selective forces appear to act on each in sympatry (Anderson and Oakeshott, 1984; David and Bocquet, 1975; Choudhary and Singh, 1987). However, *D. simulans* has a
narrower, more specialized niche than does *D. melanogaster* (Parsons, 1983) and shows less geographic divergence than does *D. melanogaster* (David *et al.*, 1984; Singh *et al.*, 1987; Choudhary and Singh, 1987). In homogeneous environments, *D. melanogaster* is usually the superior competitor in the laboratory (Wallace, 1975; Barker, 1983; Gilpin *et al.*, 1986) and appears to be preadapted to such an environment (Parsons, 1983; Carracedo and Casares, 1986). *D. simulans* appears to be adapted to avoiding competition as its fecundity and larval mortality are more affected by population density than is *D. melanogaster* (Barker, 1983; Mueller, 1985; Gilpin *et al.*, 1986).

Exploitative larval competition is important in *Drosophila* (Atkinson, 1979b; Barker, 1983) and, in laboratory experiments at least, *D. simulans* is at a competitive disadvantage because of pupal burial by foraging larvae because it pupates more on the surface of the medium whereas *D. melanogaster* tends to pupate on food-tube walls (Herskowitz, 1953; Sameoto and Miller, 1968; Barker, 1971). There can also be competition between adults. Male *D. melanogaster* court vigorously and indiscriminately and are territorial. This often prevents *D. simulans* from mating so that, at high population densities, most *D. simulans* females remain unfertilized (Shorey and Bartell, 1970; Moth, 1974; Barker, 1983; Hoffman, 1987). In addition, oviposition by *D. simulans* is inhibited by the presence of large numbers of larvae in the medium (Moth, 1974).

There have been few experiments on competition between these two species which have involved spatially heterogeneous resources or
environments. Most experiments have dealt with factors such as
temperature, the evolution of competitive ability and frequency
dependence in homogeneous environments where spatial heterogeneity
would complicate matters (Barker, 1983; Mueller, 1985). Indeed, even
in a simple and homogeneous experimental environment, the outcome of
two-species competitive interactions can be complex and difficult to

Even in apparently homogeneous environments there can be
heterogeneity in resource use leading to differences in realised
niches: D. simulans has a greater tendency to oviposit in the centre
of medium (Moore, 1952; Barker, 1971) and is more likely to lay eggs
on the surface rather than inserting them into the medium (Takamura,
1984). D. simulans larvae form a greater proportion of the larvae
found in the lower half of the medium (Barker, 1971) and D. melanogaster
is more likely to pupate on the walls of food tubes
(Sameoto and Miller, 1968). These microenvironmental differences can
effect interspecific competition: coexistence between D.
melanogaster and D. hydei on a single, undivided resource is
possible if there was sufficient medium depth for there to be
resource partitioning by differences in the larval depth (Arthur,
1986). Moore (1952) found differences in oviposition preference in
mixed D. melanogaster and D. simulans populations for old and for
fresh food surfaces. In population cages founded from eggs laid on
the edges of fresh food the frequency of D. melanogaster rose to
100%. In the two cages founded from eggs in the centre of old media,
the frequency of D. melanogaster declined (to 0 and 4%
respectively). As old food is unfavourable to both species (in single species populations neither species showed a preference for the centre of old food) the centre of old food cups are a refuge for *D. simulans* females which more readily oviposit in this site.

4.3 Environmental Factors and Coexistence

*D. melanogaster* and *D. simulans* respond differently to temperature, ethanol and light. In heterogeneous environments, coexistence might be possible if the two species can use one or more of these factors as a cue for microhabitat selection.

4.3.1 Temperature

There is evidence that *D. melanogaster* has a thermal niche in the wild (Jones *et al.*, 1987) while David *et al.*, (1983) report that Zwicky (1948) found that in a temperature gradient from 8° to 40°C, the preferred temperatures for *D. melanogaster* and *D. simulans* were 24.2°C and 23.5°C respectively. In similar experiments but with nearly 100% humidity, Prince and Parsons (1977) found that the two species had preferences of 32.1°C and 28.9°C. How such preferences may promote coexistence is unclear because at temperatures of 25°C and above, *D. simulans* is generally outcompeted by *D. melanogaster* in population cages (Moore, 1952), while at 15°C *D. simulans* may sometimes prevail (Moore, 1952; Tantawy and Soliman, 1967; Carracedo and Casares, 1986). Furthermore, *D. simulans* is eliminated from such population cages when the temperature is raised to 25°C (Moore, 1952; Tantawy and Soliman, 1967).
In the laboratory, *D. melanogaster* can tolerate higher and greater variation in temperature ([Hosgood and Parsons, 1966; Levins, 1969; Wallace, 1981; Parsons, 1983; David et al., 1983] and similar results have been found in a number of two species competition experiments [Merrel, 1951; Ayala, 1966, 1969a, 1969b; Mourão and Ayala, 1971]. Few experiments have used intermediate or varying temperatures [Barker, 1983] although Carracedo and Casares (1986) found that, though still outcompeted, *D. simulans* survived better in a constant (21°C) rather than in a variable temperature regime (a 17-21°C cycle).

In the wild, seasonal variation in the relative frequencies and absolute numbers of *D. melanogaster* and *D. simulans* in the field also vary with temperature [McKenzie and Parsons, 1974]. In the USA *D. simulans* is the more common species in the Southern States where the climate is more constant and the winters less severe, whilst in the harsher Northern States, *D. melanogaster* is dominant [Wallace, 1968]. However, *D. simulans* has recently increased in range and frequency without any appreciable change in climate [Ives, 1954; Hoenigsberg, 1968; Tantawy et al., 1970; Watanabe and Kawinishi, 1976] and *D. melanogaster* and *D. simulans* are also often sympatric in areas with temperatures at which *D. simulans* is outcompeted in the laboratory [Tantawy and Mallah, 1961]. Although there is no doubt that temperature can act as a macroenvironmental factor which limits the general distributions of *D. melanogaster* and *D. simulans*, there is little evidence the two species use it for interspecific microhabitat partitioning.
4.3.2 Ethanol

Ethanol concentration also affects competition: *D. simulans* cannot tolerate as high ethanol concentrations as can *D. melanogaster* (3.4% and 12% respectively [McKenzie and Parsons, 1972; McKenzie and McKechnie, 1979]). The success of *D. melanogaster* in colonising more northern climes is in part due to its high ethanol tolerance (David, 1979; Parson, 1983) and this difference also suggests that there might be differences in microhabitat selection. *D. melanogaster* is found both inside and outside wineries while *D. simulans* is found only outside. During the vintage *D. melanogaster* moves towards the cellars while *D. simulans* moves away (McKenzie, 1974).

In the laboratory, however, there are conflicting results over whether ethanol concentration is used in microhabitat selection. In population cages with food containing 0 and 9% alcohol, *D. simulans* preferred standard (non-alcohol) medium (McKenzie and Parsons, 1972). However, female *Drosophila* do not necessarily choose their oviposition sites with respect to ethanol concentration (Cavener, 1979). Arthur (1980a) found that in population cages with standard medium *D. simulans* outcompeted *D. melanogaster* while *D. melanogaster* won on 8% ethanol medium. There was no consistent winner with intermediate ethanol concentration (4%). These cages were homogeneous (with each cage using a single ethanol concentration) and, in cages with medium heterogeneous for ethanol concentration, there was no coexistence: *D. simulans* won in cages with media with 0 and 8% ethanol while *D. melanogaster* was the winner on media with either 0 and 10% or 0 and 12% (Arthur, 1980b).
Interspecific differences in ethanol tolerance do not seem to facilitate coexistence and the presence of *D. simulans* is only possible at low ethanol concentration. For example, in piles of grape residues *D. melanogaster* and *D. simulans* can be found when ethanol concentrations are below 3%, but during fermentation (when the ethanol concentration reaches 7%) only *D. melanogaster* remain (McKenzie and McKechnie, 1979). However, Capy et al., (1987) found that in grape-breeding communities of *Drosophila* in Southern France there was little correlation between ethanol concentration and species frequencies so that coexistence must be due to some other factor.
4.3.3 Light Preferences

Light intensity and visual acuity is important for most Dipterans: visual guidance plays a crucial role in spatial orientation during locomotion both walking and flight (Grossfield, 1978; Gotz, 1980; Wehner, 1981). Dipterans will not fly when the light conditions degrade visual acuity: flight activity in diurnal insects is inhibited by too low (or too high) light intensity (Johnson, 1969; McInnis et al., 1982). Vision is also involved in orientation towards other objects including potential mates so that lighting conditions can have an important effect on species interactions. Light intensity is also used as an environmental cue to synchronise the physiological state of potential mates so that the sexes reach sexual maturity at the same time and are brought together. Light intensity can also act as a threshold for sexual behaviour and any interspecific differences in the threshold level required may reduce the chance of hybridisation or interference between closely related sympatric species (Andrewartha and Birch, 1984). Light also affects many important behaviours in Drosophila such as the readiness to oviposit, flight activity and dispersal as well as habitat selection (David et al., 1983).

As D. simulans disperses to brighter light than D. melanogaster (McDonald and Parsons, 1973; Kekić and Marinković, 1979), and F, D. simulans offspring are more photopositive than F, D. melanogaster reared from adults collected at the same site (Kekić and Marinković, 1979; Kekić, 1982; Seiger and Khamis, 1987), differences in light preferences might also be important in promoting coexistence by
microhabitat selection. In a light gradient, D. simulans oviposits in brighter areas than does D. melanogaster (Kawanishi and Watanabe, 1978). D. melanogaster larvae also pupate in darker areas than D. simulans larvae (Manning and Markow, 1981). Rizki and Davies (1953) found that D. melanogaster larvae tended to pupate away from a light source whereas D. willistoni larvae did the opposite and that this difference increased in mixed populations thus reducing interspecific interactions.

Light preferences may, therefore, lead to differences in species distributions at the microhabitat level. For example, the attraction of D. melanogaster to the darker interiors of buildings (David, 1979) is consistent with its more photonegative light preference and, unlike D. melanogaster, the more photopositive D. simulans is rarely found inside buildings (Brncic, 1970; McKenzie, 1974; Watanabe and Kawanishi, 1976; Parsons, 1983; Capy et al., 1987).

The facultative dark mating of D. simulans is also unusual. All other cosmopolitan species of Drosophila (including D. melanogaster) have light-independent mating behaviour (Speith and Hsu, 1950; Grossfield, 1972). This gives greater flexibility in mating ability and the exploitation of the diverse lighting conditions in man-made habitats (Grossfield, 1972). The unusual light-dependent behaviour of D. simulans may be due to its close relationship with D. melanogaster. Although it restricts the light conditions in which mating is successful, the dark-inhibited mating of D. simulans may reduce interspecific contacts and reinforce ethological isolation.
(Grossfield, 1972). The differences in photopreferences between the two species may also be adaptive in causing divergence in ecological niches (Basden, 1954; Grossfield, 1978; Kawinishi and Watanabe, 1978; Parsons and Stanley, 1981, David et al., 1983).

At the habitat level, D. simulans is usually found further away from human habitation and in more suburban areas than D. melanogaster (Dobzhansky, 1965; Kawinishi and Watanabe, 1978). Such habitat differences may indeed promote coexistence; for example, since 1972 D. simulans has become widely established on mainland Japan, and yet D. melanogaster has not been displaced. Instead, D. simulans is found mainly in the more open suburbs and D. melanogaster in the more built-up areas (Watanabe et al., 1984).

Such differences do not show whether light preferences may promote coexistence within habitats. Indeed, D. melanogaster and D. simulans are now found in sympatric populations in Japan (Watada et al. 1986). At the microhabitat level, however, light preferences have been rarely investigated, although the proportion of D. simulans can drop in as short a distance as across an open window (Fuyama and Watada, 1980; Takamura, 1984). The effects of spatial heterogeneity in light conditions on interspecific competition between D. melanogaster and D. simulans have also been overlooked, (Barker, 1983). In this chapter I will investigate whether differences in photopreferences and other light-mediated behaviours between Drosophila melanogaster and D. simulans can cause microhabitat selection and hence promote coexistence by reducing
larval competition in heterogeneously lit environments. I will also investigate whether light intensity has a direct effect on competitive ability or is an arbitrary environmental cue used by the two species to reduce the overlap in species distributions.
4.4 Interspecific Differences in Light Preferences

4.4.1 Light Intensity and Microhabitat Distributions in the Field

4.4.1.1 Introduction

Here I investigate the role of light intensity in controlling the relative distributions of *D. melanogaster* and *D. simulans* in the field at the microhabitat level. This work also introduces a series of laboratory experiments on the role of light in the coexistence of these species.

4.4.1.2 Materials and Methods

A number of sites in the South and East of England were investigated (see Appendix). The traps usually consisted of plastic drinking cups, 9 cm tall with a mouth diameter of 6.5 cm, and filled with fermented fruit purées (usually apple) to a depth of about 5 cm. Glass jars were also used occasionally. The traps were scattered around the sites with varying light intensities, usually on the ground, and visited periodically during the day in a random order. Small traps were used to reduce the heterogeneity in light intensity which is possible within larger traps. The bait was made from fruit, usually apple, which was chopped up, boiled and fermented for a number of days before use. Waterlogged traps were drained and all the traps were constantly topped up with fresh bait. The cups were periodically removed and replaced by new ones.

Flies in the traps were caught in transparent plastic roasting bags which have the added advantage of being slightly electrostatic thus making the handling of the captured flies easier. Male flies
were distinguished by microscopic examination of their genitalia (Shorrocks, 1972) while females were identified through their male offspring.

Light intensity was measured with a YASHICA light exposure meter (model YEM 35) which gives exposure values (Ev's) ranging from 4 to 17. An Ev value of 17 is the brightest and each unit value represents a doubling in light intensity. These values can not be easily converted to more standard measurements such as lux but, as an illustration, indoor fluorescent lighting has a value of 9 to 10 and a Ev of 11.5 is equivalent to 170 lux (as measured by a linear light sensor). Air temperature was measured at the mouth of each trap using an environmental temperature probe.

4.4.1.3 Results

Although found at all 9 sites, bad weather (thunderstorms and rain, even in August) restricted Drosophila populations and only at four sites were the numbers of D. melanogaster caught sufficient for statistical analysis (Table 4.1). Three were in Norfolk near Ludham (map reference TG3918) during the summer of 1985 and consisted of a number of habitats (see Appendix). One was in an apple orchard, the second in a "pick your own" fruit garden and the third at a communal lawn and small vegetable garden next to dustbins. The flexibility in the light preferences can be seen from where D. melanogaster was caught, ranging from a dustbin alcove (with a light reading of less than 5), to inside a shed next to a window where homemade wine was
fermenting (mean Ev value of 10.7) and a mean light intensity of 12.3 in the orchard.

The fourth site was at Lovelace Road, Oxford, a suburban garden which was the only site where *D. simulans* was found. In 1986, 39 *D. melanogaster* and 5 *D. simulans* were identified (together with 32 unidentified *D. melanogaster/D. simulans* flies that either escaped or were females which did not produce offspring). *D. melanogaster* were caught at traps with lower light intensities than those containing *D. simulans* (mean Ev of 9.1 and 12.7 respectively; Figure 4.1, p<0.01, t-test=3.800, 5 degrees of freedom, using t-test for unequal sample sizes and with population variances not assumed to be equal, Parker, 1979).

Courting and mating flies were seen at many of the traps and, when left out for long enough, larvae and pupae were also seen in the cups. *D. melanogaster, D. subobscura, D. busckii, D. funebris* and *D. hydei* also emerged from traps brought back to laboratory from the field studies in 1985.

As only 5 wild *D. simulans* were caught, a *D. simulans* release-recapture experiment of laboratory flies was undertaken at this site. As *D. melanogaster* had already been found, only an outbred laboratory *D. simulans* stock which had been maintained in the laboratory under natural lighting conditions was released (this stock was also used to found the population cages of Experiment II, see Section 4.5). 204 females and 198 males were released in the
centre of the front garden at 14:45 on 28/9/1986. The ambient temperature was 18.4°C with an Ev light intensity of 13. Collections were started from 14:55 on the same day and ended at 14:40 on 29/9/1986, by which time a total of 229 D. simulans had been recaptured (a recapture rate of 57%). The flies were checked to make sure that only D. simulans were counted.

Like the wild D. simulans, these flies were caught at significantly higher light intensities than the wild D. melanogaster (13.7 and 9.1 respectively, \(p<0.0005\), t-test=12.239 62 d.f.). There was no significant difference in light preferences between the laboratory reared and the wild D. simulans. D. simulans at Lovelace Road were also caught at a significantly higher light intensity than D. melanogaster from any of the other sites. D. simulans were also caught at brighter light intensities than D. phalerata and D. subobscura/obscura (Table 4.2, Figure 4.1). There was no evidence for temperature selection either between sites or between species (Table 4.3). At Lovelace Road, for example, D. simulans was caught at a mean temperature of 18.0°C and D. melanogaster at 17.8°C.

These results show that light intensity can indeed control within species distributions in the wild and that light preferences in D. melanogaster and D. simulans can reduce species overlap within habitats.
4.4.2 Light Preferences of Laboratory Stocks

4.4.2.1 Introduction

Oviposition is also important in habitat selection and the readiness to oviposit of \textit{D. melanogaster} and \textit{D. simulans} in dim and bright light was investigated to test whether light preferences and the readiness to oviposit are affected by light in the same way.

4.4.2.2 Materials and Methods

Three outbred stocks were tested separately: a wildtype \textit{D. simulans} stock, a wildtype \textit{D. melanogaster} stock and a white-eye \textit{D. melanogaster} stock (\textit{D. melanogaster w}). The wildtype \textit{D. melanogaster} stock (which was also used in Chapter 3) was also crossed with a white-eye strain to produce the outbred white-eye mutant stock. This stock and the wildtype \textit{D. simulans} are also used in Experiment II of the interspecific competition cage experiments below (Section 4.5).

As in Chapter 3, dim red light and bright white light regimes were used. 25 food tubes, each with two 10-day old fertilised females and two males of each stock were kept in the two experimental light conditions. Over the following 43 hours, the number of eggs laid was counted.

Samples of the three laboratory stocks were also tested for adult light preferences in the light preference test apparatus described in Chapter 3, again using bright white light and dim red light.
4.4.2.3 Results

*D. simulans* females laid significantly more eggs in bright white light than in dim red light ($\chi^2 p<0.001$) while both *D. melanogaster* stocks laid significantly more eggs in dim red light ($\chi^2 p<0.001$). *D. simulans* was also more photopositive than *D. melanogaster* with 86% of the sample caught in the bright white light cylinder of the testing apparatus (Table 4.4) compared to only 33.7 and 26.4% for wildtype *D. melanogaster* and white-eye *D. melanogaster* respectively. Another *D. simulans* laboratory strain was also found to be highly photopositive (Table 4.4).

The readiness to oviposit is hence closely related to adult light preferences and, compared to *D. melanogaster*, *D. simulans* is photopositive having a greater tendency to disperse to and oviposit in bright white light.

4.4.3 The Effect of Experience on Light Preferences

4.4.3.1 Introduction

These experiments complement those in Chapter 3 where the effect of experience and spatial heterogeneity on habitat selection in wildtype *D. melanogaster* was investigated. Here I test whether *D. simulans* reacts in the same manner and whether a white-eye *D. melanogaster* mutant (which has pigmentless compound eyes and ocelli [Strickberger, 1962]) can also form light preferences.

4.4.3.2 Material and Methods

The two outbred stocks which had been kept in bottles in the
laboratory were a wildtype *D. simulans* stock produced by crossing 3 laboratory lines (Foumbot, Seychelles and Yaoundé) and a *D. melanogaster* w line produced by crossing the outbred wildtype *D. melanogaster* stock used in Chapter 3 with a white-eye mutant line. These stocks were also used in the second population cage competition experiment in below (Section 4.5, Experiment II). The experimental set-up was the same as Chapter 3 and consisted of No-choice lines (where the flies were kept constantly in one light regime) and RW population cages (where flies can disperse freely between the two light regimes). All populations were maintained under constant light and temperature (25°C). The two light regimes consisted of dim red light (light intensity of 0.7 lux) and bright white light (170 lux) and the flies were tested in light preference testing apparatus as described in Chapter 3 (Section 3.2.2).

4.4.3.3 Results

To investigate whether adults of the two stocks could form preferences, 50 pairs of each stock (with two pairs of flies per food tube) were randomly assigned to each of the light regimes. After 5 days, both *D. simulans* and *D. melanogaster* w adults kept in dim red light were more photonegative than flies kept in bright white light ($\chi^2 p<0.01$ and $p<0.001$, respectively, Table 4.5).

In experiment 2, adults were tested after 10 days. *D. melanogaster* w kept in dim red light were more photonegative ($\chi^2 p<0.001$). No difference, however, was found between *D. simulans* lines. In both
experiments the *D. simulans* lines were more photopositive than the equivalent *D. melanogaster* line.

Offspring from Experiment 1 (50 pairs) were also used to found long term No-choice lines (Figure 4.2). Overall, there was a consistent difference between lines. In each generation, adults from the lines kept in dim red light regime were more photonegative (p<0.005, n=17, Wilcoxon matched-pairs signed rank test; Table 4.6).

In the RW cages, *D. melanogaster* w from the dim red light sector samples were significantly more photonegative than samples from the bright white light sectors (p<0.025, n=7 Wilcoxon matched-paired signed-rank test). No such difference was found between the *D. simulans* lines, indeed, the opposite was found in a number of *D. simulans* trials with samples from the dim red light sector being more photopositive (Table 4.6).

Light preferences of adult flies living in the cages were also tested. *D. simulans* adults caught in the dim red light sectors were significantly more photonegative than adults caught in the bright white light sectors whereas no significant difference was found for caught *D. melanogaster* w adults (Table 4.6).

4.4.4 The Effect of Stressful Conditions

4.4.4.1 Materials and Methods

Stress can affect preferences (Hoffman and Turelli, 1985) and here I test whether overcrowding (which can cause stress in *Drosophila*)
alters light preferences. Adults from No-choice lines of all three stocks (*D. simulans* and *D. melanogaster* w and wildtype *D. melanogaster*) were kept in crowded conditions so that instead of the usual two pairs, 20 or more pairs were kept in each food vial. The flies were tested after 3 days in these conditions.

Another form of stress might be the presence of another species especially as male *Drosophila* court indiscriminately. This was investigated in a second series of experiments where mated two-week old females were put two to a tube (either two females or males of the other species) and kept in either dim red light or bright white light. This gave three combinations and two light regimes: female *D. simulans* with *D. melanogaster* w females, *D. simulans* females with *D. melanogaster* w males, and *D. melanogaster* w females with *D. simulans* males. 25 tubes of each interaction were kept in each of light regimes for 15 days when the adult flies were removed and their light preferences tested (Figure 4.3).

4.4.4.2 Results

After 3 days of overcrowding, the two *D. melanogaster* stocks still had significant differences in light preferences between lines after 3 days (p<0.001, *D. melanogaster* and p<0.005, *D. melanogaster* w, χ² test. Table 4.7) while there was no difference between *D. simulans* lines which suggests that *D. simulans* is more affected by overcrowding. Small sized *D. simulans* from an overcrowded stock bottle did not exhibit the usual highly photopositive preference either whereas larger flies which had developed from a less dense
bottle stock did (Table 4.7). In another experiment, the difference in preferences between *D. melanogaster* lines disappeared after 7 days (Table 4.7). The sexes can react differently: females kept on food in which larvae and pupae were present still exhibited a significant difference in light preferences. However, this difference was lost after these flies had been kept in crowded conditions for a day whereas the opposite was found with the males (Table 4.7).

In the second series of experiments, flies in two of the three combinations had altered light preferences (Table 4.8). In the female *D. melanogaster w* and *D. simulans* combination, neither species showed a significant difference between light regimes whereas both species in the female *D. simulans* and male *D. melanogaster w* combination did. Both female *D. simulans* and male *D. melanogaster w* from the bright white light regime were more photopositive (Table 4.8).

The most interesting combination was between female *D. melanogaster w* and male *D. simulans*. Male *D. simulans* from the dim red light regime were significantly more photopositive than males from the bright white light regime (*p*<0.05, $\chi^2$ test). There was no significant difference between female *D. melanogaster w* although those from the dim red light were also more photopositive. Furthermore, hybrid females (identified by having pigmented eyes and being sterile) emerged from the dim red light food tubes of the female *D. melanogaster* and male *D. simulans* combination. This last result also underlines the effect of light conditions on
interspecific matings which were possible here because female
*Drosophila* remate once they have used up sperm from previous
matings, usually within 14 days (Gromko and Pyle, 1978).
4.5 Competition and Microhabitat Selection in Population Cages

4.5.1 Introduction

Inspite of the difference in light preferences between \textit{D. melanogaster} and \textit{D. simulans} (and other sibling species pairs of \textit{Drosophila}) and the effect of light on mating behaviour, there have been few experiments on the effects of light on interspecific competition (Barker, 1983). Here I will investigate whether, in a spatially heterogeneous light environment, differences in light preferences reduce species overlap (and hence interspecific competition) and also whether light has a direct affect on mating ability and interspecific competition between \textit{D. melanogaster} and \textit{D. simulans} exploiting the same resource.

4.5.2 Materials and Methods

Population cages, 24×24×12cm in size, which varied only in the degree of spatial heterogeneity in light were constructed. The walls and floors were made from polystyrene tiles and the tops from glass. They were divided into two sectors by a partition wall with a small hole (20x5mm) at the top to permit dispersal between the two sides. The room temperature was maintained at 25°C and the cages were illuminated from above by three 40 watt fluorescent white lights positioned 17cm above the glass.

Two light regimes - bright white light and dim red light were used. The dim red light was provided by fixing 10 layers of ROSCO CINELUX 621 RED LIGHT FILTER onto the glass tops of the cages, while the bright white light illuminated sectors had just bare glass. The
red light sectors were over 200 times less bright than the bright white light sectors ("Exposure values" or EVs of 4 and 11.5 or 0.7 and 170 lux respectively). In the field, for example, I caught *D. simulans* at light intensities (Ev) of 12 to 13 and *D. melanogaster* at an Ev of 9 or less (Section 4.4.1). The walls and floors of the red light sectors were painted matt black and the white light sectors were painted matt white.

Three types of cages were used (Figure 4.3):

i) Spatially heterogeneous "RW" cages, with one sector illuminated with bright white light.

ii) Spatially homogeneous "WW" cages with both sectors illuminated with bright white light.

iii) "RR" homogeneously lit cages with both sectors illuminated with dim red light.

I hope to test whether differences in light preferences can indeed lead to microhabitat partitioning and perhaps coexistence, with the more photopositive *D. simulans* dispersing to and ovipositing in the White light sectors of the RW cages and the more photonegative *D. melanogaster* dispersing to the dim red light sectors.

The homogeneously lit cages examine the effects of light on competition and test whether coexistence is possible at particular light intensities without spatial heterogeneity. In RR cages, *D. simulans* might be at a competitive disadvantage because its mating
is disrupted while in the WW cages, *D. simulans* may be able to mate normally and may hence be at less of a disadvantage (for the temperature was maintained at 25°C which is normally too high for coexistence [Barker, 1983]).

Dim red light has a number of advantages over complete darkness. The red light filters allow sufficient energy to pass through for there to be less than a 0.4°C difference in temperature between the dim red light and the bright white light regimes. The most important reason is that red light can act as the missing screening pigments of white-eye mutants (Cosens and Briscoe, 1972) so that the effect of light on mating ability and interspecific competition can be tested directly. In dim red light, visual acuity of white-eye *D. melanogaster* is restored, whereas the pigmented eyes of wildtype flies are blinded (Geer and Green, 1962; Burnet and Connolly, 1973).

A vermilion-eye mutant was chosen because it acted as a control for the *D. melanogaster* w mutant because dim red light has the same effect on vision in the vermilion-eye mutant as on wildtype fly—both have red eye pigments and hence equally blinded and, although it lacks the normal brown screening pigment of wildtype flies, it is behaviourally very similar to wildtype *D. melanogaster* (Grossfield, 1975, Markow and Scavarda, 1977). The mutant was used instead of a wildtype *D. melanogaster* because it also has the advantage that females are distinguishable from wildtype *D. simulans*, which wildtype *D. melanogaster* is not.
In both experiments outbred stocks were used. In experiment I, the *D. simulans* stock consisted of 4 laboratory strains of *D. simulans* (2 Leeds, Foumbot and Seychelles strains) which were crossed together. Similarly, an outcrossed stock of vermilion eyed *D. melanogaster* was created from a vermilion-eyed strain crossed with wildtype strains (Kaduna, Leeds, Rhodes, Norwich and a Canary strain). The fourth generation adults of both stocks were used to found the cage populations. As well as allowing female *D. melanogaster* and *D. simulans* to be identified, the use of vermilion-eye *D. melanogaster* will also show if the light independent mating behaviour of *D. melanogaster* is an advantage in dim light when in competition with *D. simulans*.

In experiment II, a white eyed outbred stock of *D. melanogaster* (*D. melanogaster w*) was produced from crossing the mutant strain with males from 15 isofemale lines caught by myself at Condom, Southwestern France nine months previously and maintained in the laboratory. An outbred stock of *D. simulans* (as above except that Yaoundé was used instead of the Leeds strains) was used and again fourth generation adults were used to set up the cages. Experiment II used wildtype *D. simulans* and, to examine the effects of light conditions on mating ability and, therefore, competition, a white-eye mutant of *D. melanogaster* for the reasons given above. The use of this mutant (which lacks screening eye pigments) also has the same effect on *D. melanogaster* as would increasing the brightness of the white light sectors but without any further problems of
temperature control which would increase if brighter lights were
used.

To minimize initial population size fluctuations the founding
adults were put into the cages over a three week period with 40
fertilized females of each species being introduced into each cage
every week. The flies were counted using cold anaesthesia and 20 of
the recovered flies were put into each cage sector.

Standard Drosphila maize meal medium seeded with active yeast
giving 5.65g of fresh food per vial with 12 vials per population
cage sector. A third of each sector's vials were changed each week
giving a cage life of 3 weeks for each vial. There was hence a cont­
inuous adult cage population with overlapping generations.

To assess the relative frequencies of the two species four sample
vials per sector were put into the cages every three weeks for 24
hours and then removed. The frequencies of the two species was
calculated by counting the emerging adults.

To examine whether there had been any change in photopreferences
during the course of the experiments, equal numbers of male and
female offspring from sample tubes were released in clean, unused RW
cages under the same conditions as for the experimental population
cages. Each species was tested separately, and after 24 hours the
distribution of the flies over the two sectors was measured.
4.5.3 Results

The overlap in species distributions was measured by $\theta$, an index of overlap where:

$$\theta_{ij} = 1 - 0.5 \sum_{h} |P_{ih} - P_{jh}|$$

where $P_{ih}$ is the proportion of $D. \ melanogaster$ found in cage sector $h$ and $P_{jh}$ is the proportion of $D. \ simulans$ in cage sector $h$. The index $\theta$ ranges from zero (no overlap) to a value of 1 where overlap is total (Colwell and Futuyma, 1971; Southwood, 1978; Price, 1984).

Experiment I: Vermilion-eye $D. \ melanogaster$ and $D. \ simulans$

Experiment I consisted of 16 cages: 6 RW heterogeneously lit cages and 5 WW and 5 RR homogeneously lit cages. It was started on 1/3/82 and ended 47 weeks later. $\theta$ was significantly less in the RW cages (with a mean value of 0.506 for all samples compared to means of 0.757 and 0.754 for the RR and WW cages respectively, $p<0.001$, ANOVA from Parker, 1979), and there was no significant difference in $\theta$ between RR and WW cages (Figure 4.5; Tables 4.9 and 4.10). The last two samples (9 and 10) are not included in these analyses because there were too few $D. \ simulans$ left in the cages in these sample for $\theta$ and other statistics to be calculated.

It was not possible to use the vermilion-eye colour to distinguish the two species: in the samples, there was too much variation in the hue of the eyes mainly due to variation in age (wildtype young $D. \ simulans$ have very bright red eyes) for consistent identification of females. This led to the flies in sample 1 being
lost. In later samples the proportion of the two species was scored by examining the male genitalia.

The reduction in species overlap in the RW cages led to a difference in the relative survival of the two species. In each RW cage, the frequency of *D. melanogaster* was lower in the bright white light sector than in the equivalent red light sector (Figure 4.6; p<0.005, Wilcoxon matched-pairs signed-ranks test, calculated over all samples for each individual RW cage) and, inspite of the steady decline of *D. simulans* in all cages, the frequency of *D. simulans* was always higher in the white light sectors (Tables 4.11 and 4.12) and *D. simulans* also survived longer in the white light sectors of RW cages than in the red light sectors (an average of 27.8 weeks and 19.5 weeks respectively; p<0.02, n=6 Sign Test).

The frequency *D. simulans* in the white light sectors of the RW cages was also consistently higher than that in the WW and RR cages (Table 4.12, p<0.008, n=7. Sign test for mean percentage of *D. simulans* in WofRW compared to RR and WW means for each sample). However, when compared by analysis of variance, for each sample, the transformed percentage of *D. simulans* in the RW cages was not significantly different from that in the RR and WW cages (Table 4.12). WW cage number 12 was omitted from the analysis because at the start of the experiment, this cage had a consistently higher frequency of *D. simulans*. This was due to this cage being in a cooler area than the other cages. Once moved, the frequency of *D. simulans* dropped to that of the other WW cages.
Experiment II: White-eye *D. melanogaster* and *D. simulans*

Experiment II consisted of 12 cages (4 of each type). It was started on 18/5/84 and lasted for 48 weeks. As in experiment I, there was a significant reduction in overlap (θ) in the RW cages compared to the WW and RR cages (p<0.001, analysis of variance: Figure 4.7; Table 4.13 and 4.14) and the percentage *D. simulans* was significantly higher in the bright white light sectors than in the dim red light sectors of the RW cages (p<0.005, calculated over all samples, Wilcoxon matched-pairs signed-ranks test, Figure 4.8; Table 4.15). This reduction in species overlap in the RW cages did not lead to longterm coexistence either. However, there was coexistence in the WW cages for the 48 weeks of the experiment. Furthermore, the frequency of *D. simulans* was significantly higher in the WW cages than either the RR or RW cages (p<0.025 or less, analysis of variance for each of the samples and p<0.008, n=7, Sign Test; Table 4.16).

Coexistence in the WW cages shows the important effect of light on competition. The effect of light is resilient because, although the frequency of *D. simulans* dropped during a period when temperature control problems led to high temperatures (30°C during the day and 18°C at night), once the temperature returned to normal the percentage *D. simulans* in the WW cages increased again (Figure 4.9). This contrasts with Experiment I, in which there was no coexistence between vermilion-eyed *D. melanogaster* and wildtype *D. simulans* in any of the cages.
The results from the RW cages of Experiment II are somewhat surprising. There was a significant separation in species distributions for the first sample (sample A, 5 weeks after the start of the experiment) which presumably led to a decrease in interspecific competition. The mean frequency of *D. simulans* in the white light sectors of the RW cages was 78% (with an overall mean over both sectors of the RW cages of 43% *D. simulans*), significantly higher than in the RR cages (a mean of 60.1%, *p*<0.05, t-test). In the following samples, however, there was a dramatic decrease in the percentage *D. simulans* so that by sample C (13 weeks) the mean percentage of *D. simulans* in the white light sectors of the RW cages had dropped to 15% while the mean percentage for the WW cages and RR cages was 64.8% and 38.4% respectively. For the remainder of the experiment the mean frequency of this species in the white light sectors of the RW cages was not significantly different from that of the RR cages (and its frequency in the WW cages was significantly higher in all the samples). This may be due to the effect of disturbance on light preferences in *D. melanogaster w* (see below).

**Photopreference Results**

Adults from both experiment I and II were tested to see if there had been any change in photopreferences during the course of the experiments.

In experiment I, adults collected from sample 6 (week 22) were tested. There were changes in photopreferences of flies from the RW cages compared to the photopreferences of samples from the
homogeneously lit WW and RR cages (Table 4.17). Vermilion-eye *D. melanogaster* from the RW cage samples were significantly more photonegative (as measured by the percentage dispersing to dim red light) than *D. melanogaster* flies from the WW cages (p<0.001, \(\chi^2\) test, Table 4.17). No comparison is possible with samples from RR cages as there was significant heterogeneity in the results from the RR cage samples. *D. simulans* from the one RW cage tested were significantly more photopositive (percentage dispersing to bright white light) than *D. simulans* tested from either the RR and WW cage samples (p<0.001, \(\chi^2\) test, Table 4.17). There was no significant heterogeneity in cage types for the *D. simulans* results.

Irrespective of cage type, *D. simulans* flies were more photopositive than vermilion *D. melanogaster* flies from the same cage sample (p<0.05, Wilcoxon matched-pairs signed-rank test, Table 4.18). This shows the more photopositive behaviour of *D. simulans* in general. Furthermore, the differences in light preferences are largely genetical because the flies tested were the offspring of samples taken from the population cages and kept under the same conditions. Unfortunately, it was not possible to obtain sufficient numbers of *D. simulans* from later samples for photopreference tests to be repeated.

The photopreference tests for experiment II were carried out at an earlier stage than those in experiment I (sample B, week 9). Unlike experiment I, however, there was no evidence for change in photopreferences in either species (Table 4.19). These tests could
not be repeated with later samples because of the rapid drop in the frequency of *D. simulans* in the RW cages from sample C onwards.

**Dispersal Behaviour of *D. melanogaster w* alone in RW cages**

Lewontin (1959) found that *Drosophila* which are normally photonegative become highly photopositive when disturbed and, if *D. melanogaster w* has a similar escape response, this may have had an important effect on population interactions in the RW cages of Experiment II. To investigate this, *D. melanogaster w* from the same stocks used to initiate experiment II were maintained in RW cages which had food tubes in only one of the two sectors. Three had 12 food tubes in the dim red light sectors only ("R*W" cages) and three others had food tubes in the bright white light sectors only ("RW*" cages, Figure 4.10). Otherwise, the experimental conditions were the same as for Experiments I and II except that, during the changing of food vials, the hole between cage sectors was stopped up with cotton wool and not removed for about 15 minutes by which time the disturbed flies had settled down. Periodically, sample tubes were placed in the cage sectors which had the food tubes and the number of eggs laid and adults emerging counted.

The experiment was set up on 11/7/84 and ran for 49 weeks. In the absense of *D. simulans*, there was no significant difference in the number of eggs laid or adults emerging in the two types of cages for the first 7 samples (Table 4.20, signed-ranked matched-paired Wilcoxon test). Samples 8 and 9 (weeks 40 and 43) were different in
that sample tubes were put on both sides of the cages. Again, there was no consistent trend (Table 4.21).

No flies were found on foodless white light sides of the Rw cages throughout the experiment unless there was some disturbance. If the hole between the two cage sectors was not stoppered during the changing of the food tubes, or the cage top was tapped, 50 or more flies would then disperse from the red light sectors into the foodless white light sectors of the Rw cages. The flies moving to the foodless sector had some difficulty in returning to the red light sector and many dead flies were subsequently found on the foodless whitelight sectors of the Rw cages.

This escape response may be important in the outcome of competition between D. melanogaster w and D. simulans in the RW cages of experiment II because every time the food tubes were changed, the normal difference in photopreferences would be eliminated. The normally photonegative D. melanogaster w became disturbed and hence photopositive and dispersed to the white light sectors where they were unable to return to the dim red light sector.
4.6 Discussion

Most field studies have investigated *Drosophila* distributions at too small a scale (between habitats, for example) or have not differentiated between the *D. melanogaster* and *D. simulans* as well as neglecting the role of light mediated microhabitat differences. However, Pavan et al. (1950) believe that in their studies *Drosophila* were responding to light intensity and using it as a cue for changes in temperature and humidity. Seiger and Khamis (1987) found interspecific differences in light preferences for oviposition sites in four sympatric (but not closely related) species of Drosophilids—while Kekić and Marinković (1979) found that the distributions of *Drosophila* were influenced by light intensity in Batajnica Wood, 30 km north of Belgrade, Jugoslavia. Species distributions were related to the photopreferences of *F*₁ offspring from adults caught in the wood. When tested, *D. simulans* offspring were more photopositive than *D. melanogaster*. Their field data, however, suggest that *D. simulans* was not always caught in brighter areas than *D. melanogaster*. Indirect evidence, however, comes from observations that *D. simulans*, unlike *D. melanogaster*, is rarely found inside buildings (Brncic, 1970; McKenzie, 1974; Watanabe and Kawinishi, 1976; Parsons, 1983; Capy et al., 1987). In my field studies as well, only *D. melanogaster* caught indoors.

Other species of *Drosophila* often sympatric with *D. melanogaster* do not have different light preferences to *D. melanogaster* but, instead, show resource partitioning (Atkinson and Shorrocks, 1977; Marinković et al., 1980; Prince and Parsons, 1980; Kekić, 1982;
Maveety and Seiger, 1982). In my field studies, for example, *D. phalerata* and *D. funebris* were caught at similar light intensities to that of *D. melanogaster* and, unlike *D. simulans*, both show resource partitioning: *D. phalerata* normally breeds on woodland fungi (Shorrocks, 1972, 1982) and *D. funebris* can utilise decaying substrates (Shorrocks, 1972) or older food (Merrell, 1951).

Light can also affect sexual behaviour. *Drosophila* fall into three classes with respect to light and mating behaviour; *D. melanogaster* (like most cosmopolitan species) readily mates in both light and the dark, whereas mating in *D. simulans* is greatly inhibited by darkness (Speith and Hsu, 1950). *D. simulans* has a greater dependence on visual cues and stimuli and its courtship is disrupted in darkness and dim light where the visual acuity of this species is degraded (Grossfield, 1972; Cobb et al., 1985). Light can, therefore, have a significant effect on mating success and, because mating speed is an important component of fitness (Ehrman and Parsons, 1981), it is not surprising that *D. simulans* aggregates in areas where the light is bright enough for mating to proceed successfully. This can be seen in Section 4.4.2 where *D. simulans* is a more photopositive species when tested for oviposition and adult light preferences.

The difference in light preferences led to microhabitat selection in the RW population cages where there was significant reduction in species overlap in both Experiments I and II. This is probably an adaptation in *D. simulans* to reduce interspecific competition
because *D. simulans* survived better in the brighter cage sectors of the heterogeneously lit RW cages. This did not lead to long term coexistence, however. This may have been due to the cage design. The bright white light cage sectors appear not to have been bright enough for a complete separation in species distributions to be possible. In my field studies there was a range of light intensities over which there was an overlap in species distributions: at light intensities (Ev's) of lower than 10, only *D. melanogaster* was found (and above an Ev of 13, only *D. simulans*) whereas between 10 to 13 Ev the two species distributions overlapped. It is not surprising, therefore, that a small number of *D. melanogaster* was always found on the white light sector of the RW cage (which had an Ev of 11.5, well within the range of overlap found in the field) so that, unlike in the field, *D. simulans* was unable to disperse completely away from *D. melanogaster*. As *D. simulans* soon vacated the red light sectors of the RW cages, *D. simulans* was limited to the white light sector of the RW cages whereas *D. melanogaster* continued to exploit both sectors as well as having a refuge in the dim red light sectors.

This is important because there were overlapping generations and no control of population densities which will produce intense competition for fresh breeding sites in the cages. *D. simulans* with its greater sensitivity to high population density will suffer more from reduced fecundity and fertility at such densities (Shorey and Bartell, 1970; Moth, 1974; Moth and Barker, 1981; Barker, 1983). The greater tolerance of *D. melanogaster* to high population density
probably enabled *D. melanogaster* numbers to build up in the Red light sectors of the RW cages where few *D. simulans* remained. In the white light sectors, however, both species were present so that without the availability of a refuge, interspecific competition placed *D. simulans* at a disadvantage. This can be seen by the overall numbers of *D. melanogaster* and *D. simulans* in the RW cages. Although the frequency of *D. simulans* was higher in the white light sectors, the overall frequency of *D. simulans* in the RW cages was no higher than in the homogeneous RR and WW cages.

After an initial high frequency of *D. simulans* in the RW cages in Experiment II (five weeks, equivalent to four generations at 25°C), there was a rapid increase in the frequency of white-eye *D. melanogaster* in the white light sectors. A possible cause may be the dispersal behaviour of *D. melanogaster w* which can become photopositive when disturbed by the changing of food tubes (Section 4.5.3, page 170). A similar change from photonegative to photopositive behaviour when disturbed can be found in *D. pseudoobscura* (Lewontin, 1959). The difference here is that white-eye *D. melanogaster w* has difficulty in returning to the dim red light cage sectors so that the difference in light preferences is negated. In this situation the normally adaptive photopositive light preferences of *D. simulans* is maladaptive because *D. melanogaster w* will have a refuge from competition in the red light cage sectors.

The difference in light preference may be due *D. simulans* having a greater tolerance threshold to light intensity. This is similar to
eye mutants where light intensity can stimulate differential dispersal. Yellow-eyed and wildtype house flies *Musca domesticus*, for example, have similar emigration rates and locomotory activity in a light intensity of 86 lux, but, in brighter light (17,233 lux), the yellow-eyed mutant emigrates at twice the rate of the wildtype flies. This difference is probably caused by the reduced shielding pigment in the yellow-eye mutation which can not, therefore, tolerate as bright light (Chadbora and Kessler, 1977).

Light can also affect competitive ability. In intraspecific competition experiments, white-eye *D. melanogaster* is eliminated by wildtype flies (Reed and Reed, 1948, 1950; Merrel and Underhill, 1956) under normal light conditions. In darkness, however, the white-eye mutant survives better (Hedrick, 1972, 1978).

The reduced fitness of *D. melanogaster w* is largely caused by its reduced visual acuity (due to the lack of screening eye pigments in the adult) and hence mating ability (Parsons and Green, 1959; Connolly et al., 1969; Speith and Ringo, 1983). In the RW cages in Experiment II, *D. melanogaster w* may be at an advantage if *D. melanogaster w* females are fertilised in the red light sectors before dispersing to the white light sectors where *D. melanogaster w* larvae will be able to outcompete *D. simulans*. In the WW cages, this refuge is not available and coexistence — perhaps because of the reduced mating ability of *D. melanogaster w* — was then possible. In dim red light the opposite occurs: the more light orientated mating
behaviour of *D. simulans* is disrupted, and at a disadvantage — which can be seen by its elimination in the RR cages of both experiments.

The difference in competitive ability in the homogeneously lit cages demonstrates that light is not an arbitrary environmental factor. Higher light intensity may, therefore, counteract otherwise adverse conditions so that in very bright conditions spatial heterogeneity may not be necessary for coexistence. In Experiment II, the competitive ability of *D. simulans* was improved so that there was coexistence in the WW cages at 25°C, a temperature at which it is usually eliminated (Barker, 1983). Indeed, this was the only case of long term coexistence in my experiments which demonstrates that light can directly affect competitive ability and thus act as an additional resource set (in the sense of Price [1984]) or niche dimension. An area may, therefore, become more favourable to *D. simulans* if it is more brightly lit. Hoenisberg (1968) observed that the removal of certain plants species during the building of a road near his study area led to a dramatic increase in the frequency of *D. simulans*. This may have been due to the area becoming more open and hence brighter.

White-eye *D. melanogaster* have no screening eye pigments and receives 19 times more light than wildtype eyes (Grossfield, 1978) so that the use of *D. melanogaster w* in Experiment II is equivalent to putting wildtype *D. melanogaster* in very bright light. Here its visual system would also become overloaded and would be at a competitive disadvantage because *D. simulans* is able to tolerate
brighter light (Grossfield, 1978; Parsons, 1983). *D. simulans* was caught in my field studies at light intensities brighter than that for the white light sectors (an Ev of 13 compared to 11.5 of the white light cage sectors). If the white light sectors of the RW cages had been brighter, the competitive ability of *D. melanogaster* may have been reduced to such an extent as to allow coexistence (as well as the observed decrease in species overlap) in the RW cages.

Although *D. simulans* is a better competitor at lower temperatures (Barker, 1983), there was no evidence in my field studies for microhabitat temperature partitioning (although seasonal movement in *Drosophila* can be correlated with temperature [Malogowkin-Cohen et al., 1979]). This may be due to temperature not being directly linked to light intensity in temperate climates such as in England where it can still be bright when overcast with little direct sunlight so that any temperature difference between traps in brighter areas is reduced. It would be interesting to repeat these studies in warmer, sunny climates where brighter areas are also more likely to be hotter. However, between 20 and 30°C, *D. simulans* is consistently more photopositive than *D. melanogaster* (Markow, 1979) while Waddington *et al.*, (1954) observed that although *D. melanogaster* mutants respond to differences in light, there was no environmental selection with respect to temperature. Furthermore, *Drosophila* are active at specific temperatures (Grossfield, 1978; David et al., 1983) so that neither species are likely to be attracted to areas outside of their permissible temperature ranges irrespective of the light intensity. McInnis *et al.* (1982), for example, found that
(with the possible exception of very high temperatures) dispersal rate was not affected by temperature or any other environmental factor apart for low light intensity. It is also interesting that in my studies the *D. melanogaster* from the different sites were caught at similar temperatures.

Temperature did have an effect on competition in my experiments, however. At the start of Experiment I, one WW cage (cage number 12) was inadvertently placed in a cooler area than the other cages and, until moved, there was a consistently higher frequency of *D. simulans* in this cage. The WW cages of experiment II (where there was coexistence between *D. melanogaster* and *D. simulans*) clearly demonstrate the interaction between light intensity and temperature on interspecific competition. In the early part of the experiment when the cooling system broke down there was a wide range in temperature (from 30°C for short periods to 18°C), the frequency of *D. simulans* dropped in all the cages. The period of high temperature did not affect species overlap in the RW cages in Experiment II, although the frequency of *D. simulans* did decrease and perhaps helped the invasion of *D. melanogaster w* into the white light sectors of the RW cages. In the WW cages, once temperature control had been restored, *D. simulans* numbers recovered and coexisted with *D. melanogaster w*. In the RR cages, the frequency of *D. simulans* also declined during the period of high temperature but, unlike the WW cages, *D. simulans* did not recover when the temperature control was restored. Light intensity may hence be crucial to coexistence even where other environmental factors intrude.
The effect of temperature on competitive ability is unclear (Parsons, 1980; Barker, 1983; David et al., 1983) especially as temperature can be confounded by dessication (which is critical for small insects such as Drosophila [Levins, 1969]). However, developmental time decreases as temperature rises which may be important in interspecific competition because D. simulans develops much faster than D. melanogaster at 15°C; an advantage that disappears at 25°C (Tantawy and Soliman, 1967; David et al., 1983). Temperature also affects mating ability (Speiss, 1970; McKenzie, 1978; Parsons, 1983; David et al., 1983) and D. melanogaster can mate at higher temperatures (Schnebel and Grossfield, 1984).

Another reason for considering light as a niche dimension is that there is evidence that photopreferences changed during the course of experiment I. D. simulans from the RW cage tested were more photopositive than D. simulans from the RR and WW cages whereas D. melanogaster from the RW cages were less photopositive than those from the WW cage samples. Since the flies tested were from samples reared under the same conditions, the differences in photopreferences were probably genetical and had arisen from the interspecific interactions in the RW cages over the previous 22 weeks the experiment had been running, this may be an example of behavioural character displacement. D. melanogaster was the probable cause of this response because, in the absence of D. melanogaster, D. simulans expands its niche and has a more even distribution in RW cages. In Experiments I and II, for example, 90.6 and 91.4% of the overall number of D. simulans were found in the white light sectors.
whereas only 57.2% of the total were found on the white light sectors when *D. simulans* was alone in similar RW cages (J.S. Jones unpublished data; p<0.001, t-tests).

In the RW cages, therefore, there is a balance between intra- and interspecific competition. Wildtype, and to a lesser extent white-eyed, *D. melanogaster* increased their niche breadth when alone in the RW cages and became subdivided into photopositive (and hence exploited the usual *D. simulans* bright white light niche) and photonegative populations while competition with *D. simulans* in the RW cages led to a reduction in species overlap (θ) and, in Experiment I, a change in light preferences.

A natural example of my experiments may be occurring in Africa where there are semi-wild populations *D. melanogaster* and *D. simulans* and it is thought that they were originally allopatric (Western and Eastern Africa respectively) with many zones of contact in central Africa (Lachaise et al., 1988). It would be interesting to test allopatric and sympatric populations of these two species to see if there has been any character displacement in light preferences similar to those found in the RW cages in Experiment I. Lachaise et al., (1988) did not find any reproductive character displacement but they did not consider changes in light preferences between ancestral allopatric populations and those in sympathy.

*D. melanogaster* has an effect on *D. simulans*: *D. simulans* becomes more photopositive in a light gradient when mixed with *D.*
melanogaster (although *D. melanogaster* does not appear to become more photonegative [Kawinishi and Watanabe, 1978]). Even in constant light conditions, *D. simulans* disperses faster when mixed with *D. melanogaster* (Wallace, 1975) so that this within-generation (i.e. nonevolutionary) change in light preferences or dispersal enables *D. simulans* to respond rapidly to the presence of *D. melanogaster* and hence avoid interspecific competition. As *D. simulans* is a cosmopolitan species, this learned component also enables *D. simulans* to have some of the flexibility of other cosmopolitan species such as *D. melanogaster* have so that when a superior competitor such as *D. melanogaster* is absent, *D. simulans* is able to track variation in resources and thus expand its niche and exploit less brightly lit areas in spatially heterogeneous environments. This can be seen in the No-choice lines (Section 4.4.3) where *D. simulans* became behaviourally subdivided into two populations with respect to light preferences. *D. simulans* is less flexible, however, because in the intraspecific RW cage experiments on light preferences, the *D. simulans* populations, unlike *D. melanogaster*, did not become behaviourally subdivided. Indeed, *D. simulans* samples from the dim red light sectors were more photopositive than samples from the bright light sectors (although adults caught in the cages did have differences in preferences).

The presence of individuals may be stressful and, as expected from its greater sensitivity to high population densities, *D. simulans* was more likely to change its preferences in overcrowded conditions (Section 4.4.4). *D. melanogaster* may also act as a stress...
factor and in my mixed species preference tests (where the two species were kept together for 16 days), *D. simulans* males did indeed change their preferences when kept with female *D. melanogaster* w (Section 4.4.4). The importance of light on interspecific mating discrimination is also shown here because in this dim red light combination (where *D. simulans* males are blinded), interspecific hybrids were produced (see page 158). In the photopreference tests in Experiments I and II, however, I tested each species separately.

Light preferences may be most important in promoting coexistence where resource partitioning in the more usual sense is not possible. Without the differences in light preferences to exploit spatial heterogeneity in light conditions, microhabitat partitioning and hence coexistence may not be possible between *D. melanogaster* and *D. simulans*. Light preferences may also be important in reducing the chances of interspecific matings and may also bring together mates efficiently which may be particularly important when *Drosophila* numbers are small such as early in the breeding season or when an area is first colonized.

In homogeneous environments, other environmental factors may permit coexistence by altering relative competitive abilities, for example, low temperature or ethanol concentration increase the chances of *D. simulans* coexisting with *D. melanogaster*. As pointed out above, *D. simulans* is frequently found in the field at temperatures which it is outcompeted by *D. melanogaster* in the
laboratory. The greater tolerance to bright light of \textit{D. simulans} may also counteract the advantage of \textit{D. melanogaster} at high temperatures so that, if bright enough, coexistence, like in WW cages in Experiment II, may be possible in a homogeneous environment at temperatures at which \textit{D. simulans} is usually eliminated.

Patchiness in breeding sites may in itself promote coexistence (Atkinson and Shorrocks, 1981; Ives and May, 1985; Shorrocks and Rosewell, 1986). These models assume that there is no spatial heterogeneity in patch quality — which is not the case here. Experiment II shows that light intensity has a significant effect on competition between \textit{D. melanogaster} and \textit{D. simulans} so that, for example, \textit{D. simulans} has a competitive advantage in brighter patches. Spatial heterogeneity in light intensity may, therefore, be superimposed on other forms of patches and resource heterogeneity so that differential dispersal among patches is possible even when competing for one resource.

Light intensity is not the only cue used by \textit{Drosophila} species. Olfactory cues can be involved in the creation of species aggregations (Hoffman, 1985; Parsons and Hoffman, 1985, 1986) and some \textit{Drosophila} species can respond to other environmental factors (Grossfield, 1978; Markow and Fogleman, 1981; David \textit{et al.}, 1983). It is interesting to note, however, that one member of most pairs of sympatric sibling species of \textit{Drosophila} has a greater dependence on light for mating, greater phototaxis and is more tolerant to brighter light intensities (Seiger and Seiger, 1979; David \textit{et al.}, 1983).
1983; Parsons, 1983). Light mediated behaviours, therefore, may be an important mechanism in coexistence between many sibling species of *Drosophila* at the microhabitat level.
4.7 Summary

Field and population cage studies show that the innate interspecific differences in light preferences between *D. melanogaster* and *D. simulans* can reduce species overlap. In the field, *D. simulans* was caught in brighter traps, and species overlap (0) was less in the heterogeneously lit (RW) population cages than in the homogeneously lit cages (all bright white light [WW] or all dim red light [RR]). The reduction in species overlap also reduced interspecific competition (experiment I). The effect of light intensity on competition was investigated by the use of white-eyed *D. melanogaster* (which is blinded in bright white light) and wildtype *D. simulans* (mating in this species is disrupted in dim red light). In this experiment there was no long term coexistence in either the RW cages (which may have been due to the experimental set up) or the RR cages while there was coexistence in the WW cages. This demonstrates that light can have a significant effect on competition in *Drosophila* and also suggests that spatial heterogeneity need not always be necessary for coexistence.

Light preferences were investigated in both interspecific and intraspecific interactions. In the former, there was evidence for a significant change in light preferences (Experiment I) while intraspecific experiments on *D. simulans* showed that, like in *D. melanogaster* (see Chapter 3), light preferences are not fixed but could be changed by experience.
Figure 4.1

Light intensities of Drosophila caught, Lovelace Rd.
i) No-choice Lines:

Base Laboratory Stock Population

Dim Red Light Regime

F₀: 50 pairs

F₁, and subsequent generations:

- 50 randomly chosen pairs found next generation

Bright White Light Regime

F₀: 50 pairs

F₁, and subsequent generations:

- 50 randomly chosen pairs found next generation

ii) RW "Choice" Cages

Base Laboratory Stock Population

RW Cage

Dim Red Light Sector ↔ Bright White Light Sector

Note:
Subsequent generations can mate and move freely between cage sectors.

Figure 4.2

No-choice and RW Population Cage Lines

(D. simulans and D. melanogaster w)
## LIGHT REGIME:

<table>
<thead>
<tr>
<th>Combination:</th>
<th>Dim Red light</th>
<th>Bright White light</th>
</tr>
</thead>
<tbody>
<tr>
<td>1.</td>
<td>a)\textit{D. simulans}</td>
<td>b)\textit{D. simulans}</td>
</tr>
<tr>
<td>2.</td>
<td>a)\textit{D. simulans}</td>
<td>b)\textit{D. simulans}</td>
</tr>
<tr>
<td>3.</td>
<td>a)\textit{dD. simulans}</td>
<td>b)\textit{dD. simulans}</td>
</tr>
</tbody>
</table>

--- Light preferences tested after 16 days ---

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**Figure 4.3**

The effect of another species on light preferences in *Drosophila*
Figure 4.4

Types of population cages used
Figure 4.5

Experiment I: species overlap, $\theta$ for all cage types
Experiment I: relative survival of *D. simulans* in the RW cage sectors
Figure 4.7

Experiment II: species overlap, 0 for all cage types
Figure 4.8
Experiment II: relative survival of *D. simulans* in the RW cage sectors
Figure 4.9
The effect of temperature on *D. simulans* survival in the WW cages
1. R*W Cage: food tubes on dim red light sector only

2. RW* Cage: food tubes on bright white light sector only

Figure 4.10
Population cages used in the experiment on the dispersal behaviour of *D. melanogaster* w when alone
TABLE 4.1

Mean light intensities (Ev) at which *D. melanogaster* were caught (for the four sites where 5 or more *D. melanogaster* were caught).

<table>
<thead>
<tr>
<th>SITE</th>
<th>DATE</th>
<th>MEAN LIGHT INTENSITY</th>
<th>S²</th>
<th>N</th>
</tr>
</thead>
<tbody>
<tr>
<td>Norfolk 1985:</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>School Close (17/8-24/8)</td>
<td>&lt;5¹</td>
<td>0.00</td>
<td>9</td>
<td></td>
</tr>
<tr>
<td>Newmans (17/8-18/8)</td>
<td>10.7²</td>
<td>0.20</td>
<td>5</td>
<td></td>
</tr>
<tr>
<td>How Hill Farm (17/8-18/8)</td>
<td>12.3</td>
<td>2.99</td>
<td>36</td>
<td></td>
</tr>
<tr>
<td>Oxford 1986:</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Lovelace Rd (26/7-20/9)</td>
<td>9.7</td>
<td>3.17</td>
<td>39</td>
<td></td>
</tr>
</tbody>
</table>

Notes:
1 At this site *D. melanogaster* was only found in a dustbin alcove.
2 At this site *D. melanogaster* was only found in a shed.

Mean values were calculated from individual trap measurements for every collection.
Table 4.2
Mean Light Intensities for *Drosophila* caught.

i) Mean light intensities and ANOVA for 4 *Drosophila* species caught at the Lovelace Road Garden site, 1986.

<table>
<thead>
<tr>
<th>Species</th>
<th>Mean Light Intensity</th>
<th>S²</th>
<th>N</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>D. phalerata</em></td>
<td>9.8</td>
<td>4.22</td>
<td>20</td>
</tr>
<tr>
<td><em>D. subobscura/D. obscura</em></td>
<td>11.0</td>
<td>4.54</td>
<td>870</td>
</tr>
<tr>
<td><em>D. melanogaster</em></td>
<td>9.7</td>
<td>3.17</td>
<td>39</td>
</tr>
<tr>
<td><em>D. simulans</em> Sim-mix</td>
<td>13.7</td>
<td>5.32</td>
<td>229</td>
</tr>
</tbody>
</table>

**ANOVA**

<table>
<thead>
<tr>
<th>Sources of Variation</th>
<th>S. S</th>
<th>d.f.</th>
<th>M. S</th>
<th>F</th>
</tr>
</thead>
<tbody>
<tr>
<td>Between species</td>
<td>1429.3</td>
<td>3</td>
<td>476.4</td>
<td>102.4 ***</td>
</tr>
<tr>
<td><em>D. simulans</em> vs</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>other species</td>
<td>1334.8</td>
<td>1</td>
<td>1334.8</td>
<td>286.8 ***</td>
</tr>
<tr>
<td><em>D. melanogaster</em> vs</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>D. phalerata</em></td>
<td>0.1</td>
<td>1</td>
<td>0.1</td>
<td>0.02 ns</td>
</tr>
<tr>
<td>Error</td>
<td>5356.4</td>
<td>1151</td>
<td>4.65</td>
<td></td>
</tr>
</tbody>
</table>

*** p<0.001;

ii) ANOVA of light intensities at which *D. simulans* and *D. melanogaster* were caught in the *D. simulans* release-recapture experiment and for *D. melanogaster* caught at the four sites (see Table 4.1).

<table>
<thead>
<tr>
<th>Sources of Variation</th>
<th>S. S</th>
<th>d.f.</th>
<th>M. S</th>
<th>F</th>
</tr>
</thead>
<tbody>
<tr>
<td>Between sites</td>
<td>1190.8</td>
<td>4</td>
<td>297.70</td>
<td>64.77 ***</td>
</tr>
<tr>
<td><em>D. simulans</em> vs</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>D. melanogaster</em> sites</td>
<td>733.05</td>
<td>1</td>
<td>733.05</td>
<td>159.49 ***</td>
</tr>
<tr>
<td>Between <em>D. melanogaster</em> sites</td>
<td>457.75</td>
<td>1</td>
<td>457.75</td>
<td>99.59 ***</td>
</tr>
<tr>
<td>Error</td>
<td>1438.6</td>
<td>313</td>
<td>4.596</td>
<td></td>
</tr>
</tbody>
</table>

*** p<0.001;
Table 4.3

Mean Temperatures at which *Drosophila* were caught.

i) Mean temperature (°C) and ANOVA for 4 *Drosophila* species caught at the Lovelace Road Garden site, 1986.

<table>
<thead>
<tr>
<th>Species</th>
<th>Mean Temperature</th>
<th>$S^2$</th>
<th>N</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>D. phalerata</em></td>
<td>17.6</td>
<td>1.49</td>
<td>20</td>
</tr>
<tr>
<td><em>D. subobscura</em>/<em>D. obscura</em></td>
<td>18.0</td>
<td>2.11</td>
<td>923</td>
</tr>
<tr>
<td><em>D. melanogaster</em></td>
<td>17.8</td>
<td>2.03</td>
<td>38</td>
</tr>
<tr>
<td><em>D. simulans</em> Sim-mix</td>
<td>18.0</td>
<td>1.85</td>
<td>229</td>
</tr>
</tbody>
</table>

ANOVA

<table>
<thead>
<tr>
<th>Sources of Variation</th>
<th>S.S.</th>
<th>d.f.</th>
<th>M.S.</th>
<th>F</th>
</tr>
</thead>
<tbody>
<tr>
<td>Between species</td>
<td>5.568</td>
<td>3</td>
<td>1.856</td>
<td>0.904 ns</td>
</tr>
<tr>
<td>Error</td>
<td>2475.8</td>
<td>1206</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

ii) Temperature (°C) at which *D. melanogaster* and *D. simulans* Sim-mix were caught (for the four main *D. melanogaster* sites).

<table>
<thead>
<tr>
<th>Species</th>
<th>Mean Temperature</th>
<th>$S^2$</th>
<th>N</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>D. melanogaster</em></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>How Hill Farm</td>
<td>18.1</td>
<td>1.756</td>
<td>36</td>
</tr>
<tr>
<td>Newmans</td>
<td>18.8</td>
<td>0.059</td>
<td>5</td>
</tr>
<tr>
<td>School Close</td>
<td>17.7</td>
<td>0.000</td>
<td>9</td>
</tr>
<tr>
<td>Lovelace Rd</td>
<td>17.8</td>
<td>2.026</td>
<td>38</td>
</tr>
<tr>
<td><em>D. simulans</em></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sim-mix, Lovelace Rd</td>
<td>18.0</td>
<td>1.851</td>
<td>229</td>
</tr>
</tbody>
</table>

ANOVA

<table>
<thead>
<tr>
<th>Sources of Variation</th>
<th>S.S.</th>
<th>d.f.</th>
<th>M.S.</th>
<th>F</th>
</tr>
</thead>
<tbody>
<tr>
<td>Between sites</td>
<td>6.4625</td>
<td>4</td>
<td>1.6156</td>
<td>0.8996 ns</td>
</tr>
<tr>
<td>Error</td>
<td>560.32</td>
<td>312</td>
<td>1.7959</td>
<td></td>
</tr>
</tbody>
</table>
Table 4.4
Laboratory stocks light preferences and readiness to oviposit in dim red and bright white light.

<table>
<thead>
<tr>
<th>Stock</th>
<th>Light preference (%W)</th>
<th>%Eggs laid in white light 24hrs</th>
<th>$\chi^2$</th>
<th>43hrs</th>
<th>$\chi^2$</th>
</tr>
</thead>
<tbody>
<tr>
<td>D. simulans</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sim-mix</td>
<td>86.0</td>
<td>93.3</td>
<td>***</td>
<td>58.8</td>
<td>***</td>
</tr>
<tr>
<td>Sim ++</td>
<td>81.1</td>
<td>-</td>
<td>-</td>
<td></td>
<td></td>
</tr>
<tr>
<td>D. melanogaster</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>D. melanogaster w</td>
<td>26.4</td>
<td>0.0</td>
<td>***</td>
<td>31.2</td>
<td>***</td>
</tr>
<tr>
<td>D. melanogaster ++</td>
<td>33.7</td>
<td>41.9</td>
<td>***</td>
<td>29.1</td>
<td>***</td>
</tr>
</tbody>
</table>

*** p<0.001, $\chi^2$ test for significant deviation from 50:50 distributions, where %W is the percentage of adults found in the bright white light cylinder of the testing apparatus.
Table 4.5
No-choice Lines: Light preferences (%W) for the initial exposure experiments (28/10/85 and 11/12/85).

i) 5 day exposure:

<table>
<thead>
<tr>
<th>Light Regime</th>
<th>White light (n)</th>
<th>Dim red light (n)</th>
<th>W-R</th>
<th>χ²</th>
</tr>
</thead>
<tbody>
<tr>
<td>D. simulans</td>
<td>90.8 (76)</td>
<td>70.6 (51)</td>
<td>+20.2*</td>
<td></td>
</tr>
<tr>
<td>D. melanogaster w</td>
<td>75.0 (85)</td>
<td>45.7 (81)</td>
<td>+29.3 n.s.</td>
<td></td>
</tr>
</tbody>
</table>

ii) 10 day exposure:

<table>
<thead>
<tr>
<th>Light Regime</th>
<th>White light (n)</th>
<th>Dim red light (n)</th>
<th>W-R</th>
<th>χ²</th>
</tr>
</thead>
<tbody>
<tr>
<td>D. simulans</td>
<td>94.1 (34)</td>
<td>94.7 (19)</td>
<td>+0.6 n.s.</td>
<td></td>
</tr>
<tr>
<td>D. melanogaster w</td>
<td>88.9 (72)</td>
<td>61.3 (119)</td>
<td>+26.6 ***</td>
<td></td>
</tr>
</tbody>
</table>

* p<0.01, *** p<0.001, where %W is the percentage of flies found in the bright white light tube of the test apparatus.

ii) No-choice Lines: Light preferences (%W) of F₁, and following generations (28/10/85 - 24/5/86).

<table>
<thead>
<tr>
<th>Light Regime</th>
<th>White light</th>
<th>Dim red light</th>
<th>W-R</th>
<th>χ²</th>
</tr>
</thead>
<tbody>
<tr>
<td>a) D. simulans</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>(F₀)</td>
<td>90.8</td>
<td>70.6</td>
<td>+20.2*</td>
<td></td>
</tr>
<tr>
<td>f₁</td>
<td>80.0</td>
<td>69.6</td>
<td>+10.4 n.s.</td>
<td></td>
</tr>
<tr>
<td>f₂</td>
<td>80.2</td>
<td>75.3</td>
<td>+4.9 n.s.</td>
<td></td>
</tr>
<tr>
<td>f₃</td>
<td>77.9</td>
<td>60.0</td>
<td>+17.9*</td>
<td></td>
</tr>
<tr>
<td>f₄</td>
<td>91.9</td>
<td>66.7</td>
<td>+25.2 ***</td>
<td></td>
</tr>
<tr>
<td>f₅</td>
<td>72.8</td>
<td>62.4</td>
<td>+10.2 n.s.</td>
<td></td>
</tr>
<tr>
<td>f₆</td>
<td>86.2</td>
<td>86.3</td>
<td>-0.1 n.s.</td>
<td></td>
</tr>
<tr>
<td>f₇</td>
<td>76.0</td>
<td>56.8</td>
<td>+19.2*</td>
<td></td>
</tr>
</tbody>
</table>

Overall, p<0.01; (N=8; Wilcoxon match-paired signed-rank test).

b) D. melanogaster w

<table>
<thead>
<tr>
<th>Light Regime</th>
<th>White light</th>
<th>Dim red light</th>
<th>W-R</th>
<th>χ²</th>
</tr>
</thead>
<tbody>
<tr>
<td>(F₀)</td>
<td>75.0</td>
<td>45.7</td>
<td>+29.3 ***</td>
<td></td>
</tr>
<tr>
<td>f₁</td>
<td>69.1</td>
<td>58.0</td>
<td>+11.1 n.s.</td>
<td></td>
</tr>
<tr>
<td>f₂</td>
<td>91.4</td>
<td>56.3</td>
<td>+35.1 ***</td>
<td></td>
</tr>
<tr>
<td>f₃</td>
<td>77.4</td>
<td>63.5</td>
<td>+13.9 n.s.</td>
<td></td>
</tr>
<tr>
<td>f₄</td>
<td>91.2</td>
<td>75.0</td>
<td>+16.2*</td>
<td></td>
</tr>
<tr>
<td>f₅</td>
<td>75.2</td>
<td>58.8</td>
<td>+16.4 **</td>
<td></td>
</tr>
<tr>
<td>f₆</td>
<td>76.5</td>
<td>74.2</td>
<td>+2.3 n.s.</td>
<td></td>
</tr>
<tr>
<td>f₇</td>
<td>50.6</td>
<td>65.6</td>
<td>-15.0 n.s.</td>
<td></td>
</tr>
<tr>
<td>f₈</td>
<td>77.5</td>
<td>43.3</td>
<td>+34.2 **</td>
<td></td>
</tr>
</tbody>
</table>

Overall, p<0.025; (N=9; Wilcoxon match-paired signed-rank test).
Table 4.6

RW Choice cages:

i) Light preferences (%W) of cage samples (17/12/85 - 6/3/86).

<table>
<thead>
<tr>
<th>Cage Sector</th>
<th>White light</th>
<th>Red light</th>
<th>W-R</th>
<th>χ²</th>
</tr>
</thead>
<tbody>
<tr>
<td>a) D. simulans</td>
<td>38.8</td>
<td>45.7</td>
<td>-6.9</td>
<td>ns</td>
</tr>
<tr>
<td></td>
<td>46.5</td>
<td>80.5</td>
<td>-34.4</td>
<td>*</td>
</tr>
<tr>
<td></td>
<td>65.0</td>
<td>60.3</td>
<td>+4.7</td>
<td>ns</td>
</tr>
<tr>
<td></td>
<td>86.1</td>
<td>57.2</td>
<td>+28.9</td>
<td>***</td>
</tr>
<tr>
<td></td>
<td>56.5</td>
<td>87.5</td>
<td>-31.0</td>
<td>***</td>
</tr>
<tr>
<td></td>
<td>41.5</td>
<td>82.5</td>
<td>-41.0</td>
<td>***</td>
</tr>
</tbody>
</table>

Overall, not significant (N=6; Wilcoxon match-paired signed-rank test).

b) D. melanogaster w

<table>
<thead>
<tr>
<th>Cage Sector</th>
<th>White light</th>
<th>Red light</th>
<th>W-R</th>
<th>χ²</th>
</tr>
</thead>
<tbody>
<tr>
<td>i)</td>
<td>78.3</td>
<td>55.7</td>
<td>+22.6</td>
<td>*</td>
</tr>
<tr>
<td>ii)</td>
<td>65.9</td>
<td>66.7</td>
<td>-0.8</td>
<td>ns</td>
</tr>
<tr>
<td>iii)</td>
<td>61.5</td>
<td>33.8</td>
<td>+27.7</td>
<td>*</td>
</tr>
<tr>
<td>iv)</td>
<td>72.4</td>
<td>47.2</td>
<td>+25.2</td>
<td>ns</td>
</tr>
<tr>
<td>v)</td>
<td>62.5</td>
<td>49.0</td>
<td>+13.5</td>
<td>ns</td>
</tr>
<tr>
<td>vi)</td>
<td>73.7</td>
<td>44.9</td>
<td>+28.8</td>
<td>***</td>
</tr>
<tr>
<td>vii)</td>
<td>76.0</td>
<td>64.8</td>
<td>+11.2</td>
<td>ns</td>
</tr>
</tbody>
</table>

Overall, p<0.025 (N=7; Wilcoxon match-paired signed-rank test).


<table>
<thead>
<tr>
<th>Cage Sector</th>
<th>White light</th>
<th>Red light</th>
<th>W-R</th>
<th>χ²</th>
</tr>
</thead>
<tbody>
<tr>
<td>D. simulans</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>i)</td>
<td>93.8</td>
<td>67.7</td>
<td>+27.1</td>
<td>***</td>
</tr>
<tr>
<td>ii)</td>
<td>91.1</td>
<td>62.3</td>
<td>+28.8</td>
<td>***</td>
</tr>
<tr>
<td>D. melanogaster w</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>i)</td>
<td>39.1</td>
<td>20.9</td>
<td>+18.2</td>
<td>ns</td>
</tr>
<tr>
<td>ii)</td>
<td>65.0</td>
<td>55.3</td>
<td>+9.7</td>
<td>ns</td>
</tr>
<tr>
<td>iii)</td>
<td>60.0</td>
<td>70.0</td>
<td>-10.0</td>
<td>ns</td>
</tr>
<tr>
<td>iv)</td>
<td>79.7</td>
<td>79.3</td>
<td>+0.4</td>
<td>ns</td>
</tr>
<tr>
<td>D. melanogaster</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>i)</td>
<td>86.2</td>
<td>59.0</td>
<td>27.2</td>
<td>***</td>
</tr>
<tr>
<td>ii)</td>
<td>78.9</td>
<td>63.3</td>
<td>+15.6</td>
<td>**</td>
</tr>
<tr>
<td>iii)</td>
<td>82.1</td>
<td>72.3</td>
<td>+9.8</td>
<td>ns</td>
</tr>
</tbody>
</table>

Overall, p<0.01; (N=9; Wilcoxon match-paired signed-rank test).

* * * p<0.001, ** p<0.025, * p<0.05, where %W is the percentage of flies found in the bright white light tube of the test apparatus.
Table 4.7
The effect of overcrowding on light preferences (%W).

1. F₃ surplus flies kept under crowded conditions for two days (9/1/86):

<table>
<thead>
<tr>
<th>Light Regime</th>
<th>White light</th>
<th>Red light</th>
<th>χ²</th>
</tr>
</thead>
<tbody>
<tr>
<td>a) D. simulans</td>
<td>72.8</td>
<td>62.9</td>
<td>ns</td>
</tr>
<tr>
<td>b) D. melanogaster w</td>
<td>75.2</td>
<td>58.7</td>
<td>**</td>
</tr>
<tr>
<td>c) D. melanogaster</td>
<td>83.3</td>
<td>63.7</td>
<td>***</td>
</tr>
</tbody>
</table>

2. Light preferences (%W) of adults from D. melanogaster No-choice lines kept in crowded conditions for 7 days from 12/5/86:

<table>
<thead>
<tr>
<th></th>
<th>%W</th>
<th>χ²</th>
</tr>
</thead>
<tbody>
<tr>
<td>White light line</td>
<td>69.2</td>
<td></td>
</tr>
<tr>
<td>Red light line</td>
<td>74.1</td>
<td>ns</td>
</tr>
</tbody>
</table>

3. Light preferences (%W) of No-choice line D. melanogaster adults which were kept in food tubes with larvae and pupae, tested (19/5/86) then retested after a day of being kept in crowded conditions:

<table>
<thead>
<tr>
<th></th>
<th>χ²</th>
<th>χ²</th>
</tr>
</thead>
<tbody>
<tr>
<td>a) 19/5/86</td>
<td></td>
<td></td>
</tr>
<tr>
<td>White light line</td>
<td>77.8</td>
<td>76.9</td>
</tr>
<tr>
<td>Red light line</td>
<td>55.3</td>
<td>* 86.7</td>
</tr>
<tr>
<td>b) 20/5/86</td>
<td></td>
<td></td>
</tr>
<tr>
<td>White light line</td>
<td>60.0</td>
<td>100.0</td>
</tr>
<tr>
<td>Red light line</td>
<td>44.4</td>
<td>ns 66.7</td>
</tr>
</tbody>
</table>

4. Light preferences (%W) of laboratory stock D. simulans adults which had developed in overcrowded and normal conditions (13/11/86):

<table>
<thead>
<tr>
<th></th>
<th>%W</th>
<th>χ²</th>
</tr>
</thead>
<tbody>
<tr>
<td>Overcrowded, small D. simulans</td>
<td>36.5</td>
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</tr>
<tr>
<td>Normal D. simulans</td>
<td>76.3</td>
<td>***</td>
</tr>
</tbody>
</table>

* p<0.05, ** p<0.005, *** p<0.001.
Table 4.8
The effect of another species on light preferences (%W) of adults (9/12/85).

i) 2♀ D. simulans with 2♀ D. melanogaster ♀

<table>
<thead>
<tr>
<th>Light Regime</th>
<th>White light</th>
<th>Red light</th>
<th>$\chi^2$</th>
</tr>
</thead>
<tbody>
<tr>
<td>♀ D. simulans</td>
<td>100.0</td>
<td>97.6</td>
<td>ns</td>
</tr>
<tr>
<td>♀ D. melanogaster ♀</td>
<td>86.5</td>
<td>74.3</td>
<td>ns</td>
</tr>
</tbody>
</table>

ii) 2♀ D. simulans with 2♂ D. melanogaster ♀

<table>
<thead>
<tr>
<th>Light Regime</th>
<th>White light</th>
<th>Red light</th>
<th>$\chi^2$</th>
</tr>
</thead>
<tbody>
<tr>
<td>♀ D. simulans</td>
<td>100.0</td>
<td>84.8</td>
<td>*</td>
</tr>
<tr>
<td>♂ D. melanogaster ♀</td>
<td>92.9</td>
<td>73.8</td>
<td>*</td>
</tr>
</tbody>
</table>

iii) 2♂ D. simulans with 2♀ D. melanogaster ♀

<table>
<thead>
<tr>
<th>Light Regime</th>
<th>White light</th>
<th>Red light</th>
<th>$\chi^2$</th>
</tr>
</thead>
<tbody>
<tr>
<td>♂ D. simulans</td>
<td>73.3</td>
<td>100.0</td>
<td>*</td>
</tr>
<tr>
<td>♀ D. melanogaster ♀</td>
<td>85.7</td>
<td>90.9</td>
<td>ns</td>
</tr>
</tbody>
</table>

* $p<0.05$.  

-204-
Table 4.9

Experiment I: Degree of overlap of species distributions between cage sectors of the three cage types using \( \theta_{ij} = 1 - 0.5 \sum_{k} |P_{ik} - P_{jk}| \) where a value of \( \theta = 1 \), indicates complete overlap and \( \theta = 0 \) no overlap in distributions (see text for further explanation).

<table>
<thead>
<tr>
<th>SAMPLE (WEEKS)</th>
<th>2(9)</th>
<th>3(12)</th>
<th>4(15)</th>
<th>5(18)</th>
<th>6(22)</th>
<th>7(25)</th>
<th>8(31)</th>
</tr>
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<tr>
<td><strong>RW CAGES:</strong></td>
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<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>2 RW</td>
<td>0.407</td>
<td>0.255</td>
<td>---</td>
<td>0.494</td>
<td>0.556</td>
<td>---</td>
<td>---</td>
</tr>
<tr>
<td>4 RW</td>
<td>0.546</td>
<td>0.558</td>
<td>0.444</td>
<td>0.956</td>
<td>0.466</td>
<td>0.306</td>
<td>0.525</td>
</tr>
<tr>
<td>5 RW</td>
<td>0.384</td>
<td>0.631</td>
<td>0.609</td>
<td>0.381</td>
<td>0.567</td>
<td>0.524</td>
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</tr>
<tr>
<td>10RW</td>
<td>0.122</td>
<td>0.409</td>
<td>0.359</td>
<td>0.590</td>
<td>0.681</td>
<td>0.646</td>
<td>0.346</td>
</tr>
<tr>
<td>13RW</td>
<td>0.235</td>
<td>0.511</td>
<td>0.590</td>
<td>0.349</td>
<td>0.488</td>
<td>0.483</td>
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</tr>
<tr>
<td>16RW</td>
<td>0.509</td>
<td>0.738</td>
<td>0.832</td>
<td>0.567</td>
<td>0.849</td>
<td>0.274</td>
<td>0.539</td>
</tr>
<tr>
<td><strong>WW CAGES:</strong></td>
<td></td>
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<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1WW</td>
<td>0.748</td>
<td>0.639</td>
<td>0.769</td>
<td>---</td>
<td>---</td>
<td>---</td>
<td>---</td>
</tr>
<tr>
<td>8WW</td>
<td>0.867</td>
<td>0.819</td>
<td>0.777</td>
<td>0.770</td>
<td>0.535</td>
<td>---</td>
<td>0.435</td>
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<tr>
<td>12WW</td>
<td>0.764</td>
<td>0.825</td>
<td>0.789</td>
<td>0.985</td>
<td>0.912</td>
<td>0.463</td>
<td>0.854</td>
</tr>
<tr>
<td>14WW</td>
<td>0.953</td>
<td>0.679</td>
<td>0.556</td>
<td>0.875</td>
<td>0.756</td>
<td>0.392</td>
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</tr>
<tr>
<td><strong>RR CAGES:</strong></td>
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</tr>
<tr>
<td>3RR</td>
<td>0.903</td>
<td>0.694</td>
<td>0.541</td>
<td>0.895</td>
<td>0.412</td>
<td>---</td>
<td>0.684</td>
</tr>
<tr>
<td>7RR</td>
<td>0.634</td>
<td>0.816</td>
<td>0.480</td>
<td>0.927</td>
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<tr>
<td>9RR</td>
<td>0.951</td>
<td>0.821</td>
<td>0.568</td>
<td>0.887</td>
<td>0.919</td>
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<td>0.981</td>
</tr>
<tr>
<td>11RR</td>
<td>0.995</td>
<td>0.912</td>
<td>0.713</td>
<td>0.860</td>
<td>0.618</td>
<td>0.899</td>
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</tr>
<tr>
<td>15RR</td>
<td>0.637</td>
<td>0.613</td>
<td>0.583</td>
<td>0.921</td>
<td>0.839</td>
<td>0.409</td>
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</tr>
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</table>
Table 4.10
Experiment I: Mean values of degree of overlap θ results presented in Table 2.

<table>
<thead>
<tr>
<th>SAMPLE (weeks)</th>
<th>2(9)</th>
<th>3(12)</th>
<th>4(15)</th>
<th>5(18)</th>
<th>6(22)</th>
<th>7(26)</th>
<th>8(31)</th>
</tr>
</thead>
<tbody>
<tr>
<td>CAGE TYPE:</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>RW</td>
<td>0.357</td>
<td>0.517</td>
<td>0.567</td>
<td>0.569</td>
<td>0.601</td>
<td>0.447</td>
<td>0.470</td>
</tr>
<tr>
<td>WW</td>
<td>0.833</td>
<td>0.741</td>
<td>0.723</td>
<td>0.877</td>
<td>0.734</td>
<td>0.678</td>
<td>0.645</td>
</tr>
<tr>
<td>RR</td>
<td>0.824</td>
<td>0.771</td>
<td>0.577</td>
<td>0.898</td>
<td>0.707</td>
<td>0.653</td>
<td>0.833</td>
</tr>
</tbody>
</table>

---

ANOVA of θ values, over all 7 samples

<table>
<thead>
<tr>
<th>Sources of Variation</th>
<th>d.f.</th>
<th>S.S</th>
<th>M.S.</th>
<th>F</th>
</tr>
</thead>
<tbody>
<tr>
<td>Between cage types</td>
<td>2</td>
<td>1.363</td>
<td>0.6815</td>
<td>24.15***</td>
</tr>
<tr>
<td>RW/WW &amp; RR cage types</td>
<td>1</td>
<td>1.332</td>
<td>1.332</td>
<td>47.23***</td>
</tr>
<tr>
<td>Between RR &amp; WW cages</td>
<td>1</td>
<td>0.031</td>
<td>0.031</td>
<td>1.099 n.s.</td>
</tr>
<tr>
<td>(Error</td>
<td>85</td>
<td>2.399</td>
<td>0.0282</td>
<td></td>
</tr>
</tbody>
</table>

(* ***p<0.001)

Where the means, over all 8 samples are:

RW: 0.506; WW: 0.757; RR: 0.754
Table 4.11
Experiment I: Relative survival of *D. melanogaster* and *D. simulans* in the spatially heterogeneous RW cages, showing the percentage of *D. melanogaster* on the Red light (R) and White light (W) sectors of the RW Cages.

<table>
<thead>
<tr>
<th>SAMPLE (WEEKS)</th>
<th>2(9)</th>
<th>3(12)</th>
<th>4(15)</th>
<th>5(18)</th>
<th>6(22)</th>
<th>7(26)</th>
<th>8(31)</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>CAGE:</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>2 R</td>
<td>100.0</td>
<td>100.0</td>
<td>100.0</td>
<td>100.0</td>
<td>98.3</td>
<td>100.0</td>
<td>100.0</td>
</tr>
<tr>
<td>W</td>
<td>53.2</td>
<td>93.3</td>
<td>100.0</td>
<td>95.5</td>
<td>88.9</td>
<td>100.0</td>
<td>100.0</td>
</tr>
<tr>
<td>4 R</td>
<td>83.3</td>
<td>97.9</td>
<td>100.0</td>
<td>84.5</td>
<td>98.2</td>
<td>100.0</td>
<td>100.0</td>
</tr>
<tr>
<td>W</td>
<td>29.9</td>
<td>69.4</td>
<td>66.7</td>
<td>82.0</td>
<td>61.8</td>
<td>62.5</td>
<td>94.6</td>
</tr>
<tr>
<td>5 R</td>
<td>95.1</td>
<td>90.9</td>
<td>100.0</td>
<td>95.5</td>
<td>99.1</td>
<td>100.0</td>
<td>100.0</td>
</tr>
<tr>
<td>W</td>
<td>43.1</td>
<td>63.4</td>
<td>83.7</td>
<td>51.2</td>
<td>93.8</td>
<td>98.5</td>
<td>100.0</td>
</tr>
<tr>
<td>10 R</td>
<td>100.0</td>
<td>98.8</td>
<td>100.0</td>
<td>91.1</td>
<td>93.0</td>
<td>97.2</td>
<td>100.0</td>
</tr>
<tr>
<td>W</td>
<td>31.0</td>
<td>66.7</td>
<td>85.7</td>
<td>63.5</td>
<td>75.5</td>
<td>86.9</td>
<td>94.4</td>
</tr>
<tr>
<td>13 R</td>
<td>100.0</td>
<td>97.4</td>
<td>100.0</td>
<td>100.0</td>
<td>100.0</td>
<td>100.0</td>
<td>100.0</td>
</tr>
<tr>
<td>W</td>
<td>65.7</td>
<td>81.9</td>
<td>89.5</td>
<td>95.0</td>
<td>69.0</td>
<td>100.0</td>
<td>100.0</td>
</tr>
<tr>
<td>16 R</td>
<td>97.2</td>
<td>89.2</td>
<td>89.2</td>
<td>98.2</td>
<td>70.8</td>
<td>100.0</td>
<td>99.0</td>
</tr>
<tr>
<td>W</td>
<td>59.4</td>
<td>80.6</td>
<td>73.9</td>
<td>57.8</td>
<td>56.8</td>
<td>87.3</td>
<td>88.5</td>
</tr>
<tr>
<td><strong>Means</strong></td>
<td></td>
<td></td>
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<tr>
<td>R</td>
<td>95.9</td>
<td>96.8</td>
<td>97.9</td>
<td>94.9</td>
<td>93.2</td>
<td>99.5</td>
<td>99.8</td>
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<tr>
<td>W</td>
<td>47.2</td>
<td>75.9</td>
<td>84.1</td>
<td>74.2</td>
<td>74.3</td>
<td>89.0</td>
<td>96.2</td>
</tr>
</tbody>
</table>

Overall, p<0.005 (n=36), Wilcoxon matched-pairs signed ranks test for relative survival of *D. melanogaster* on the Red light sectors (R) versus the White light sectors (W) of the RW cages, for all samples.
Table 4.11 cont.
Experiment I: Relative survival of *D. melanogaster* and *D. simulans* in the spatially homogeneous cages, showing the percentage of *D. melanogaster* in each cage.

<table>
<thead>
<tr>
<th>SAMPLE (WEEKS)</th>
<th>2(9)</th>
<th>3(12)</th>
<th>4(15)</th>
<th>5(18)</th>
<th>6(22)</th>
<th>7(26)</th>
<th>8(31)</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>WW CAGES:</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1WW</td>
<td>57.4</td>
<td>89.0</td>
<td>96.3</td>
<td>90.7</td>
<td>100.0</td>
<td>100.0</td>
<td>100.0</td>
</tr>
<tr>
<td>6WW</td>
<td>100.0</td>
<td>100.0</td>
<td>100.0</td>
<td>100.0</td>
<td>100.0</td>
<td>100.0</td>
<td>100.0</td>
</tr>
<tr>
<td>8WW</td>
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<td>79.7</td>
<td>89.1</td>
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<td>86.1</td>
<td>100.0</td>
<td>99.4</td>
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<td>51.6</td>
<td>23.1</td>
<td>34.4</td>
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<td>96.3</td>
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<td>97.6</td>
<td>93.7</td>
<td>77.4</td>
<td>96.7</td>
<td>100.0</td>
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<td>93.8</td>
<td>99.1</td>
<td>99.0</td>
<td>97.8</td>
<td>100.0</td>
<td>99.6</td>
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</tr>
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<td>60.5</td>
<td>85.3</td>
<td>63.4</td>
<td>78.7</td>
<td>100.0</td>
<td>100.0</td>
</tr>
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<td>57.5</td>
<td>79.4</td>
<td>73.3</td>
<td>95.1</td>
<td>89.0</td>
<td>98.8</td>
<td>100.0</td>
</tr>
<tr>
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<td>80.9</td>
<td>97.3</td>
<td>72.0</td>
<td>96.6</td>
<td>96.5</td>
<td>100.0</td>
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<tr>
<td><strong>Means</strong></td>
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<td></td>
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<tr>
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<td>67.8</td>
<td>77.4</td>
<td>83.5</td>
<td>74.9</td>
<td>77.3</td>
<td>97.0</td>
<td>99.3</td>
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<tr>
<td>WW without Cage 12 (see text)</td>
<td>71.9</td>
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<td>95.7</td>
<td>90.2</td>
<td>90.9</td>
<td>99.2</td>
<td>99.8</td>
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<tr>
<td>RR</td>
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<td>81.7</td>
<td>90.7</td>
<td>82.9</td>
<td>91.8</td>
<td>99.1</td>
<td>99.9</td>
</tr>
</tbody>
</table>
Table 4.12
Experiment I: Mean relative survival of *D. melanogaster* in the three cage types for each sample calculated from the individual percentages presented in Table 3.3, where WofRW is the white light sectors of the RW cages and WW$_{12}$ is the mean of all the WW cages except for cage 12 (see text for further details).

<table>
<thead>
<tr>
<th>SAMPLE (WEEKS)</th>
<th>2(9)</th>
<th>3(12)</th>
<th>4(15)</th>
<th>5(18)</th>
<th>6(22)</th>
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<th>8(31)</th>
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<tbody>
<tr>
<td>Cage type:</td>
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<td></td>
<td></td>
<td></td>
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</tr>
<tr>
<td>WofRW</td>
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<td>84.1</td>
<td>74.2</td>
<td>74.3</td>
<td>89.0</td>
<td>96.2</td>
</tr>
<tr>
<td>WW$_{12}$</td>
<td>71.9</td>
<td>91.0</td>
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<td>90.2</td>
<td>90.9</td>
<td>99.2</td>
<td>99.8</td>
</tr>
<tr>
<td>RR</td>
<td>66.7</td>
<td>81.7</td>
<td>90.7</td>
<td>82.9</td>
<td>91.8</td>
<td>99.1</td>
<td>99.9</td>
</tr>
</tbody>
</table>

ANOVA of Sample 2

<table>
<thead>
<tr>
<th>Sources of Variation</th>
<th>d.f.</th>
<th>S.S</th>
<th>M.S.</th>
<th>F</th>
</tr>
</thead>
<tbody>
<tr>
<td>Between cage types</td>
<td>2</td>
<td>840.8</td>
<td>420.4</td>
<td>3.163 n.s.</td>
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<tr>
<td>WofRW/WW &amp; RR cage types</td>
<td>1</td>
<td>736.8</td>
<td>736.8</td>
<td>5.544 *</td>
</tr>
<tr>
<td>Between RR &amp; WW cages</td>
<td>1</td>
<td>104.1</td>
<td>104.1</td>
<td>0.783 n.s.</td>
</tr>
<tr>
<td>(Error)</td>
<td>12</td>
<td>1594.8</td>
<td>132.9</td>
<td></td>
</tr>
</tbody>
</table>

* p<0.05.
Table 4.13

Experiment II: Degree of overlap of species distributions between cage sectors of the three cage types using \( \theta_{ij} = 1 - 0.5|P_i - P_j| \)
where a value of \( \theta = 1 \), indicates complete overlap and \( \theta = 0 \) no overlap in distributions (see text for further explanation).

<table>
<thead>
<tr>
<th></th>
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<th></th>
<th></th>
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</tr>
</thead>
<tbody>
<tr>
<td><strong>RW CAGES:</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>3 RW</td>
<td>0.894</td>
<td>0.440</td>
<td>0.570</td>
<td>---</td>
<td>---</td>
<td>---</td>
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</tr>
<tr>
<td>7 RW</td>
<td>0.441</td>
<td>0.457</td>
<td>---</td>
<td>---</td>
<td>0.319</td>
<td>0.410</td>
<td>0.482</td>
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<tr>
<td>9 RW</td>
<td>0.236</td>
<td>0.333</td>
<td>0.284</td>
<td>0.247</td>
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<tr>
<td>12RW</td>
<td>0.561</td>
<td>0.248</td>
<td>0.152</td>
<td>---</td>
<td>0.337</td>
<td>0.595</td>
<td>---</td>
</tr>
<tr>
<td><strong>WW CAGES:</strong></td>
<td></td>
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<td></td>
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<td></td>
<td></td>
</tr>
<tr>
<td>2WW</td>
<td>0.676</td>
<td>0.766</td>
<td>0.429</td>
<td>0.709</td>
<td>0.864</td>
<td>0.909</td>
<td>0.963</td>
</tr>
<tr>
<td>6WW</td>
<td>0.566</td>
<td>0.575</td>
<td>0.666</td>
<td>0.966</td>
<td>0.863</td>
<td>0.607</td>
<td>0.846</td>
</tr>
<tr>
<td>10WW</td>
<td>0.803</td>
<td>0.804</td>
<td>0.846</td>
<td>0.980</td>
<td>0.872</td>
<td>0.653</td>
<td>0.802</td>
</tr>
<tr>
<td>11WW</td>
<td>0.648</td>
<td>0.426</td>
<td>0.867</td>
<td>0.736</td>
<td>0.555</td>
<td>0.763</td>
<td>0.672</td>
</tr>
<tr>
<td><strong>RR CAGES:</strong></td>
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<td></td>
<td></td>
<td></td>
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<td></td>
<td></td>
</tr>
<tr>
<td>1RR</td>
<td>0.978</td>
<td>0.666</td>
<td>0.857</td>
<td>0.983</td>
<td>---</td>
<td>0.258</td>
<td>0.818</td>
</tr>
<tr>
<td>4RR</td>
<td>0.295</td>
<td>0.682</td>
<td>0.870</td>
<td>0.851</td>
<td>---</td>
<td>---</td>
<td>---</td>
</tr>
<tr>
<td>5RR</td>
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<td>0.859</td>
<td>0.560</td>
<td>0.404</td>
<td>---</td>
<td>---</td>
<td>---</td>
</tr>
<tr>
<td>8RR</td>
<td>0.263</td>
<td>0.909</td>
<td>0.660</td>
<td>0.204</td>
<td>0.516</td>
<td>---</td>
<td>---</td>
</tr>
</tbody>
</table>
Table 4.14

Experiment II: Mean values of degree of overlap \( \theta \) results presented in Table 3.

|---------------|------|------|-------|-------|-------|-------|-------|

CAGE TYPE:

- **CAGE**:  
  - **RW**: 0.533, 0.372, 0.335 (0.247), 0.328, 0.502 (0.482)
  - **WW**: 0.673, 0.643, 0.702, 0.848, 0.788, 0.733, 0.821
  - **RR**: 0.597, 0.779, 0.739, 0.610 (0.516), (0.258), (0.818)

ANOVA of \( \theta \) values, over all 7 samples

<table>
<thead>
<tr>
<th>Sources of Variation</th>
<th>d.f.</th>
<th>S.S</th>
<th>M.S.</th>
<th>F</th>
</tr>
</thead>
<tbody>
<tr>
<td>Between cage types</td>
<td>2</td>
<td>1.073</td>
<td>0.536</td>
<td>13.26***</td>
</tr>
<tr>
<td>RW/WW &amp; RR cage types</td>
<td>1</td>
<td>0.996</td>
<td>0.996</td>
<td>24.6 ***</td>
</tr>
<tr>
<td>Between RR &amp; WW cages</td>
<td>1</td>
<td>0.077</td>
<td>0.077</td>
<td>1.894 n.s.</td>
</tr>
<tr>
<td>(Error</td>
<td>64</td>
<td>2.590</td>
<td>0.041</td>
<td></td>
</tr>
</tbody>
</table>

(***p<0.001)

Where the means, over all 7 samples are:

- **RW**: 0.413;  **WW**: 0.715;  **RR**: 0.657
Table 4.15
Experiment II: Relative survival of *D. melanogaster* and *D. simulans* in the spatially heterogeneous RW cages, showing the percentage of *D. melanogaster* on the Red light (R) and White light (W) sectors of the RW cages.

<table>
<thead>
<tr>
<th></th>
<th></th>
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<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>CAGE:</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>3 R</td>
<td>67.3</td>
<td>100.0</td>
<td>100.0</td>
<td>100.0</td>
<td>100.0</td>
<td>100.0</td>
<td>100.0</td>
</tr>
<tr>
<td>W</td>
<td>56.5</td>
<td>63.0</td>
<td>88.0</td>
<td>100.0</td>
<td>100.0</td>
<td>100.0</td>
<td>100.0</td>
</tr>
<tr>
<td>7 R</td>
<td>95.3</td>
<td>93.8</td>
<td>100.0</td>
<td>100.0</td>
<td>100.0</td>
<td>100.0</td>
<td>98.6</td>
</tr>
<tr>
<td>W</td>
<td>25.6</td>
<td>43.1</td>
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<td>100.0</td>
<td>90.2</td>
<td>97.0</td>
<td>76.9</td>
</tr>
<tr>
<td>9 R</td>
<td>95.7</td>
<td>100.0</td>
<td>100.0</td>
<td>100.0</td>
<td>100.0</td>
<td>100.0</td>
<td>100.0</td>
</tr>
<tr>
<td>W</td>
<td>27.6</td>
<td>51.7</td>
<td>92.7</td>
<td>74.0</td>
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<td>100.0</td>
<td>100.0</td>
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<tr>
<td>12R</td>
<td>62.9</td>
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<td>100.0</td>
<td>100.0</td>
<td>100.0</td>
<td>100.0</td>
<td>100.0</td>
</tr>
<tr>
<td>W</td>
<td>18.6</td>
<td>17.1</td>
<td>60.0</td>
<td>100.0</td>
<td>96.7</td>
<td>99.2</td>
<td>100.0</td>
</tr>
</tbody>
</table>

Means

<table>
<thead>
<tr>
<th></th>
<th>R</th>
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<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>80.3</td>
<td>98.4</td>
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<td>100.0</td>
<td>100.0</td>
<td>100.0</td>
</tr>
<tr>
<td></td>
<td>32.1</td>
<td>43.7</td>
<td>85.2</td>
<td>93.5</td>
<td>96.7</td>
<td>99.0</td>
<td>94.2</td>
</tr>
</tbody>
</table>

Overall, p<0.005 (n=17), Wilcoxon matched-pairs signed ranks test for relative survival of *D. melanogaster* on the Red light sectors (R) versus the White light sectors (W) of the RW cages, for all samples.

Cont.,
Table 4.15 cont.

Experiment II: Relative survival of *D. melanogaster* and *D. simulans* in the spatially homogeneous cages, showing the percentage of *D. melanogaster* in each cage.

<table>
<thead>
<tr>
<th></th>
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<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>WW CAGES:</td>
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<td></td>
<td></td>
</tr>
<tr>
<td>2WW</td>
<td>36.3</td>
<td>10.0</td>
<td>37.4</td>
<td>31.3</td>
<td>76.7</td>
<td>22.0</td>
<td>26.9</td>
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<tr>
<td>6WW</td>
<td>9.5</td>
<td>4.4</td>
<td>23.1</td>
<td>62.9</td>
<td>83.2</td>
<td>37.1</td>
<td>22.2</td>
</tr>
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<td>10WW</td>
<td>41.9</td>
<td>10.1</td>
<td>54.0</td>
<td>73.7</td>
<td>87.2</td>
<td>63.6</td>
<td>61.7</td>
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<tr>
<td>11WW</td>
<td>18.3</td>
<td>2.8</td>
<td>26.2</td>
<td>59.4</td>
<td>92.1</td>
<td>35.9</td>
<td>44.8</td>
</tr>
<tr>
<td>RR CAGES:</td>
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<td></td>
<td></td>
</tr>
<tr>
<td>1RR</td>
<td>45.0</td>
<td>9.8</td>
<td>44.5</td>
<td>90.0</td>
<td>100.0</td>
<td>95.4</td>
<td>99.7</td>
</tr>
<tr>
<td>4RR</td>
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<td>49.4</td>
<td>65.8</td>
<td>93.4</td>
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<td>100.0</td>
<td>100.0</td>
</tr>
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<td>57.6</td>
<td>48.8</td>
<td>80.4</td>
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<td>100.0</td>
<td>100.0</td>
</tr>
<tr>
<td>8RR</td>
<td>71.0</td>
<td>42.1</td>
<td>55.6</td>
<td>99.5</td>
<td>98.4</td>
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<tr>
<td>Means</td>
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<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>WW</td>
<td>26.5</td>
<td>6.8</td>
<td>35.2</td>
<td>56.8</td>
<td>84.8</td>
<td>39.6</td>
<td>38.9</td>
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<tr>
<td>RR</td>
<td>60.1</td>
<td>37.5</td>
<td>61.6</td>
<td>95.3</td>
<td>99.6</td>
<td>98.8</td>
<td>99.9</td>
</tr>
</tbody>
</table>
Table 4.16

Experiment II: Mean relative survival of *D. melanogaster* in three cage types for each sample (calculated from the individual percentages presented in table 3.7).

<table>
<thead>
<tr>
<th></th>
<th></th>
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<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>CAGE TYPE:</td>
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<tr>
<td>RW</td>
<td>57.3</td>
<td>67.3</td>
<td>95.3</td>
<td>98.0</td>
<td>98.9</td>
<td>99.6</td>
<td>97.0</td>
</tr>
<tr>
<td>WW</td>
<td>26.5</td>
<td>6.8</td>
<td>35.2</td>
<td>56.8</td>
<td>84.4</td>
<td>39.6</td>
<td>38.9</td>
</tr>
<tr>
<td>RR</td>
<td>60.1</td>
<td>37.5</td>
<td>61.6</td>
<td>95.3</td>
<td>99.6</td>
<td>98.8</td>
<td>99.9</td>
</tr>
</tbody>
</table>

ANOVA: ** * ** ** n.s. ** ** (**p<0.01), (*p<0.05)
Table 4.17
Experiment I: Photopreference tests on offspring from cage samples taken on week 22 (sample 6).

i) D. melanogaster

a) RR cages:

<table>
<thead>
<tr>
<th></th>
<th>%W</th>
<th>n</th>
</tr>
</thead>
<tbody>
<tr>
<td>3</td>
<td>72.2</td>
<td>36</td>
</tr>
<tr>
<td>7</td>
<td>63.8</td>
<td>99</td>
</tr>
<tr>
<td>9</td>
<td>61.3</td>
<td>93</td>
</tr>
<tr>
<td>11</td>
<td>42.6</td>
<td>94</td>
</tr>
<tr>
<td>15</td>
<td>43.9</td>
<td>66</td>
</tr>
</tbody>
</table>

Heterogeneity \( \chi^2 \) 44.85 (p<0.001)

b) WW cages:

<table>
<thead>
<tr>
<th></th>
<th>%W</th>
<th>n</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>58.9</td>
<td>90</td>
</tr>
<tr>
<td>8</td>
<td>69.6</td>
<td>91</td>
</tr>
</tbody>
</table>

c) RW cages:

<table>
<thead>
<tr>
<th></th>
<th>%W</th>
<th>n</th>
</tr>
</thead>
<tbody>
<tr>
<td>5</td>
<td>56.5</td>
<td>101</td>
</tr>
<tr>
<td>10a</td>
<td>64.5</td>
<td>84</td>
</tr>
<tr>
<td>10b</td>
<td>60.5</td>
<td>77</td>
</tr>
<tr>
<td>13</td>
<td>31.8</td>
<td>85</td>
</tr>
<tr>
<td>16</td>
<td>57.4</td>
<td>101</td>
</tr>
</tbody>
</table>

\( \chi^2 \) test on RW cage and WW photopreference scores:

<table>
<thead>
<tr>
<th>Sources of Variation</th>
<th>d.f.</th>
<th>( \chi^2 )</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>Deviation from WW score</td>
<td>1</td>
<td>17.78</td>
<td>***</td>
</tr>
<tr>
<td>Heterogeneity</td>
<td>3</td>
<td>0.17</td>
<td>n.s.</td>
</tr>
<tr>
<td>(Total)</td>
<td>4</td>
<td>17.95</td>
<td></td>
</tr>
</tbody>
</table>

*** p<0.001.

where %W is the percentage of flies found in the White light sector of the RW photopreference testing cage (see text for details).
Table 4.17 cont.
Experiment I: Photopreference tests on offspring from cage samples taken on week 22 (sample 6).

ii) *D. simulans*

a) RR cages

<table>
<thead>
<tr>
<th>%W</th>
<th>n</th>
</tr>
</thead>
<tbody>
<tr>
<td>3</td>
<td>20.7</td>
</tr>
<tr>
<td>9</td>
<td>36.0</td>
</tr>
<tr>
<td>11</td>
<td>29.5</td>
</tr>
</tbody>
</table>

b) WW cages:

<table>
<thead>
<tr>
<th>%W</th>
<th>n</th>
</tr>
</thead>
<tbody>
<tr>
<td>8</td>
<td>28.1</td>
</tr>
<tr>
<td>14a</td>
<td>15.8</td>
</tr>
<tr>
<td>14b</td>
<td>5.7</td>
</tr>
</tbody>
</table>

c) RW cages:

<table>
<thead>
<tr>
<th>%W</th>
<th>n</th>
</tr>
</thead>
<tbody>
<tr>
<td>16</td>
<td>0.0</td>
</tr>
</tbody>
</table>

where %W is the percentage of flies found in the White light sector of the RW photopreference testing cage (see text for details).

χ² tests on *D. simulans* photopreference scores:

<table>
<thead>
<tr>
<th>Cage types</th>
<th>χ²</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>RW and RR cages</td>
<td>21.4</td>
<td>***</td>
</tr>
<tr>
<td>RW and WW cage 8</td>
<td>21.0</td>
<td>***</td>
</tr>
<tr>
<td>RW and WW cage 14</td>
<td>4.77</td>
<td>*</td>
</tr>
</tbody>
</table>

*** p<0.001, * p<0.05.
Table 4.18
Comparison of photopreference scores of *D. melanogaster* and *D. simulans* samples from the same cages.

<table>
<thead>
<tr>
<th>Cage No.</th>
<th>%W <em>D. simulans</em></th>
<th>%W <em>D. melanogaster</em></th>
<th>Diff.</th>
</tr>
</thead>
<tbody>
<tr>
<td>3RR</td>
<td>79.3</td>
<td>72.2</td>
<td>+7.1</td>
</tr>
<tr>
<td>9RR</td>
<td>64.0</td>
<td>61.3</td>
<td>+2.7</td>
</tr>
<tr>
<td>11RR</td>
<td>70.5</td>
<td>42.6</td>
<td>+27.9</td>
</tr>
<tr>
<td>8WW</td>
<td>71.9</td>
<td>69.6</td>
<td>+2.3</td>
</tr>
<tr>
<td>16RW</td>
<td>100.0</td>
<td>57.4</td>
<td>+42.6</td>
</tr>
</tbody>
</table>

Overall, p<0.05 (n=5), Wilcoxon matched-pairs signed ranks test of *D. simulans* photopreference score compared to the equivalent *D. melanogaster* score for each cage, where %W is the percentage of flies found in the White light sector of the RW photopreference testing cage (see text for details).
Table 4.19  
Experiment II: Photopreference tests on offspring from cage samples taken on week 9 (sample B).

i) \textit{D. melanogaster w}

\begin{tabular}{lcc}
 & \%W & n \\
\hline
1RR & 60.9 & 23 \\
4RR & 60.5 & 76 \\
\hline
\end{tabular}

\begin{tabular}{lcc}
 & \%W & n \\
\hline
2+10 & 46.2 & 26 \\
\hline
\end{tabular}

\begin{tabular}{lcc}
 & \%W & n \\
\hline
3RW & 29.0 & 107 \\
7RW & 26.7 & 45 \\
9RW & 50.0 & 92 \\
12RW & 60.0 & 55 \\
\hline
\end{tabular}

Heterogeneity $\chi^2 = 23.41$, (p$<$0.001).

ii) \textit{D. simulans}

\begin{tabular}{lcc}
 & \%W & n \\
\hline
1RR & 80.8 & 78 \\
4RR & 60.5 & 76 \\
\hline
\end{tabular}

Heterogeneity $\chi^2 = 6.694$ (p$<$0.01).

\begin{tabular}{lcc}
 & \%W & n \\
\hline
10WW & 78.9 & 71 \\
\hline
\end{tabular}

\begin{tabular}{lcc}
 & \%W & n \\
\hline
3RW & 63.2 & 38 \\
7RW & 71.7 & 46 \\
9RW & 69.6 & 56 \\
12RW & 80.0 & 20 \\
\hline
\end{tabular}

Cont.,
Table 4.19 Cont.

Experiment II. Comparison of photopreference scores of *D. melanogaster* w and *D. simulans* samples from the same cages.

<table>
<thead>
<tr>
<th>Cage No.</th>
<th>%W <em>D. simulans</em></th>
<th>%W <em>D. melanogaster</em></th>
<th>Diff.</th>
</tr>
</thead>
<tbody>
<tr>
<td>1RR</td>
<td>80.8</td>
<td>60.9</td>
<td>+19.9</td>
</tr>
<tr>
<td>4RR</td>
<td>60.5</td>
<td>60.5</td>
<td>0.0</td>
</tr>
<tr>
<td>2+10WW</td>
<td>78.9</td>
<td>46.2</td>
<td>+32.7</td>
</tr>
<tr>
<td>3RW</td>
<td>63.2</td>
<td>29.0</td>
<td>+34.2</td>
</tr>
<tr>
<td>7RW</td>
<td>71.7</td>
<td>27.7</td>
<td>+45.0</td>
</tr>
<tr>
<td>9RW</td>
<td>69.6</td>
<td>50.0</td>
<td>+19.6</td>
</tr>
<tr>
<td>12RW</td>
<td>80.0</td>
<td>60.0</td>
<td>+20.0</td>
</tr>
</tbody>
</table>

Overall, p<0.025 (n=6), Wilcoxon matched-pairs signed ranks test of *D. simulans* photopreference score compared to the equivalent *D. melanogaster* score for each cage, where %W is the percentage of flies found in the White light sector of the RW photopreference testing cage (see text for details).
Table 4.20
Dispersal behaviour of white-eye *D. melanogaster* alone in RW population cages

i) Samples 1 to 7:

a) Eggs laid:

<table>
<thead>
<tr>
<th>SAMPLE:</th>
<th>1</th>
<th>3</th>
<th>4</th>
<th>5</th>
<th>6</th>
<th>7</th>
</tr>
</thead>
<tbody>
<tr>
<td>R*WCages</td>
<td>3</td>
<td>63</td>
<td>159</td>
<td>133</td>
<td>188</td>
<td>23</td>
</tr>
<tr>
<td>5</td>
<td>89</td>
<td>128</td>
<td>259</td>
<td>161</td>
<td>29</td>
<td>522</td>
</tr>
<tr>
<td>7</td>
<td>86</td>
<td>182</td>
<td>101</td>
<td>224</td>
<td>25</td>
<td>359</td>
</tr>
<tr>
<td>Mean</td>
<td>79.3</td>
<td>156.3</td>
<td>164.3</td>
<td>191</td>
<td>25.7</td>
<td>857</td>
</tr>
</tbody>
</table>

| Mean | 72.5 | 115 | 277.3 | 176.0 | 56.7 | 635.7 |

These cages were normal RW cages which had food tubes in one sector only: R*W cages had food tubes in the red light sectors only and the RW* cages had food tubes on the white light sectors. Sample tubes were put in the cage sectors which already contained food tubes.

b) Adults emerging:

<table>
<thead>
<tr>
<th>SAMPLE:</th>
<th>1</th>
<th>3</th>
<th>4</th>
<th>5</th>
<th>6</th>
<th>7</th>
</tr>
</thead>
<tbody>
<tr>
<td>R*WCages</td>
<td>3</td>
<td>-</td>
<td>60</td>
<td>67</td>
<td>155</td>
<td>16</td>
</tr>
<tr>
<td>5</td>
<td>-</td>
<td>74</td>
<td>73</td>
<td>136</td>
<td>18</td>
<td>229</td>
</tr>
<tr>
<td>7</td>
<td>-</td>
<td>61</td>
<td>94</td>
<td>186</td>
<td>17</td>
<td>225</td>
</tr>
<tr>
<td>Mean</td>
<td>-</td>
<td>65</td>
<td>78</td>
<td>159</td>
<td>17</td>
<td>180.7</td>
</tr>
</tbody>
</table>

| Mean | - | 50.3 | 126.7 | 131 | 34.7 | 200.7 |

Overall, Not significant, for either eggs laid or adults emerging between the two cage types; Wilcoxon matched-pairs signed ranks test.
Table 4.20
Dispersal behaviour of white-eye *D. melanogaster* alone in RW population cages:

**ii) Samples 8 and 9:**
(Samples 8 and 9 are different to the first seven samples in that sample tubes were put in both sectors of each cage.)

### a) Eggs laid

<table>
<thead>
<tr>
<th>Rsectors</th>
<th>Wsectors</th>
<th>%W sector</th>
<th>R*WCages</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sample 8</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>3</td>
<td>147</td>
<td>203</td>
<td>58.0</td>
</tr>
<tr>
<td>5</td>
<td>162</td>
<td>141</td>
<td>46.5</td>
</tr>
<tr>
<td>7</td>
<td>205</td>
<td>87</td>
<td>29.8</td>
</tr>
</tbody>
</table>

Mean: 171.3 143.6 44.8

($\chi^2$ Heterogeneity: ***)

### b) Adults emerging

<table>
<thead>
<tr>
<th>Rsectors</th>
<th>Wsectors</th>
<th>%W sector</th>
<th>R*WCages</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sample 8</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>3</td>
<td>102</td>
<td>145</td>
<td>58.7</td>
</tr>
<tr>
<td>5</td>
<td>137</td>
<td>113</td>
<td>45.2</td>
</tr>
<tr>
<td>7</td>
<td>137</td>
<td>86</td>
<td>38.6</td>
</tr>
</tbody>
</table>

Mean: 125.3 114.7 47.8

($\chi^2$ Heterogeneity: ***)

<table>
<thead>
<tr>
<th>RW*Cages</th>
<th>Rsectors</th>
<th>Wsectors</th>
<th>%W sector</th>
<th>R*WCages</th>
</tr>
</thead>
<tbody>
<tr>
<td>4</td>
<td>234</td>
<td>256</td>
<td>52.2</td>
<td>n.s.</td>
</tr>
<tr>
<td>8</td>
<td>139</td>
<td>210</td>
<td>59.1</td>
<td>***</td>
</tr>
<tr>
<td>10</td>
<td>53</td>
<td>321</td>
<td>85.8</td>
<td>***</td>
</tr>
</tbody>
</table>

Mean: 142.0 262.3 65.7

($\chi^2$ Heterogeneity: n.s.)
Table 4.20 cont.

a) Eggs laid

<table>
<thead>
<tr>
<th>Sample 9</th>
</tr>
</thead>
<tbody>
<tr>
<td>Rsects</td>
</tr>
<tr>
<td>----------</td>
</tr>
<tr>
<td>RW*Cages</td>
</tr>
<tr>
<td>3</td>
</tr>
<tr>
<td>5</td>
</tr>
<tr>
<td>7</td>
</tr>
<tr>
<td>Mean</td>
</tr>
</tbody>
</table>

(χ² Heterogeneity: ***)

<table>
<thead>
<tr>
<th>Sample 9</th>
</tr>
</thead>
<tbody>
<tr>
<td>Rsects</td>
</tr>
<tr>
<td>----------</td>
</tr>
<tr>
<td>RW*Cages</td>
</tr>
<tr>
<td>4</td>
</tr>
<tr>
<td>8</td>
</tr>
<tr>
<td>10</td>
</tr>
<tr>
<td>Mean</td>
</tr>
</tbody>
</table>

(χ² Heterogeneity: ***)

b) Adults emerging

<table>
<thead>
<tr>
<th>Sample 9</th>
</tr>
</thead>
<tbody>
<tr>
<td>Rsects</td>
</tr>
<tr>
<td>----------</td>
</tr>
<tr>
<td>RW*Cages</td>
</tr>
<tr>
<td>3</td>
</tr>
<tr>
<td>5</td>
</tr>
<tr>
<td>7</td>
</tr>
<tr>
<td>Mean</td>
</tr>
</tbody>
</table>

(χ² Heterogeneity: *)

<table>
<thead>
<tr>
<th>Sample 9</th>
</tr>
</thead>
<tbody>
<tr>
<td>Rsects</td>
</tr>
<tr>
<td>----------</td>
</tr>
<tr>
<td>RW*Cages</td>
</tr>
<tr>
<td>4</td>
</tr>
<tr>
<td>8</td>
</tr>
<tr>
<td>10</td>
</tr>
<tr>
<td>Mean</td>
</tr>
</tbody>
</table>

(χ² Heterogeneity: n.s.)

Where χ² test is for significant deviation from an expected 50:50 distribution of eggs laid or adults emerging from the two cage sectors.
CHAPTER 5

GENERAL DISCUSSION

5.1 Microhabitat Dispersal and Light Preferences in *Drosophila*

5.1.1. Variation in Light Preferences

Chapters 3 and 4 show that in a heterogeneously lit environment microhabitat dispersal in *D. melanogaster* and *D. simulans* can be mediated by light preferences. These have both a genetic and a behavioural component and the relative importance of each component depends on the interaction with a balance of selective forces acting on the two components.

At the interspecific level, genetic or innate differences in light preferences can be more important. The more photopositive *D. simulans* disperses to brighter areas than the more photonegative *D. melanogaster*. This is adaptive because interspecific competition is reduced. The learned component of intraspecific light preferences demonstrated in Chapter 3 may enable individuals with flexible preferences to track changes in resources and exploit vacant, previously unfavourable niches or suboptimal habitats more rapidly than individuals relying on longer term, genetic or evolutionary between-generation changes. This ability means that when alone in heterogeneously lit population cages, both *D. melanogaster* and *D. simulans* can rapidly disperse to and exploit a vacant light niche which, in interspecific interactions is usually unfavourable because it is occupied by the other species. In the absence of *D. simulans*, *D. melanogaster* — which is normally photonegative — disperses into
bright light (Chapter 3) and the normally photopositive *D. simulans* disperses into dim red light sectors in the patchy cages (Chapter 4).

Light is an advantageous cue for small animals with limited behavioural repertoires such as *Drosophila* because it gives less ambiguous and longer ranged information on the suitability of an area than might temperature or humidity. Many invertebrates use light in the initial stages of habitat selection (van Alphen and Vet, 1986). *D. melanogaster* and *D. simulans* may use it in microhabitat selection and possibly breeding site choice because substrate-based are less important than are extrinsic cues in tracking unpredictable resources. Moreover, females of many parasitoid and cosmopolitan species often exploit different substrates to that from which they emerged.

The anomalous light preferences of *D. simulans* — which can reduce species overlap — may have evolved in order to allow coexistence with *D. melanogaster* in the absence of resource partitioning. Another cosmopolitan species (*Drosophila immigrans*) often sympatric with *D. melanogaster* and *D. simulans* has photoneutral light preferences and the light independent mating behaviour characteristic of cosmopolitan species of *Drosophila* (Grossfield, 1966; Marinković et al., 1980; Kekić, 1982; Maveety and Seiger, 1982) but, unlike *D. simulans*, shows resource partitioning with *D. melanogaster* by exploiting decaying vegetables (Atkinson and Shorrock, 1977; Atkinson, 1979b; Prince and Parsons, 1980).
Although Parsons (1981) believes that coexistence between these three species is due to different tolerances to ethanol and to "competitive speciation" by the partitioning of this single resource, he now neglects the potential role of light preferences in coexistence. My results support his earlier view (Parsons, 1973) because, even when exploiting the same resource, *D. melanogaster* and *D. simulans* can reduce species overlap by their different light preferences.

Intraspecific and interspecific interactions affect variation in light preferences differently. In patchy RW population cages there was a genetic change in light preferences, presumably in response to interspecific competition. However, learned changes appeared to be more important in intraspecific interactions: even after more than 80 generations there was no evidence for any accumulated genetic divergence between the *D. melanogaster* longterm "No-choice" lines (Chapter 3). Unlike most experiments on variation for light preferences, there was no active selection for choice of light regime in my experiments. Once set up, the lines were kept in the same light regime with no selection for greater preferences for that light regime—I used random pairs to found the next generation of the two lines (Section 3.2.3.1, Chapter 3).

Some form of disruptive selection between light regimes may be required for genetic divergence in light preferences. Divergent populations for photopositive and photonegative light preferences can be rapidly selected from a base population (see Rockwell and
Seiger, 1973; Grossfield, 1978 for references) which can also produce changes in morphology (Hadler, 1964a; Kečić and Valvajter, 1978), mating ability and oviposition preference (Marinković, 1974; Markow, 1975). In support of this, genetic changes in preference — where *D. simulans* became more photopositive and *D. melanogaster* more photonegative in the RW cages of experiment I, Chapter 4 — suggest that there was selection for interspecific divergence. If individuals of a species dispersed to the 'wrong' light patch, overlap and hence interspecific competition is increased and fitness reduced.

In other words, simple experience of a light regime may not be enough to produce genetic changes in light preferences in *D. melanogaster*. Interestingly, mating behaviour in *D. melanogaster* can also remain stable over many generations in darkness (Lambert and Harper, 1985) and Thorpe (1938) found that although *Nemeritis* adults could be conditioned to the odour of a new host (*Meliphora* larvae), there was no genetic change in preference so that the proportion choosing the new host did not increase even after 11 generations of exposure to the new host.

Mates can be difficult to find in patchy environments because they are dispersed at relatively low density among the patches. There may hence be selection for host-fidelity. Colwell (1986a), for example, found many selective forces acting on host-fidelity in his study of interactions in hummingbird flower mite species. Although there was interspecific competition, specialization in host plant
species was caused by host-fidelity which increased the effective
density of potential mates. These mites are colonizers and must
disperse to new flowers. Disembarkation at the right host plant
species can reduce time and energy wasted on courtship and mating
with the wrong species of mite. Host-plant specialization is, hence,
promoted by a form of sexual selection acting on differential mating
success. The reinforcement of reproductive isolation is by host-
plant fidelity rather than by interspecific competition (Colwell,
1986a).

*D. melanogaster* and *D. simulans* are also colonizers and similar
selection for host-fidelity (mediated by light preferences) may act
on them. Although host-plant affiliations in the Hummingbird flower
mites are largely arbitrary (Colwell, 1986) so that host-fidelity
can arise by the exploitation of an arbitrary factor, for *D.
melanogaster* and *D. simulans*, light is not an arbitrary factor as it
directly affects competitive ability (Chapter 4).

5.1.2 Adaptive Nature of Flexible Light Preferences
Flexible light preferences are adaptive for species which exploit
ephemeral, patchy and hence unpredictable breeding sites. This flex-
ibility permits the rapid colonization, the tracking of new
resources and the exploitation of vacant niches. Habitat selection
which arises from experience does not require the linkage between
habitat choice and fitness needed for genetic changes in
preferences. For example, dispersing Hummingbird flower mites do not
have completely fixed or "hardwired" preferences but can make

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"mistakes" in host choice at a rate of about ½% (Colwell, 1986a). This guarantees the rapid colonization of host plant species which are mite-free. This is analogous to the opportunist behaviour of *D. melanogaster* where the lack of fixed light preferences helps the exploitation of new or under-used breeding sites in heterogeneous environments. Flexibility of light preferences in *Drosophila* may also help males to find females (which mate, feed and oviposit at the same sites [Spieth and Ringo, 1983; Rice, 1985]).

5.1.3 Interspecific Variation in Light Preferences

Although *D. simulans* uses light to reduce overlap and interspecific competition with *D. melanogaster*, there remains an advantage in having learned preferences because *D. simulans* is a colonizing and cosmopolitan species. Learned preferences also means that in the absence of a superior competitor a species can exploit niches which are often occupied by competitors without the cost of individual genetic specialization. For example, learned and flexible light preferences allow *D. simulans* to increase its niche with respect to light intensity when *D. melanogaster* is absent and contract it when this species is present. This may explain why, in Chapter 4, *D. simulans* formed a preference for dim red light because although it is then almost blind this is a major disadvantage only when *D. melanogaster* is also present. Similarly, white-eye *D. melanogaster* also formed preferences for bright white light in which it is blinded — a preference mal-adaptive only when the mutant is in competition with other strains or species.
Learned flexibility in light preferences is particularly effective in *D. simulans* because it often reaches new areas before *D. melanogaster* (Nunney, Manuscript). It will have the first choice of breeding sites and can then respond to the later arrival of *D. melanogaster* by becoming more photopositive. The extent of behavioural flexibility in *D. simulans* is, however, less than in *D. melanogaster* as might be expected by its narrower and more specialized niche. For example, in RW (choice) cage lines (Chapter 4), *D. simulans* offspring from the sample tubes in the two sectors did not form different preferences although adults caught in the cage sectors did. This suggests that *D. simulans* emerge with an innate photopositive light preference which can be subsequently altered by experience. On the other hand, preferences in *D. melanogaster* can be formed in the pupal and early adult stages.

The photopositive preference of *D. simulans* reduces the chance of interspecific contacts: *D. melanogaster* adults are more likely to court in dimly lit areas reducing interspecific interference in mating. Males of both species form small territories on feeding sites and *D. melanogaster* males are more likely to displace the generally smaller *D. simulans* males in interspecific contests (Jacobs, 1978; Hoffman, 1987).

Light can also counteract the effects of temperature in spatially homogeneous environments. In experiment II, where the use of a white-eye mutant was equivalent to exposing pigmented wildtype eyed *D. melanogaster* to brighter light, there was coexistence in the
homogeneously lit WW cages (where white-eye *D. melanogaster* was at a disadvantage because it is blinded in bright light) even though the temperature was too high (25°C) for coexistence usually to occur. Light intensity was, therefore, acting like an additional resource axis superimposed onto the homogeneous environment.

5.1.4 Light Preferences and Habitat Selection: Conclusions

There are several interspecific and intraspecific selective pressures acting on light preferences in *D. melanogaster* and *D. simulans*. Competition can lead generalists to evolve into divergent specialists with an increased efficiency in resource exploitation (Lawlor and Maynard Smith, 1976). It may also promote the use of new resources if limiting resources are not equally utilized (MacArthur and Levin, 1964, 1967; Pontin, 1982). Differences in light preferences between *D. melanogaster* and *D. simulans* are, therefore, intricately interrelated with a balance between intraspecific and interspecific variation. There is also a frequency-dependent component which can change niche width (Wilson and Turelli, 1986; Tauber and Tauber, 1989). Host-fidelity also leads to sexual selection, which like competition, can narrow host choice while selection based on resource availability tends to broaden it.

There are two components involved in habitat selection here: genetic and learned or behavioural. Most studies concentrate on the genetic component and do not consider the possibility of learning. Any important variation in habitat selection or host fidelity is assumed to be genetical: which is odd given the view that behaviour...
is important in the first stages of speciation (Diehl and Bush, 1989; Tauber and Tauber, 1989).

In my experiments, the importance of the two components—learned and innate preferences—depends on whether the interaction is interspecific or intraspecific. Interspecific differences in light preferences have a large genetic component; the changes in light preferences of offspring under interspecific competition are also genetical (Chapter 4). In contrast, there is a large learned component to changes in light preferences at the intraspecific level so that experience had an important effect on preferences in single species populations of *D. melanogaster* (Chapter 3) and *D. simulans* (Chapter 4). Even in the longterm experiment (Chapter 3) there is no evidence for a genetic changes in light preferences. This may result from the absence of niche choice and divergent selection pressure on the "No-choice" lines whereas in the interspecific competition experiment of Chapter 4 selection for avoidance of interspecific competition by reduced overlap was mediated by the divergence in light preferences between the two species.

In spatially heterogeneous environments, light preferences can also increase the efficiency of finding mates among patchy breeding sites particularly when population densities are low. Interspecific differences in light preferences may be important in *D. melanogaster* and *D. simulans* because light affects not only mating behaviour, but also affects oviposition and larval feeding which can all occur at
the same sites (mating at the restaurant, so to speak [Labeyrie, 1978]).

The details of speciation in *D. melanogaster* and *D. simulans* are uncertain (David and Capy, 1988; Lachaise et al, 1988), but light mediated behaviours are involved with *D. simulans* exploiting a brighter niche. Genes identified for photopositive and photonegative preferences in *D. simulans* are all on autosomal chromosomes while, in *D. melanogaster*, genes for photopositive behaviour are autosomal and genes for photonegative behaviour are sex-linked (Markow and Smith, 1977).

The relevance of photic behaviour to reproductive isolation is illustrated by a fertile white-eye mutation in *Drosophila subobscura*. In a strain selected for light-independent mating behaviour a white-eye mutant spontaneously occurred which, unlike previous white-eye *D. subobscura*, was fertile (Springer, 1973). Previous mutants were sterile because they could not see the essential visual stimuli on which mating in this species is dependent (Wallace and Dobzhansky, 1946). The fertile white-eye mutant was fertile because the strain selected for light-independence in which it arose was less dependent on visual cues for mating than unselected *D. subobscura* (Springer, 1983). This might produce reproductive isolation in a patchy environment because only the *D. subobscura* mutant can mate in darkness (which unlike wildtype *D. subobscura*, is inhibited in light).
5.2 Spatial Heterogeneity, Dispersal and Coexistence

5.2.1 Patchiness and Dispersal

Spatial heterogeneity is important in interspecific and intraspecific interactions as variation in dispersal or preferences is dependent on it. In my experiments, species overlap was reduced by spatial heterogeneity. In single species cages, both *D. melanogaster* and *D. simulans* populations became behaviourally subdivided when there was spatial heterogeneity. Dispersal in these experiments was mediated by environmental rather than by resource-based heterogeneity. Such environmental patchiness can maintain a polymorphism for a deleterious allele: Jones and Probert (1980) showed that in homogeneously lit population cages, a white-eye *D. simulans* mutant was eliminated by a wildtype strain. In a heterogeneous light environment, however, a white-eye:wildtype polymorphism was maintained. In the patchy cages, there was differential dispersal. The net migration of the photopositive wildtype flies into the white light sectors provided the white-eye mutant with a refuge in the red light sector. This refuge was necessary because in the homogeneous RR cages — where no such refuge was available — the white-eye mutant was eliminated.

Narise (1968) also found that differential dispersal provided vestigial winged *D. melanogaster* with a refuge from wildtype flies in patchy environments. Mixed populations were introduced into either a homogeneous environment (a single population cage) or a patchy environment (10 connected migration tubes with the same total food area in both environments). The mutant was not eliminated in the patchy environment, its survival was due to faster dispersal of
the vestigial flies among the migration tubes (which provided a 
refuge from the wildtype flies). Indeed, the dispersal rate of Vg 
flies was higher in the presence of wildtype flies.

5.2.2 Species Coexistence in Patchy Environments

Patchiness — even two patches — can promote coexistence if there is 
differential dispersal between competitors (Skellam, 1951; Horn and 
MacArthur, 1972; Levin, 1974; LLoyld and White, 1980; Shorrocks and 
Rosewell, 1984; Hassell and May, 1985; Chesson and Case, 1986;
Philips and Hubbard 1989). However, in spite of the differences in 
dispersal between D. melanogaster and D. simulans, I did not find 
coexistence in my two-patch RW cages (Chapter 4). This may have been 
due to several factors. Perhaps the white light patches were not 
bright enough. In my field studies there was a range of light 
intensities where both species were caught and the bright white 
light used in the RW cages falls in this range (Chapter 4). If the 
white light sectors had been brighter there may have been greater 
divergence in species distributions reducing overlap and making 
coexistence more likely. However, the use of white-eyed D. 
melanogaster in experiment II was roughly equivalent to placing 
wildtype D. melanogaster in brighter light, and this too failed to 
lead to long term coexistence.

The lack of coexistence in the RW cages may have been due to the 
photopositive light preferences of D. simulans restricting it to the 
Bright white light sectors of the RW cages whereas D. melanogaster 
was found in both sectors. This, together with the greater
sensitivity of *D. simulans* to high population density, further reduced the frequency of this species.

The cages may have been too simple: greater patchiness may have provided greater opportunity for dispersal giving *D. simulans* more chance to find refugia. This is important as *D. simulans* avoids direct competition with *D. melanogaster* (Barker, 1983; Mueller, 1985; Gilpin *et al.*, 1986). Increased patchiness in many models also increases the chance of coexistence and Kneidel (1985) found that the overlap in species distributions of two Dipteran species (*Fannia howardi* and *Megaselia scalaris*) decreased when they oviposited among more subdivided breeding sites. Increased patchiness can also promote coexistence because dispersal can produce refugia reducing the effect of competitive exclusion and allowing coexistence (Levin, 1974; Casewell, 1978; Atkinson and Shorrocks, 1981). My results do show that there are differences in light preferences and dispersal even with limited complexity.

In Levin's (1974) model, coexistence is possible in two patches so long as there is differential dispersal between them and each species has some advantage in its favoured patch. In the RW cage, the heterogeneity in light provided the patchiness and the interspecific differences in light preferences, the differential dispersal. The advantage that each species had in its preferred patch was probably due to the effect of light on mating ability. Light preferences increased this advantage because differential dispersal also led to each species having superior numbers in its
preferred patch. This is important because, in *Drosophila*, the competitor with the greater initial number or frequency tends to prevail (Narise, 1965; Hedrick, 1972; Barker, 1983). *D. simulans* oviposits faster than *D. melanogaster* in brighter lit areas (see Chapter 4) which will also benefit *D. simulans* in the bright white light patches. *D. simulans* larvae are most common at the edges of food medium whereas *D. melanogaster* tends to lay more eggs at the edges so that, if *D. simulans* females oviposit first, their larvae will destroy most of the later laid *D. melanogaster* eggs (Barker, 1971; Moth and Barker, 1976).

The increase in the numbers of *D. melanogaster* white eyed flies and the rapid dispersal of such flies when disturbed may have made coexistence less likely in the RW cages by reducing the differential dispersal caused by light preferences so that the RW cages may effectively have become a single patch. As Levin (1974) suggests, this will lead to the elimination of the weaker competitor. There was, however, a significant reduction in species overlap and a high proportion of *D. simulans* for the first few generations in the RW cages. Restarting such cages every few generations may well have led to longterm coexistence rather than simply to a reduced rate of decline in the relative frequency of *D. simulans* in the two sectors of the RW cages.

Coexistence does not necessarily imply that species frequencies are equal. *D. simulans* in the wild may be rare and found in only a few of the available patches. Spencer (1968), for example, found *D. 
\textit{D. simulans} (which is rarer than \textit{D. melanogaster} in his study region in Ohio, USA) in only one trap. These flies were probably descended from a small local population as 10\% of them carried a recessive autosomal mutation (\textit{radius incompletus}). \textit{D. melanogaster} was found in many of the other traps and, the breaking up of breeding sites into small discrete patches or traps enabled \textit{D. simulans} to coexist with \textit{D. melanogaster} by colonizing only a part of the environment.

Patchiness does not always lead to greater population stability. Karieva (1987), for example, found that increased habitat fragmentation into smaller and more numerous patches did not stabilize predator-prey interactions but led to local population explosions of the prey species. Ims and Stenseth (1989) report that Forney and Gilpin (1989) found that \textit{Drosophila} populations were more likely to survive in undivided (i.e. homogeneous) laboratory environments.

5.3 Coexistence in Spatially Homogeneous Environments
There can be coexistence without patchiness if, for example, competitive ability is inversely related to a species frequency (De Witt, 1960, 1961; Ayala, 1971; Price, 1984). Temporal heterogeneity, although not explicitly investigated in this thesis, can have an important effect on population interactions. In Ayala's (1971) case, at least, coexistence was caused by temporal heterogeneity because the competitive advantage of one of the species of \textit{Drosophila} at one stage of their life cycle was balanced by its competitive disadvantage at another. In most models, however, temporal heterogeneity has the same or a lesser effect as spatial heterogeneity and can safely
be ignored (Turelli and Gillespie, 1980; Turelli, 1981; Chesson, 1986).

Frequency-dependent predation can also promote coexistence among prey species even in a homogeneous environment (see Chapter 1). However, as is clear from Chapter 2, the homogeneity or otherwise of an environment is organism-defined. Although the background was homogeneous, in my experiments, spatial heterogeneity arose from the spatial patterning of the prey themselves. This affected predator preferences and hence prey survival to such an extent that the usual advantage of being rare was lost when the prey were arguably in a less spatially heterogeneous distribution (the aggregated arrangement).

As discussed in Chapter 2, an effect of this spatial component of frequency-dependent predation is that the mixing of rare prey species with more common ones within patches is favoured. Rare prey which tend to disperse to patches containing other species will be relatively safer so that, even on a homogeneous background, this form of predation may provide a rare species with a refuge among more common prey. Frequency-dependence also means that predation can act at the same scale as can competition and can hence reduce the effect of competition within patches.

The within-patch effect of predator or parasitoid pressure may affect Drosophila interactions. In my field studies, for example, parasitoid wasps were found in and around traps and a number emerged
from traps and food tubes brought back to the laboratory. *D. simulans* larvae are better able to withstand such parasitism than can *D. melanogaster* larvae (Carton and Kitano, 1981). When parasitoid wasps are present, exploitation of the same breeding sites may be easier even without resource partitioning. Inspite of recent work (Carton et al., 1986), little is known about how parasitism may promote coexistence at the within-habitat scale investigated in this thesis. If there is a spatial component to any frequency-dependence involved in host choice this might promote the mixing of *D. melanogaster* and *D. simulans* at the same breeding sites even in the absence of other factors.

5.4 Concluding Remarks

There is an intricate balance of selective forces acting on population interactions between *D. melanogaster* and *D. simulans* but patchiness in light conditions can certainly facilitate coexistence by reducing species overlap or providing favoured patches where a species has increased competitive ability.

The effect of light preferences in *Drosophila* on intraspecific and interspecific habitat selection can be thought of in terms of fundamental and realized niches. The fundamental niche of each species includes both dim and bright light as each can exploit both light sectors in the absence of the other. Interspecific interactions in the RW cages narrows the realized niche and the two species disperse to different light patches. However, in my experiments, the intensity of the bright white light patches used in the RW cages was
too low, and coexistence was not possible because the realized niche of *D. melanogaster* incorporated the whole of *D. simulans* fundamental niche.

Environmental and resource patchiness may be superimposed so that spatial heterogeneity can act at more than one level. If resources are highly subdivided, interspecific differences in characters such as light preferences may not be needed. However, such preferences may have evolved when competition is strong and there is no chance for resource partitioning or coexistence through resource patchiness. In a homogeneous environment, there is a continuum from *D. melanogaster* as the superior competitor in dim red light to superiority for *D. simulans* in bright light with coexistence at intermediate light intensities. Temperature has a similar effect on competition with *D. simulans* more likely to survive at lower temperatures (Barker, 1983).

Light preferences act at most of the important stages of the *Drosophila* life cycle. It is difficult to say whether the differences in preferences between *D. melanogaster* and *D. simulans* arose to reduce interspecific competition, to minimize interspecific matings, or to increase the chances of finding a mate in a patchy environment. As Shorrocks *et al.*, (1987) emphasize, resource partitioning may be important in coexistence even for *Drosophila* competing for patchy resources (see p.48, Shorrocks and Rosewell, 1987). However, until now there has been no clear biological basis for the aggregative behaviour of each species central to their model.
For *D. melanogaster* and *D. simulans*, at least, light preferences in a heterogeneously lit environment may provide such a mechanism.
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APPENDIX

Main *Drosophila* Field Sites.

1. School Close, Ludham, Norfolk
2. Howhill Farm, Howhill, Norfolk
3. D. Newman, Ludham Rd., Catfield, Norfolk
4. 2, Lovelace Rd., Oxford
1. School Close Site, Ludham, Norfolk

Large garden with a vegetable patch including rotting cabbages. Species caught: *D. melanogaster*, *D. subobscura*, *D. funebris* and *D. busckii*. 
2. Howhill Farm Orchard, Howhill, Norfolk
Large orchard on private farm land. Apples starting to ripe; a number already fallen and are beginning to rot. Many *D. subobscura* resting on tree trunks. Species caught: *D. melanogaster* and *D. subobscura*. 
3. Ludham Road, Catfield, Norfolk
Backgarden with fresh fruit (raspberries and blackcurrents) for sale. Species caught: *D. melanogaster*, *D. subobscura*, *D. busckii*, *D. funebris*, *D. phalerata* and *D. hydei.*
4. 2, Lovelace Road, Oxford

Secluded garden surrounded by high fences and trees with a number of fruit trees (used to be part of an orchard). Species caught: *D. melanogaster, D. simulans, D. subobscura, D. busckii, D. funebris, D. phalerata, D. immigrans, D. hydei* and *D. virilis.*

Note: *D. melanogaster and D. subobscura* emmerged from traps brought back to the laboratory.