Ecological studies of the breeding sites and reproductive strategies of domestic species of *Drosophila*

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SUMMARY

The ecology and reproductive strategies of seven species of domestic Drosophila were examined at a wholesale fruit and vegetable market.

The seasonal abundance of adult Drosophila was investigated using baited traps. The value of different trapping methods was discussed.

Drosophila were reared from different fruits and vegetables brought back from the market to the laboratory. D. melanogaster, D. simulans and D. subobscura nearly always emerged from fermenting fruits, D. busckii specialised on decaying vegetables, and D. immigrans and D. hydei were generalists. Within the groups, fermenting fruit and decaying vegetables there was ccnsiderable overlap of breeding sites.

Some of the factors which might influence breeding site preferences were investigated in the field and in the laboratory. Both selection of breeding sites by ovipositing females and differential survival of the larvae seem to be important. Unlike other species of Drosophila the domestic species do not seem to separate their feeding and breeding sites.

D. immigrans, which frequently breeds in citrus fruits, was found to be particularly associated with these fruits when they were infected with the mould, Penicillium. Other species emerged more often from uninfected fruit. There may be a long standing evolutionary relationship between D. immigrans, citrus fruits and Penicillium.

The body size of D. melanogaster, caught in traps, was found to change in a regular way during the season. This was partly an effect of temperature, but partly due to intraspecific competition at the highest population densities. Intraspecific competition is unimportant in the other species, though some species suffered from interspecific competition with D. melanogaster.

The reproductive strategies of the seven Drosophila species were examined. They fell into two groups, large species with large clutches

of small eggs, and small species with small clutches of large eggs. These strategies are not consistent with r- and K- selection theory, but may have been linked to the predictability of finding breeding sites.

The ecology of domestic species of Drosophila was discussed with reference to current theories of population regulation.

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CHAPTER 1

INTRODUCTION

As ecology has developed as a science its interest has gradually shifted away from the distributions of organisms towards the dynamic ecological processes which underly them (Pearsall, 1964). The earliest studies of this sort concentrated on the ecological succession of plant communities; later, the experimental work of Gause (1934) stimulated interest in competition and lead to a formalisation of the concept of the niche by Hutchinson (1957). The dynamics of predator-prey interactions have been much studied and even the concept of diversity, which is essentially descriptive, arouses more interest for its relationship to community stability than as a static descriptive term. The emphasis, then, is firmly on dynamics. Despite this, ecologists have tended to ignore another dynamic process, evolution.

Interactions between animals and their environments have often been thought of as though they were happening in ecological time as distinct from evolutionary time. This abstraction was justified on the grounds that evolutionary events happen too slowly to have any influence over ecological processes. A change in outlook among ecologists has been stimulated by workers such as Ford (1964) and Dobzhansky (1970) who have shown that genetic changes in field populations can happen very quickly and so can affect ecological events.

For a long time the Peppered moth, Biston betularia, provided one of the few cases in which genetic changes had been observed in a population (Kettlewell, 1973). In Manchester, between 1848 and 1895 the frequency of the industrial melanic form of this moth increased from zero to 98%. This change was associated with an increase in pollution and the elimination of lichens on which the normal form of the moth is cryptic.

One might argue that even this rate of evolutionary change is too slow to influence ecological events. An example of much faster genetic change with direct ecological consequences is provided by Dobzhansky (1970). He looked at an inversion polymorphism in a

natural population of Drosophila pseudoobscura in California. The two most common inversions were called Standard and Chiricahua. In winter Standard was twice as frequent in the population as Chiricahua but during spring Chiricahua increased in frequency until it was the most common inversion. During summer Standard again became twice as frequent. Laboratory experiments showed that Standard was favoured at high temperatures, which explains its increase in the summer, but Chiricahua was favoured when competition was reduced as at the start of spring when winter mortality had reduced the population size (Birch, 1955).

Levins (1968) has noted that in the time it takes for species to interact demographically in simple competition, genetic changes can alter their competitive ability. Several laboratory studies have provided evidence for this observation. Moore (1952b) found that in competition with Drosophila melanogaster, D. simulans was usually eliminated fairly quickly. In one case, however, D. simulans remained for much longer and had evolved improved competitive ability. Pimentel et al (1965) found that in competition between houseflies and blowflies, natural selection always increased the competitive ability of the rarer species.

The new awareness of evolution among ecologists has lead to a change in thinking about the ways in which animals interact with the environment. Instead of being passively manipulated by the environment animals are now thought of as having, or acting as if they have, a strategy or set of tactics. This suggests some teleology, by analogy with human tactics which are always directed at a goal, but Stearns (1976) has defined a tactic as a set of coadapted traits designed by natural selection to solve particular ecological problems. Defined in this way, it is clear that the teleology is due to the short hand way in which biologists normally talk about natural selection (Hull, 1974). Several fields have benefited from this interest in the adaptiveness of animals' ecological characters, the most obvious being the related subjects, reproductive strategies and life history strategies. In these fields the theory is already well developed (Stearns, 1976) and has stimulated much practical work. Other fields that have benefited are the theory of foraging

strategies (MacArthur and Pianka, 1966; MacArthur, 1972) and predator avoidance strategies (Pianka, 1974). Unfortunately these subjects have been hampered because the genetic basis of the ecological characters being studied is rarely known.

The flow of information between genetics and ecology has not all been one way. There is as much a need for a knowledge of ecology in genetics as of genetics in ecology. One aspect of the ecology of their species that has concerned geneticists has been the difference between central and marginal populations. Populations at the margins of a species range are often less polymorphic and phenotypically variable than those at the centre. Lewontin (1974) has reviewed the confusion of explanations that surround this phenomenon, most of which is due to lack of ecological information. We do not know whether marginal environments are more or less diverse than those at the centre, or whether they are more or less temporarily unstable or even whether we should necessarily expect lower population densities at the margins. Ecological work is required to complement the genetics. A subject that has benefited from ecological considerations is the study of stable polymorphisms. In the past geneticists tended to think of populations as living in uniform environments and so stable polymorphisms were usually explained as the result of heterozygous advantage. Recently the application of ecological techniques has resulted in a considerable amount of evidence which indicates that genetic polymorphisms are maintained by environmental heterogeneity (Hedrick et al, 1976). Taylor and Powell (1977) have shown that there are genetic differences between collections of Drosophila persimilis from slightly different habitats within a small area, and that these differences are due to habitat choice. Such evidence of the importance of the environment to the genotype emphasises the need for geneticists to know the ecology of the animal they are studying.

Much information might, therefore, be gained by a study of either the genetics of an ecologically well known animal or the ecology of a genetically well known animal. The latter course was adopted in this project.

The domestic species of Drosophila include the animal best known genetically, D. melanogaster. Ford (1964) states that D. melanogaster provides remarkably poor ecological material, for little is known of its larval and almost nothing of its imaginal ecology. This statement is slightly unfortunate because although Ford draws attention to the lack of information about the ecology of this species he suggests that there are intractable problems to be solved before the ecology can be studied. Carson (1965) suggests that the reason cosmopolitan, domestic Drosophila are little known in the wild is that naturalists prefer to study the endemic fauna to the detriment of the cosmopolitan species. Ecologists may also have a feeling that animals that live in association with human rubbish do not have a natural ecology. Certainly there are problems associated with studying adult Drosophila in the field as there are with any flying insect which has to be attracted to traps, but there are no special problems associated with the study of the larval ecology.

The characteristics that make the domestic species of Drosophila so useful as genetic tools, such as short generation time and ease of laboratory culture, have made them popular as material for laboratory ecology. Most of the early work was concerned with studies of population growth in D. melanogaster (Pearl and Parker, 1922; Bodenheimer, 1938; Robertson and Sang, 1944; Chiang and Hodson, 1950). These studies have provided much information on the effect of density on components of fitness. Sang (1950) reviews this work. More recent laboratory ecology has concentrated on competition between different species, (Merrell, 1951; Moore, 1952a; Miller, 1964; Barker and Podger, 1970). Much of this work has been reviewed by Ayala (1970) who has himself conducted many laboratory studies on competition in Drosophila.

The field ecologist working on domestic Drosophila has, then, a vast body of genetic and ecological information gained in the laboratory with which to interpret field data.

The Biology of Domestic Drosophila

Dobzhansky (1965) uses the terms domestic species and cosmopolitan species interchangeably when reviewing the population genetics of these species of *Drosophila*. These terms emphasise the two most noticeable features of the biology of these flies. The domestic species occur in or near human habitations and are virtually cosmopolitan in distribution, having been transported round the world with human aid. Patterson and Stone (1952) recognise eight species of *Drosophila* which they referred to as cosmopolitan or nearly so; these are *D. ananassae*, *D. busckii*, *D. funebris*, *D. hydei*, *D. immigrans*, *D. melanogaster*, *D. repleta* and *D. simulans*. Of these species *D. ananassae* is more or less absent from Europe (Basden, 1954) and *D. repleta* is rare in Britain, being absent from the extensive collections of Basden (1954) and Dyson-Hudson (Shorrocks, 1977). Another species, *D. subobscura* is a common woodland species in Britain (Shorrocks, 1975) but is often found in domestic habitats also (Basden, 1954; Shorrocks, 1974). The following seven species, then, are the common domestic species in Britain and are the subject of this thesis: *Drosophila busckii* Coquillet, *D. funebris* (Fabricius), *D. hydei* Sturtevant, *D. immigrans* Sturtevant, *D. melanogaster* Meigen, *D. simulans* Sturtevant and *D. subobscura* Collin.

The genus Drosophila is divided into eight subgenera by Patterson and Stone (1952). Some of these subgenera are subdivided into species groups and some of the species groups are further divided into species subgroups. Table 1.1 shows how the seven British domestic species are classified under this scheme. The domestic species belong to three subgenera; the subgenus Sophophora includes *D. melanogaster*, *D. simulans* and *D. subobscura*, the subgenus Drosophila includes *D. funebris*, *D. immigrans* and *D. hydei*, while *D. busckii* is the only species in the monotypic subgenus Dorsilopha. Only two of the domestic species, *D. melanogaster* and *D. simulans* share the same species group, these two being sibling species. In general, then, the domestic species do not form a taxonomic group, this way of life having evidently evolved independently several times.

Table 1.1 The classification of domestic species of Drosophila

Subgenus	Species group	Species sub-group	Species
Drosophila	funebris		D. funebris
"	immigrans		D. immigrans
"	repleta	hydei	D. hydei
Sophophora	melanogaster	melanogaster	D. melanogaster
"	"	"	D. simulans
"	obscura		D. subobscura
Dorsilopha			D. buscki

Though the domestic species are now distributed worldwide it is usually inferred that each species evolved in the geographical region presently inhabited by its closest relatives. The melanogaster subgroup, for instance, contains four known endemic African species, D. yakuba, D. teissieri, D. orena and D. erecta, so it is concluded that the melanogaster subgroup as a whole, including the cosmopolitan species, D. melanogaster and D. simulans, must have evolved in Africa (Tsacas and Lachaise, 1974). The two siblings may, of course, have separated after their common ancestor became cosmopolitan. That such a later separation is possible is shown by the case of D. mauritiana, a species very closely related to D. simulans and known only from the island of Mauritius (Tsacas and David, 1974). Dobzhansky (1965) considers that D. simulans might possibly be native in parts of Brazil where there is a case of this species being found in tropical rain forests far from human dwellings. There are no endemic relatives of D. simulans in this area, however, and so the evidence is slight. The funebris group of the subgenus Drosophila evolved in Nearctic North America (Patterson and Stone, 1952). Presumably this is where D. funebris itself evolved, though Dobzhansky (1965) states that it is one of the commonest species in and out of domestic habitats in Russia and so might be native there. D. hydei comes from a species group centred in central America (Patterson and Stone, 1952) and D. immigrans comes from an Oriental species group (Spencer, 1940; Patterson and Stone, 1952). D. buscki is the only species in its subgenus, Dorsilopha, but species very close to it exist in Southeast Asia where it may have originated (Throckmorton, 1975). The evidence is, then, that all the domestic species of Drosophila, apart from D. funebris, evolved in various parts of the tropics.

Carson (1965) has outlined two alternative characteristics that might account for the wide distribution of the domestic Drosophila. These species might be closely adapted to a specific niche that man has created and so be carried around the world; for instance, D. buzzatii is specialised to breed on cacti of the genus Opuntia and has been transported to all parts of the world where Opuntia

has spread as a weed. Alternatively, the domestic Drosophila might have achieved the genetic competence to exploit a wide series of environments. Dobzhansky (1965) states that it is tempting to suppose that the domestic species of Drosophila are more ecologically versatile than their wild relatives. The difficulty which this generalisation must meet, however, is that whereas domestic Drosophila are conspicuously successful in man modified habitats, they are rarely able to colonise natural habitats to which they are introduced by man.

Some workers, especially in temperate regions, have tried to explain the lack of success of the domestic species in the wild as being due to their poor low temperature tolerance. Spencer (1940), for instance, believes that D. immigrans overwinters indoors, gives rise to small spring populations, and may only reach woodland late in the summer. This view of the mechanism restricting the domestic species to domestic habitats is difficult to extend to tropical areas where the domestic species have no need to overwinter indoors. Lachaise (1974) found that in the Ivory Coast D. melanogaster and D. ananassae are localised in human settlements and plantations and only colonise the savanna when bush fires destroy the indigenous Drosophilidae. One interpretation of this finding would be that the domestic species are usually confined to human settlements by competition from the wild Drosophila. This may be a widespread phenomenon, accounting for the lack of success of domestic Drosophila in the wild, the world over.

Little systematic information is available about the feeding and breeding sites of domestic species of Drosophila. Carson (1965) has said that the study of the breeding sites of the cosmopolitan species of Drosophila has been a much neglected phase of the study of the ecology of Drosophila. He published a list of the breeding sites from which domestic Drosophila have been reared and concluded that they show great latitude of breeding site. Sturtevant (1921) classified the larvae of D. busckii and D. funebris as

general scavengers, feeding on rotten potatoes, excretement and stale formalinised meat etc. Most of the common species he described as breeding on decaying fruit, while D. hydei was intermediate between the two types. Shorrocks (1977) has emphasised the fundamental ecological division in Drosophila between those that use substrates undergoing alcoholic fermentation and those that use decaying substrates as breeding sites. Drosophila larvae rely on microorganisms for their nutrition within breeding sites. Fruits have a low pH which favours the growth of yeasts which are the common agents of alcoholic fermentation. Vegetables, on the other hand, undergo other forms of decay caused mainly by bacteria rather than yeasts (Jay, 1970). It may be, then, that D. busckii and D. funebris larvae specialise on sources of bacterial decay, usually vegetables, while fruit feeders such as D. melanogaster and D. simulans specialise on sites of alcoholic fermentation caused by yeasts. This generalisation seems to be supported by the list of breeding sites provided by Carson (1965).

One important aspect of the ecology of domestic species of Drosophila in temperate regions is the manner in which they survive the winter. In Basden's (1954) collections from Scotland none of the domestic species were trapped outdoors in January or February, and even in Patterson's (1943) collections from as far south as Texas the domestic species were very much reduced in winter. Most authors, quite reasonably, infer from evidence such as this that the domestic Drosophila suffer very high mortality in temperate regions during the winter (Spencer, 1950), but the subject is almost impossible to investigate because when temperatures are below the fly's flight threshold they will not appear in traps even if surviving well. Most workers believe that a small number of individuals can survive indoors or in other sheltered habitats. McKenzie (1975) found that D. melanogaster adults overwintered in cellars in a vineyard in Victoria, Australia. He suggested that the population was reconstructed in the spring by females that were inseminated before the winter. Ives (1970) found that in South Amherst, Massachusetts, where temperatures fall well below freezing in winter, D. melanogaster larvae overwintered in a rotten apple pile.

Since the domestic species have been distributed around the world in association with man, movement of individuals in this way may always be important in their ecology. Hunter (1968) has shown that, perhaps as an adaptation to this, the domestic species, D. melanogaster, D. hydei and D. immigrans have much better physiological tolerance of temperature changes than the more localised wild species, D. pseudoobscura, D. viracochi and D. willistoni. In temperate regions the numbers of domestic Drosophila imported artificially could be very significant compared to the numbers surviving from the previous season. David and Boquet (1975), however, have reviewed evidence, in D. melanogaster, of latitudinal clines in the polygenic quantitative traits, adult weight, female ovariole number and alcohol tolerance. The existence of these clines suggests that human transport does not mix the flies enough to produce a uniform genotypic composition. This means that it is possible to interpret the ecology of a population of domestic Drosophila as adaptations to its own local environment rather than to a generalised worldwide domestic habitat.

The possibility of this sort of interpretations is further enhanced by studies of the dispersal ability of domestic Drosophila, reviewed by Wallace (1966). He concluded that D. melanogaster, D. willistoni and D. funebris are restricted in their dispersion; ". . . 60% to 80% of individuals of these species collected at one spot may have their points of origin lying within a radius of 25 metres." D. pseudoobscura had a much faster dispersal rate. McKenzie (1974) also found low dispersion rates in D. melanogaster and D. simulans. It is tempting to suppose that all domestic species of Drosophila have low rates of dispersal as an adaptation to exploiting large, productive, but widely separated food sources such as fruit markets, rubbish dumps or tomato fields. Within such productive areas feeding and breeding sites can be found by the flies without wide dispersal, while transport between the sites can be accomplished by human agency, avoiding hazardous flights by the adult Drosophila.

There is, then, a reasonable body of knowledge about the general

biology, genetics and laboratory ecology of the domestic species of Drosophila and this provides a context for the field ecology to be studied in this project.

This project differs from many previous ecological investigations of Drosophila in two ways.

First, the ecology was studied using standard ecological techniques. Much Drosophila ecology has been carried out by population geneticists whose ecological methods have tended to be unorthodox. Dobzhansky and Wright (1943), for instance, investigated dispersion in D. pseudoobscura using not wild flies but mutant stocks. Begon et al (1975) pointed out that information on the density of Drosophila had never been sought by applying standard mark-release-recapture techniques. Many investigators have collected large quantities of data by trapping Drosophila or rearing them from breeding sites but have not carried out the sort of analysis that would occur to most ecologists. Shorrocks (1977) has gained much new information by reanalysing such collection data from Europe.

The second difference from most previous work is that in this project the emphasis is placed on the ecology of Drosophila in relation to their breeding sites. Carson (1971) has stated that Drosophilidae show most specificity in their choice of breeding sites. This is obviously an important facet of their ecology. Carson also concluded that a considerable amount of basic information is available in the literature. Unfortunately much of this information is anecdotal and based on single observations, e.g. Gordon (1942). This is probably because the breeding sites of wild species of Drosophila are scattered and difficult to find (Carson, 1951). The domestic species, on the other hand, whose breeding sites are readily found, provide ideal subjects for quantitative investigations.

The Study Sites

The main study area was Pontefract Lane wholesale fruit and vegetable market, situated 4km. south east of the centre of Leeds. A plan of

the site is shown in Figure 1.1. The market buildings, shaded in the figure, stand in open paved grounds, about 65,000 m^2 in area. The markets consist of five buildings; one on its own is the frozen food market while the other four comprise the fresh fruit and vegetable market and are connected by covered ways. In Fig 1.1 the covered ways and awnings round the buildings are indicated by broken lines. Each building is 65m long and 34m wide.

Market trading carries on each day until about 1 p.m., after which the area is swept mechanically and by hand to remove most of the considerable quantities of fruit and vegetables left on the ground. Most of the open space around the buildings and the interiors are swept fairly thoroughly. The sweepings are removed daily so the Drosophila have to exploit those fruits and vegetables that are consistently missed by the sweepers. Frequently whole lorry loads of fruit or vegetables are found to be unsaleable and are then piled in their boxes under the awnings, where they may stay for a month or more. Between these piles of boxes sweeping is much less thorough and many individual items of discarded fruits and vegetables are regularly missed in the cleaning up.

The market provides a wide variety of potential Drosophila breeding sites. There is more trade in fruit than in vegetables at the market and this is reflected in the available breeding sites.

Pontefract Lane market is probably fairly isolated from other sources of domestic Drosophila. It stands in an open industrial estate. To the north are extensive railway sidings, to the east is open waste ground, to the south an engineering works and to the west an abattoir and meat market. The abbatoir has some livestock accommodation which might provide a source of D. funebris and D. busckii (Basden, 1954), but the openness of the area ensures that there will be little active migration of Drosophila into or out of the market.

A small amount of field work was also carried out at Kirkgate market, a retail market in the centre of Leeds. The market is in

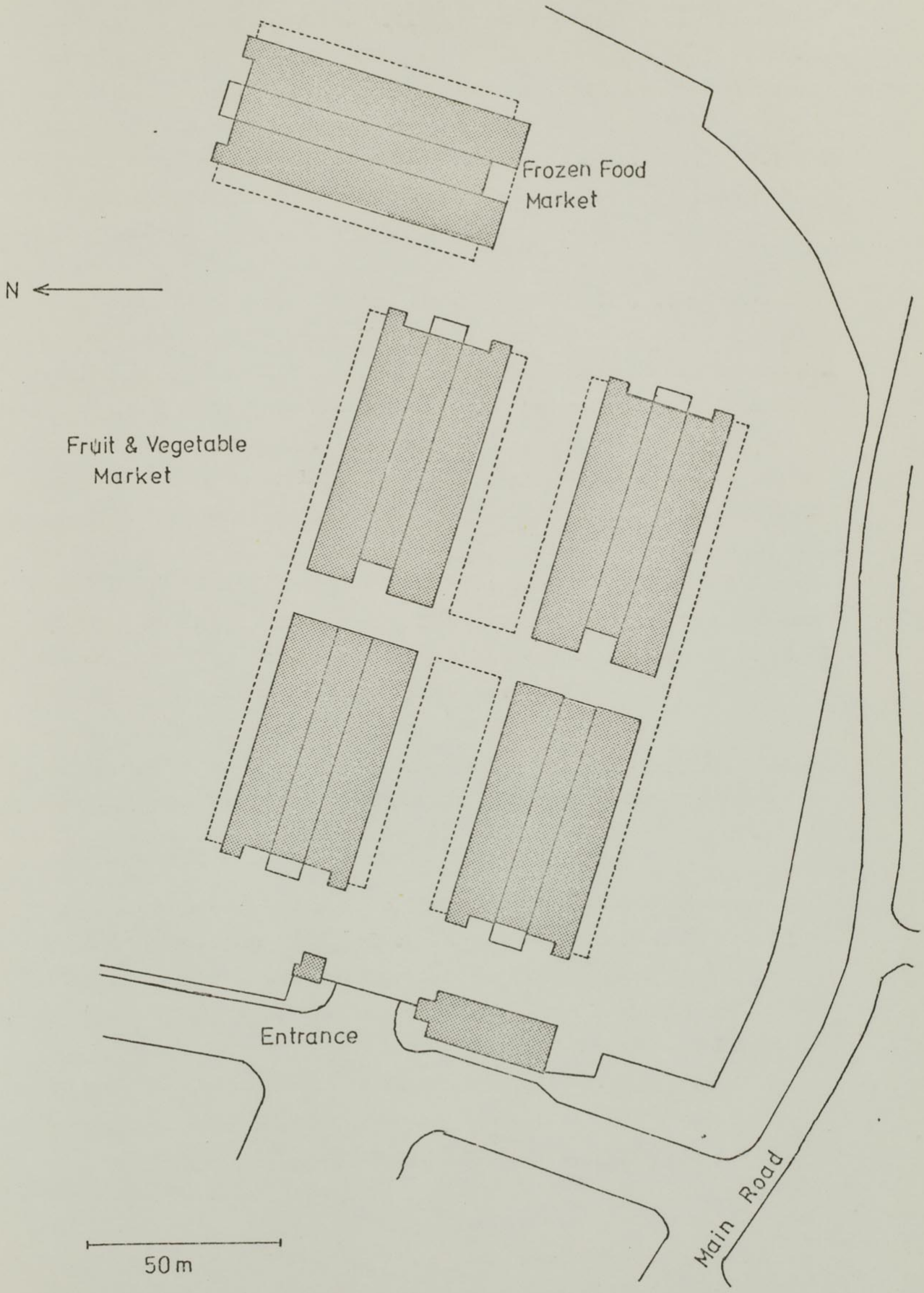


Fig 1.1 Pontefract Lane fruit and vegetable market

two sections, an indoor part and an outdoor part. Both sections include fruit and vegetable stalls.

Species Identification

The Drosophila species were identified using the keys provided by Basden (1954), Frydenberg (1956), Fonseca (1965), and Shorrocks (1972).

The only difficulty experienced was in the identification of D. melanogaster and D. simulans. Parsons (1975) states that the only satisfactory morphological mode of separation between the two species is based on differences in the external male genitalia. The posterior process of the genital tergite is much larger in D. simulans than in D. melanogaster. Moore (1952b) considers that there is no reliable rapid means of distinguishing the females.

Some workers (Patterson, 1943; Pipkin, 1952, 1965) have not tried to separate the females, others (Tantawy and Mallah, 1961; McKenzie and Parsons, 1972) have identified the females from genital differences in their male progeny. Basden (1954), however, uses morphological characters to distinguish the females of the two species, although he admits that "some female simulans were doubtless determined as melanogaster during the early stages of the investigation." The main character used by Basden to separate the species was cheek width. In D. melanogaster the width of the cheek from the lowest point of the eye to the mouth border is at least as broad as the widest part of the first tibia. In D. simulans the cheek is narrower.

In this study the number of flies to be identified precluded the rearing of male offspring to separate the melanogaster group females. During 1975 the females were not distinguished but in 1976 cheek width was used as the morphological criterion for separating the species.

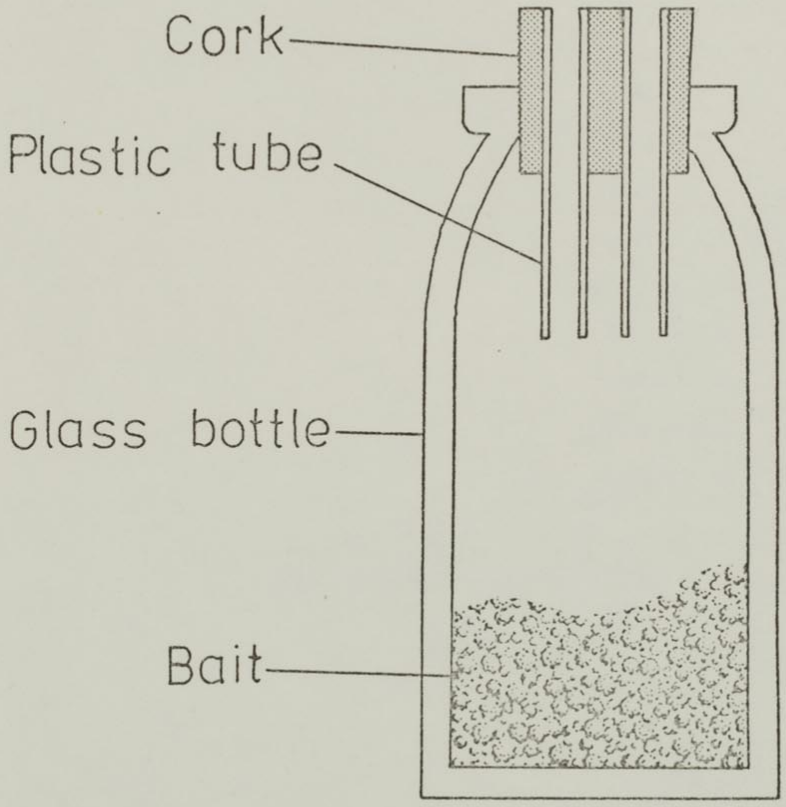


Fig 2.1 A bottle trap

CHAPTER 2

DROSOPHILA COLLECTIONS

Introduction

Adult Drosophila were collected in various ways during this study. The most usual methods involved attracting the flies to fermenting or rotting baits designed to simulate their natural feeding or breeding sites. Most ecological studies of Drosophila have used baits to attract the adults, but this method suffers serious shortcomings which must be discussed before the results are examined.

In this study baits were exposed either within bottle traps (Basden, 1954; Shorrocks, 1972) or as open bait. The bottle trap (Fig. 2.1) consisted of a $\frac{1}{3}$-pint glass bottle containing about 50ml of bait and stoppered with a cork. The cork was bored with two holes, each taking a 5cm length of plastic tubing, having an internal bore of 6mm, and projecting about 3cm inside the bottle. Drosophila, attracted by the bait, enter the trap via the two plastic tubes and try to escape by climbing up the glass sides of the bottle. They rarely encounter the openings in the plastic tubes and so they are trapped. Open bait was exposed in plastic sandwich boxes (10cm x 10cm x 7.5cm). The bait was spread over the floor of the box in a layer about 1cm thick and was covered with a sheet of absorbent tissue paper to prevent flies from sticking to it. For trapping, the box was left with its lid half on for a period and this was deftly replaced to trap any flies that had entered. Carbon dioxide was introduced through a small hole in the lid using a 'Sparklets Corkmaster' and the anaesthetised flies were removed with an aspirator.

The two methods of collecting with baits were used for different purposes. Open baits were exposed for short periods, usually two hours, and would collect large numbers of Drosophila compared to the bottle traps. The numbers of flies collected, the species proportions and sex ratios would, however, reflect the environmental conditions during the two hour trapping period as well as the true

population values. Since environmental conditions can vary greatly between such short periods open bait could not be used to provide numerical population data. Bottle traps, on the other hand, were exposed for much longer periods, one or two weeks, and so were less subject to short term environmental fluctuations. Bottle traps gave a continuous trapping record, only needing to be serviced once a week. Changes in the environment do, of course, occur from week to week and these must affect the catches of the bottle traps. Temperature, wind speed and humidity all affect the activity of Drosophila and so must affect the size of the bottle trap collections, the species proportions and sex ratios. Different baits and baits of different ages attract different biased samples of the Drosophila population and so there is an accumulation of sources of error.

It is difficult to estimate how much bias is attached to trap collections but there is some evidence that bottle traps give a fairly good estimate of the sex ratio of some flies in the wild. Basden (1954) noted that open baits produced a preponderance of males, especially in D. subobscura, whereas bottle traps gave a majority of females. Shorrocks (1975) also obtained an excess of female D. subobscura in bottle traps in Adel Dam, Leeds. Begon (1976) in a mark-release-recapture study of D. subobscura in Adel Dam found that there was a true excess of females in this population and the bottle traps of Shorrocks (1975) gave good estimates of the sex ratio. Similar data for different species and in different localities would have to be obtained before this could be said to be a general result.

It is safest, then, to treat trapping data with some caution and the results that follow are therefore presented without elaborate analysis.

Methods

Between 27.9.74 and 26.2.76 Drosophila were collected using open bait. Until June 1975 the collections were all made at Kirkgate market, but later collections were mostly made at Pontefract Lane,

where traps were disturbed less frequently. The bait used was a mixture of malt bait (Lakovaara et al, 1969) and chopped banana. On each trapping occasion ten traps were exposed for two hours. At Kirkgate the traps were exposed along a balcony within the market building and at Pontefract Lane they were exposed on the ground outside the buildings, but protected from the rain by the awnings.

From 29.4.76 to 9.12.76 bottle traps were used at Pontefract Lane. The bottles were exposed in units of four; two bottles contained chopped banana fermented for one week with baker's yeast, one contained malt bait (Lakovaara et al, 1969) prepared the previous week and one contained fresh chopped tomatoes. Four of these units were used, one at the entrance to each market building at ground level. The bottles were left out for seven days and then replaced by new ones.

Results and Discussion

The numbers of Drosophila of each species taken at every trapping occasion are given in Table 2.1 for open traps and in Table 2.2 for bottle traps. A total of 14,074 flies were captured, made up of 75% D. melanogaster and D. simulans, 11% D. immigrans, 6% D. subobscura, 5% D. hydei, 2% D. funebris and 1% D. busckii.

SEASON

Figure 2.2 shows the numbers of Drosophila caught in bottle traps each week. There are three periods when the numbers of flies trapped reaches a peak. The first is in mid June, the second in late July and the third in late September. Temperature records for the same period are given in Figure 3.4. If the peaks are merely at periods when the flies are most active then they should also be the periods of highest temperatures. In fact the peaks are not associated with high temperatures and so might reflect a genuine increase in the abundance of the flies.

Table 2.1 Collection data from open traps

Date	Site	D. melanogaster & D. simulans		D. melanogaster	D. simulans	D. subobscura		D. hydei		D. funebris		D. busckii		D. immigrans		Total
		+o		♂	♂	+o	♂	+o	♂	+o	♂	+o	♂	+o	♂	
27. 9.74	Kirkgate	4		1												5
1.10.74	"	40		19						1	4	1		1	2	68
7.10.74	"	23		7								1				31
23.10.74	"	2														2
25.10.74	"	1				1				1	2					5
28.10.74	"	2		2						1						5
30.10.74	"	1		2												3
6.11.74	"	3		5							4					12
7.11.74	"	1														1
20.11.74	"					1										1
3.12.74	"	2												1	1	4
4.12.74	"															0
22. 1.75	"															0
20. 3.75	"															0
24. 4.75	"															0
30. 4.75	"						1									1
7. 5.75	"															0
20. 5.75	"	2					1									3
22. 5.75	"	3		2			3									8
23. 5.75	"	5		2		2	7									16
3. 6.75	"					1	2				1					4
10. 6.75	"	11		17		9	5			2	1					45
13. 6.75	Pontefract L.	6		7		2				1						16
23. 6.75	Kirkgate	2				1										3
30. 6.75	Pontefract L.	215		179	19	11	2	15	20		2		1	1		465
11. 7.75	"	88		54	9	11	4							5	20	191
17. 7.75	Kirkgate	116		42	3	16	5	2	1	1	3			9	2	200
22. 7.75	Pontefract L.	69		37	10	7	2	4		6	17			2	13	167
29. 7.75	"	74		58	6	11	7	4	11	4	4		4	8	22	213
5. 8.75	"	114		105	2	17	5	2	6	2	3	1	1	3	4	265
12. 8.75	"	12		25	1	23	15	21	23	2	2	1		8	11	144
18. 8.75	Kirkgate	78		30	2	10	1	1		2	1	1	2	17	11	156
1. 9.75	Pontefract L.	836		749	7	49	44	25	67	11	22	2	3	28	83	1926
24. 9.75	Kirkgate	89		126	1	5	1	14	8	8	7	2		2	3	266
29. 9.75	Pontefract L.	27		36	1	4	12	2	1	1	1			8		93
7.10.75	"	11		13		29	11			1		1			1	67

Table 2.1 continued

Date	Site	*D. melanogaster* & *D. simulans* ♀	*D. melanogaster* ♂	*D. simulans* ♂	*D. subobscura* ♀	*D. subobscura* ♂	*D. hydei* ♀	*D. hydei* ♂	*D. funebris* ♀	*D. funebris* ♂	*D. buscki* ♀	*D. buscki* ♂	*D. immigrans* ♀	*D. immigrans* ♂	Total
14.10.75	Pontefract L.	1	1		3	2								1	8
15.10.75	"	3	3		7	3			4	4			1		25
21.10.75	Kirkgate	54	39	1	1		1	7	4	8			4		119
6.11.75	Pontefract L.				2	1									3
7.11.75	Kirkgate	3				1									4
11.11.75	"	8	6			1	2	1	5	4				1	28
21.11.75	Pontefract L.														0
3.12.75	Kirkgate														0
8. 1.76															0
26. 2.76															0
Total		1906	1567	62	227	124	93	145	57	90	10	11	94	187	4573

Fig 2.2 Bottle trap collections - the numbers of each species of Drosophila caught each week

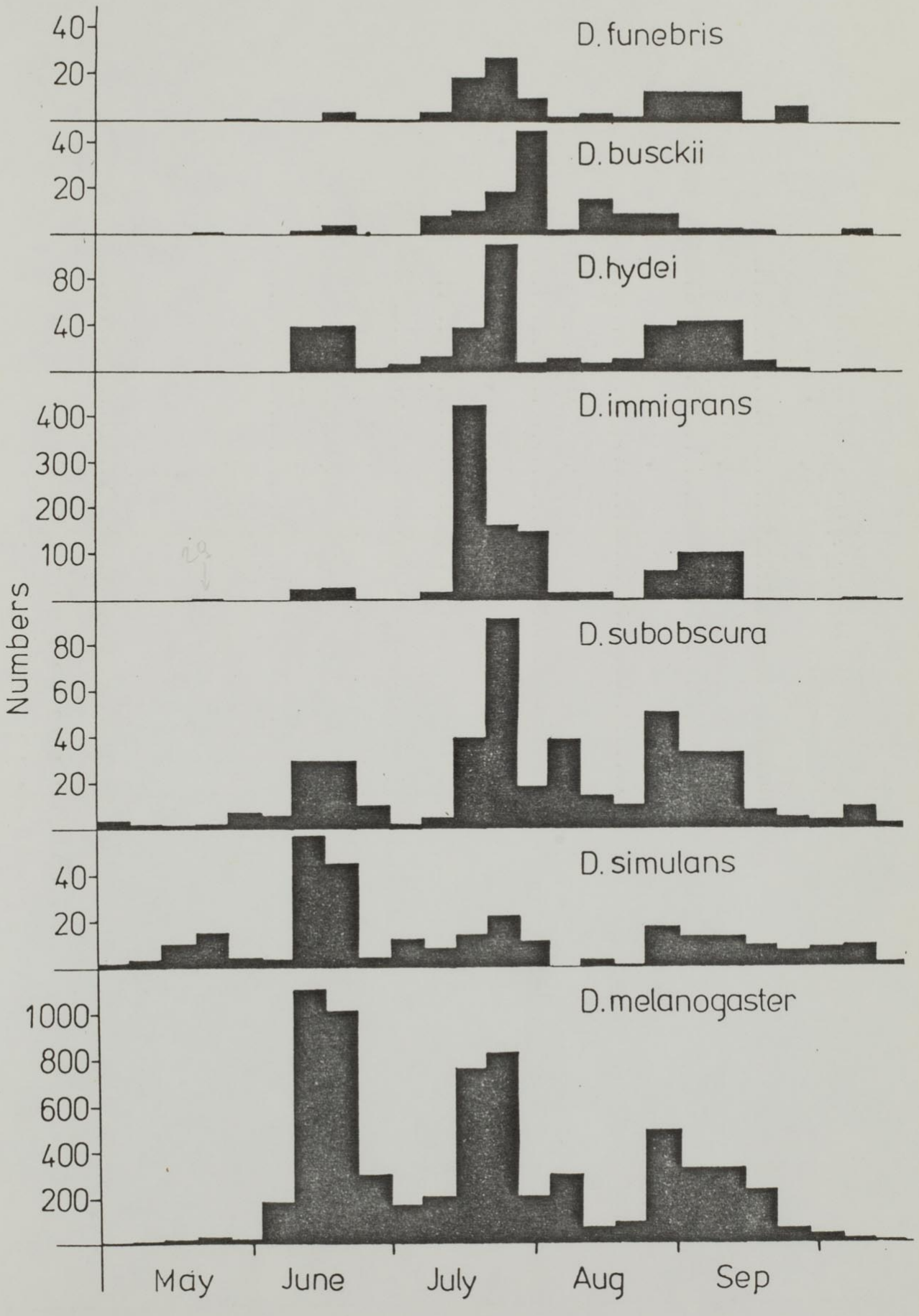


Table 2.2 Collection data from bottle traps

Week ending	D. melanogaster ♀	D. melanogaster ♂	D. simulans ♀	D. simulans ♂	D. subobscura ♀	D. subobscura ♂	D. hydei ♀	D. hydei ♂	D. funebris ♀	D. funebris ♂	D. buscki ♀	D. buscki ♂	D. immigrans ♀	D. immigrans ♂	Total
5. 5.76	2	2		1	3										8
12. 5.76	7	3	1	2	2										15
19. 5.76	12	9	5	5	1										32
26. 5.76	19	12	8	7	2		1				1		2		52
2. 6.76	15	10	2	2	7				1						37
9. 6.76	135	48	1	3	9		1								197
16. 6.76	780	320	28	29	27	3	29	14				2	8	15	1255
23. 6.76	736	277	15	30	28	2	24	17	3	1	2	2	11	16	1164
30. 6.76	196	96		4	8	2	2	1	1				1	1	312
7. 7.76	124	49	7	5	1		6	1		1			2		196
14. 7.76	138	68	3	5	4	1	11	3	4		6	2	14	4	263
21. 7.76	421	341	4	10	38	4	24	15	9	10	3	7	140	292	1318
28. 7.76	399	434	5	17	79	13	66	45	16	12	12	7	58	107	1270
4. 8.76	99	102	5	8	16	2	4	4	5	5	13	33	41	110	447
11. 8.76	157	146			36	3	8	5	3	1	4		2	15	380
18. 8.76	41	32	1	2	14	1	7		6	1	5	10	14	2	136
25. 8.76	55	40			10	1	10	1	4	1	4	5	2	2	135
1. 9.76	311	180	7	10	42	9	27	13	3	10	5	4	23	41	685
15. 9.76	385	277	10	27	54	14	30	59	8	18	1	5	70	136	1094
22. 9.76	135	100	7	2	9		7	3	1			2		1	267
29. 9.76	39	23	2	5	6		3		5	2			1		86
6.10.76	25	19	2	7	5			1						1	60
13.10.76	16	7	4	6	11		1	1				3	1	3	53
20.10.76	3	1		2	3		1							1	11
27.10.76				2	6							1	1		10
3.11.76	1							1		1			1	1	5
10.11.76		2	1		1			1							5
17.11.76					1										1
24.11.76					1										1
1.12.76					2	2			1						5
9.12.76					1										1
22.12.76															0
12. 1.77															0
Total	4251	2598	118	191	427	57	262	185	70	63	56	83	392	748	9501

Three species were present in the bottle traps at the end of April, D. melanogaster, D. simulans and D. subobscura. The other species were not found in traps until the end of May. D. melanogaster and D. simulans reached their highest levels during the first peak in mid June and tended to decline during the rest of the season. This seasonal pattern matches that shown by D. melanogaster in Southern England in Dyson-Hudson's (1954) trapping survey. The other species, which, apart from D. subobscura, had appeared in traps later, reached their highest levels during the second peak at the end of July. Most species disappeared from traps at the beginning of November but a few individuals of D. subobscura were caught in December.

Figure 2.3 shows, for each species, its percentage contribution to the total population throughout the season. The results of open trapping in 1975 are shown as well as the bottle traps in 1976. The 1975 results confirm that D. melanogaster, D. simulans and D. subobscura appear in traps before the other species. D. melanogaster is the dominant species in trap collections during most of the season, but at the beginning and end of each season D. subobscura tends to make up a larger proportion of the population. This might be expected of the native British species, adapted to lower temperatures than the cosmopolitan species. Shorrocks (1975) in his trapping records of D. subobscura in a woodland near Leeds found that the numbers in traps are at a low level until June when they begin to rise and then remain high until late January with a peak in late autumn. At Pontefract Lane the numbers of D. subobscura were on the decline by autumn and this species had more or less disappeared by the beginning of January. This difference might be explained by the fact that in woodland, in autumn, there is a flush of fruit and fungi to provide breeding sites, while at Pontefract Lane decaying fruit becomes much less plentiful in autumn after the 'soft-fruit' season is over.

SEX RATIO

Table 2.3 gives the overall sex ratio of each species of Drosophila

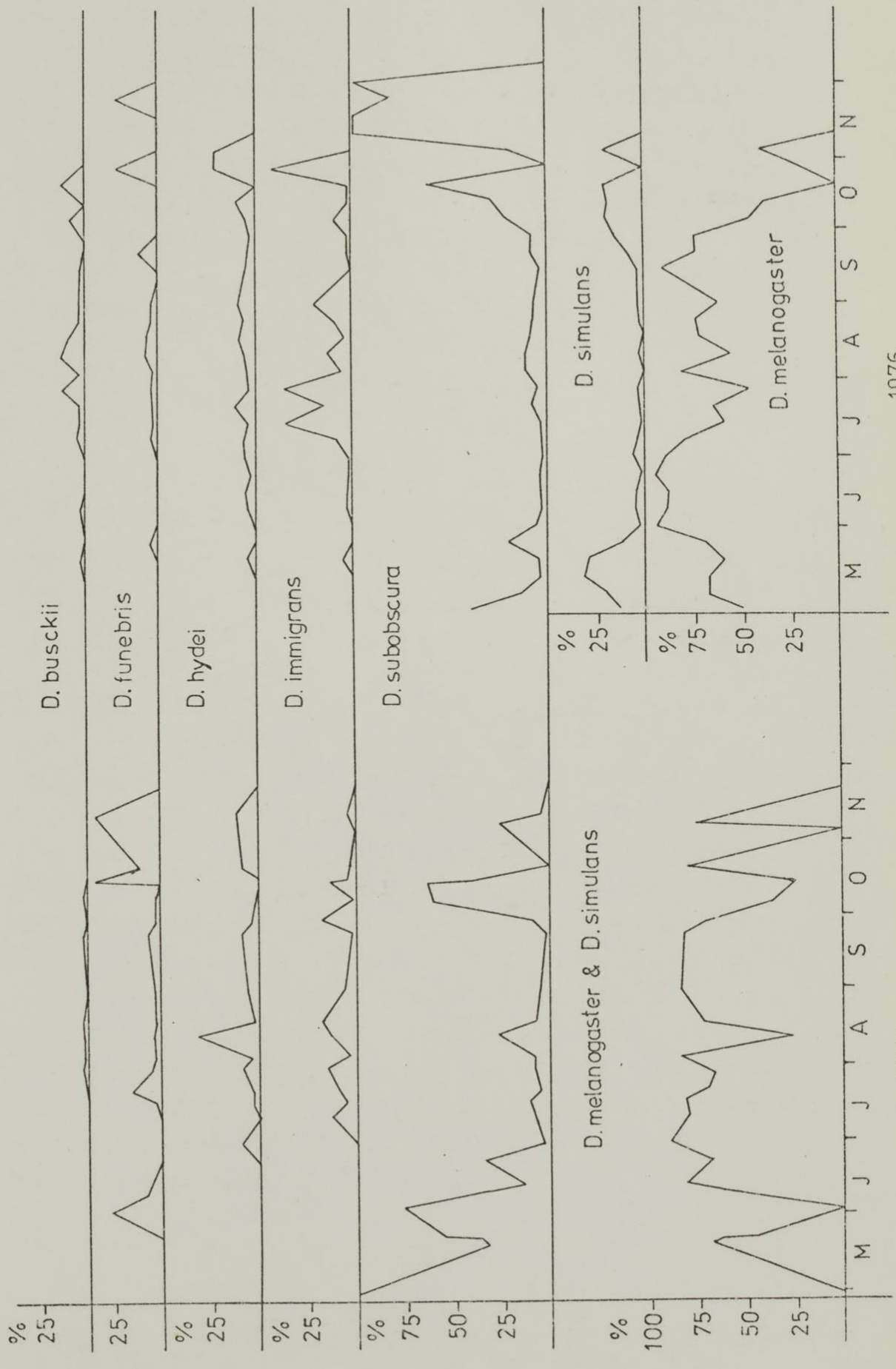


Fig 2.3 Seasonal changes in the percentage contribution of each species of Drosophila to the total collection

Table 2.3 Sex ratios expressed as percentage of females

Species	Open traps	Bottle traps
D. melanogaster)	53.9% p<0.01	62.1% p<0.01
D. simulans)		38.2% p<0.01
D. subobscura	36.5% p<0.01	88.2% p<0.01
D. immigrans	43.3% p<0.01	34.4% p<0.01
D. hydei	39.1% p<0.01	58.6% p<0.01
D. funebris	38.8% p<0.01	52.6% n.s
D busckii	47.6% n.s	40.3% p<0.05

The probability levels refer to χ^2 tests for departure from 1:1 sex ratio

from open traps and from bottle traps. Though neither necessarily reflects the true sex ratio some interesting patterns emerge. As also noted by Basden (1954), D. subobscura shows a significant excess of females from bottle traps but of males from open traps. Two other species, D. hydei and D. funebris show the same pattern while all the other species are consistent from bottle to open traps. D. immigrans and D. busckii have a consistent excess of males while D. melanogaster has an excess of females. None of the species have an excess of males in bottle traps and an excess of females in open traps. This may reflect a difference in behaviour between the sexes common to all the species.

TRAP SITES

Table 2.4 shows the frequency of each species of Drosophila at each of the four bottle trapping sites at Pontefract Lane. There is evidently an uneven distribution of flies among the sites. For each species an index of dispersion (Southwood, 1966) was calculated.

$$\chi^2 = \frac{s^2(N-1)}{\bar{x}}$$

s^2 = variance, N = number of trap sites, and $\bar{x}$ = mean number of flies

Every species had a significantly large value of χ^2 indicating an aggregated pattern. The χ^2 for heterogeneity between species was significant, showing that different species have some difference in their pattern of aggregation but this χ^2 is very much smaller than the total χ^2 which suggests that the pattern of aggregation is broadly similar for each species. In fact trap site 3 is the most popular for every species, site 2 is usually the next most popular while sites 1 and 4 are less attractive.

For D. melanogaster changes in the aggregation during the season were investigated using the index of dispersion. In this case the total χ^2 equals 4026.1 ($p < 0.01$) and the heterogeneity χ^2 equals 1795.9 ($p < 0.01$). This large and significant heterogeneity between weeks shows that the preferences of this species are not entirely

Table 2.4 Numbers collected at each bottle trap site

Species	Trap Sites 1	2	3	4	Total	Index of Dispersion χ^2	
D. melanogaster	921	2036	3203	689	6849	2336.3	$p<0.01$
D. simulans	77	68	133	31	309	69.0	$p<0.01$
D. subobscura	72	128	180	104	484	51.4	$p<0.01$
D. immigrans	54	253	790	43	1140	1291.1	$p<0.01$
D. hydei	51	143	179	74	447	95.0	$p<0.01$
D. funebris	13	22	87	11	133	117.9	$p<0.01$
D. busckii	18	36	74	11	139	68.7	$p<0.01$
Total	1206	2686	4646	963	9501		

Total χ^2 4029.4, d.f. = 21, $p<0.01$
Pooled χ^2 3626.8, d.f. = 3, $p<0.01$
Heterogeneity χ^2 402.6, d.f. = 18, $p<0.01$

consistent over the season, but even so site 3 was the preferred site in the majority of weeks.

The results suggest that the aggregation is due to a preference for certain sites rather than to mutual attraction of the flies. No obvious differences between the sites could be used to explain this preference. The most popular sites, 3 and 2, are both on the east side of the market and would probably be more sheltered from the prevailing wind than the less popular sites, 1 and 4. Any other explanation of the habitat preferences, however, would be just as plausible without further information.

CHAPTER 3

BREEDING SITE SPECIFICITY

Introduction

Carson (1971) has suggested that 'the major specificity of the ecology of Drosophila relates to the niche in which the female of the species deposits her eggs'. Unfortunately statements about the unspecialised use of breeding sites by the domestic species have been based on the range of food items used rather than their frequency of use (Shorrocks, 1977). This chapter describes how quantitative data were obtained and analysed.

The importance of different niche dimensions was determined by means of an analysis of species diversity (Levins, 1968; Shorrocks, 1975), a technique analagous to analysis of variance. Allan (1975) has advocated the use of the Shannon and Weaver (1949) diversity index (H') in analyses of this kind because it is unaffected by sample size. Estimates of H' are biased if based on samples of the total population (Pielou, 1966), but this bias can be corrected if the number of species in the population is known. In the case of the domestic species of Drosophila at Pontefract Lane the total number of species is known with some certainty and so the Shannon and Weaver index was used with the correction. These formulae are explained with the analysis.

In an analysis of diversity such as this, the total diversity is determined from the total number of flies obtained throughout the investigation. If the Drosophila species partition a niche dimension, such as season, then the average diversity calculated for each month will be less than the total diversity because the species proportions are less even. The difference between this within-month diversity and the total is the between months diversity. Its magnitude is a measure of the importance of season in the ecological separation of the Drosophila species. This analysis can be extended to cope with several niche dimensions in order to determine their relative importance.

Methods

Each week from 28.4.76 to 27.10.76 a sample of discarded fruits and vegetables from Pontefract Lane was brought back to the laboratory. The interiors of the market buildings were not sampled because regular access was difficult; therefore, the sampling was confined to the open space within 20m of the buildings. Random sampling of the breeding sites was impracticable owing to the large amount of material, so a representative sample was achieved by bringing in at least one item of each fruit or vegetable found, and, in the case of the more common species, several items in different stages of decay. When the collection was returned to the laboratory the itemswere placed separately in glass jars with the tops covered with nylon fabric. The jars were then placed in an outdoor insectary and were examined at least three times a week. Any emerged flies were removed and identified.

Results

A total of 437 potential breeding sites were investigated, of which 180 yielded *Drosophila*. The numbers of *Drosophila* emerging from each species of breeding site are shown in Table 3.1. In Table 3.2 the emergences are classified according to the month in which the breeding site was brought into the laboratory.

Niche Dimensions

The relative importance of different breeding sites and seasonal changes to the community structure was investigated by partitioning the species diversity (Levins, 1968; Shorrocks, 1975). Diversity was measured using the Shannon and Weaver (1949) formula,

$$H' = - \sum_{i=1}^{n} p_i \ln p_i$$

where p_i is the frequency of species i. If a component of diversity, j (e.g. season), is divided into n categories (e.g. months) then the between category contribution to diversity is equal to the total diversity minus the within or mean category diversity.

Table 3.1 Numbers of each Drosophila species emerging from each species of breeding site

Breeding Sites	D. busckii	D. funebris	D. hydei	D. immigrans	D. melanogaster	D. simulans	D. subobscura	Total flies	Number of breeding sites
Apple Malus pumila	1		1	6	1429	290	162	1889	75
Apricot Prunus armeniaca					51	20		71	5
Aubergine Solanum melongena				20				20	5
Banana Musa sp.				17	237	65	35	354	27
Cabbage Brassica oleracea	1	1	2					4	1
Carrot Daucus carota				7	3	1		11	4
Cauliflower Brassica oleracea	74							74	4
Celery Apium graviolens	1	4						5	3
Courgette Curcubita pepo	13			12				25	4
Cucumber Cucumis sativa		1		2				3	5
Grapefruit Citrus paradisi			14	75	490	2	28	609	15
Lemon Citrus limon	4	7	26	60	218	7	14	336	32
Lettuce Lactuca sativa	41		33	47			3	124	5
Mango Mangifera indica			11		3			14	1
Marrow Curcubita pepo						3		3	2
Melon Cucumis melo	15		124	39	97	4		279	15

Table 3.1 continued

Breeding Sites	D. busckii	D. funebris	D. hydei	D. immigrans	D. melanogaster	D. simulans	D. subobscura	Total flies	Number of breeding sites
Onion Allium cepa				29	5	32	13	79	12
Orange Citrus aurantium	1	2	35	151	789	73	31	1082	59
Peach Prunus persica			1	27	606	64	5	703	31
Pear Pyrus communis					23	65	9	97	22
Plum Prunus domestica				7	315	62	43	427	47
Potato Solanum tuberosum	24							24	9
Strawberry Fragaria sp.					4			4	6
Tomato Solanum lycopersicum			17	87	127	32	30	293	47
Yam Dioscorea sp.			131		163			294	1
Total	175	15	395	586	4560	720	373	6824	437

Table 3.2 Numbers of each Drosophila species emerging from all breeding sites collected each month

Month	D. busckii	D. funebris	D. hydei	D. immigrans	D. melanogaster	D. simulans	D. subobscura	Total flies	Number of breeding sites
April	0	0	0	0	0	0	0	0	14
May	24	0	0	0	262	39	3	328	48
June	76	4	29	28	1974	244	61	2416	83
July	73	1	259	362	815	129	57	1696	77
August	2	5	89	65	713	199	70	1143	83
September	0	5	18	122	796	109	25	1075	75
October	0	0	0	9	0	0	157	166	57
Total	175	15	395	586	4560	720	373	6824	437

$$H'_{between} = H'_{total} - \frac{1}{n}\sum_{j=1}^{n} H'_n = \frac{1}{n}\sum_{j=1}^{n}(H'_{total} - H'_n)$$

When dealing with individual breeding site items as categories, p_i was known and the Shannon and Weaver formula could be used. For other components of diversity, such as breeding site species or season, p_i could only be estimated from a sample. In these circumstances a modified formula (Hutcheson, 1970) was used,

$$H' = -\sum_{i=1}^{n} p_i \ln p_i + (s-1)/2N$$

where p_i is the proportion of species i in the sample, s is the number of species being sampled, and N is the sample size.

Since both between and within category diversities are means, standard errors of these means can be computed. In order to use these standard errors to estimate the significance of components of diversity we need to know the distribution of H'. Bowman et al (1971) have shown theoretically that the distribution of H' is asymptotically normal and Heip and Engels (1974) have demonstrated empirically that the diversities of samples of copepods as measured by H' are normally distributed.

Table 3.3 shows the analysis for niche components of Drosophila species. The smallest pure component was between months, which was significantly smaller than the within breeding sites component at the 5% level ($t = 2.3$) and was also smaller than the total between breeding sites component at the 1% level ($t = 4.7$). Partitioning of the season is evidently less important in the community than partitioning of breeding sites.

The total between breeding site diversity is made up of a larger component due to partitioning of breeding site species and a smaller component due to the partitioning of different items of the same species and the difference between them is not significant. There are, then, differences between the items, possibly in the state of decay, as well as differences between the species, which lead to exploitation by a range of Drosophila species.

Table 3.3 Niche analysis for *Drosophila* emergences

Niche Component	H'	95% Confidence limits
Within breeding site items	0.38	0.33 - 0.43
Between breeding site items, within species	0.23	0.17 - 0.28
Between breeding site species	0.37	0.25 - 0.49
Total between breeding sites	0.60	0.39 - 0.80
Between months	0.22	0.14 - 0.30
Apparent interaction (breeding sites and months)-	0.05	
Total	1.15	

The within-breeding site component of diversity is a measure of coexistence. It makes a significant contribution to the total Drosophila species diversity, indicating that partitioning of the breeding sites is not rigorous enough to entirely separate the species.

The term labelled apparent interaction in Table 3.3 is the sum of two terms, the real redundancy and the real interaction between season and breeding site. The magnitude of these two terms cannot be determined in this type of analysis. The real redundancy is a positive term that measures the non-orthogonality of dimensions and the real interaction is a negative term that measures the extra diversity accounted for by taking both dimensions together. Real redundancy in this analysis would mean that different breeding sites were found in different months. Real interaction would mean that the Drosophila species were using different breeding sites in different months. The sum of the two terms in this case is negative and so there is a small apparent interaction. If the sum were positive there would be apparent redundancy.

The magnitude of the real redundancy can be estimated by carrying out a diversity analysis on breeding site species in which the between months component of diversity is a measure of non-orthogonality. When this was done the total breeding site species diversity was 2.72 of which only 0.07 or 2.5% was between months. Thus most breeding sites occur in all months and the two dimensions are effectively orthogonal. Since the real redundancy is very small and the apparent interaction in Table 3.3 is very small then the real interaction must also be small. The Drosophila species do not then change their breeding sites significantly during the season.

Breeding Sites

The breeding sites were compared with respect to Drosophila species emerging using Raabe's percentage similarity (Southwood, 1966). Percentages for each breeding site species were weighted according

to the number of Drosophila emerging and combined to give the dendrogram in Figure 3.1.

There are two main groups of breeding sites revealed by the analysis, a group of vegetables (lettuce - celery in Fig. 3.1) and a group containing all the fruits but also some vegetables (apple - onion). Within the second group some taxonomically related breeding sites are closely associated in the analysis. The three Prunus species plum, peach and apricot are very similar in their Drosophila fauna as are the three Citrus species, lemon, orange and grapefruit. The second group (apple - onion) can be divided again into a group of nine closely associated fruits (apple - strawberry) and a group of mostly vegetable-like breeding sites (tomato - onion) which do not form a group in the analysis but will be considered separately. The justification for this is that none of these vegetable-like breeding sites seem to undergo the alcoholic fermentation characteristic of fruits. Fruits have a low pH that favours the growth of yeasts rather than the bacteria that are the common spoilage agents of vegetables. Pears are the only fruits that commonly undergo bacterial spoilage and these are associated with vegetable-like breeding sites in the analysis (Jay, 1970). The breeding sites are divided, then, into three groups; fruits (apple - strawberry), vegetables (lettuce - celery) and an intermediate group (tomato - onion). D. funebris is excluded from the following analyses because too few data were available.

Figure 3.2 is a histogram showing the proportion of each Drosophila species emerging from the three different breeding site groups. It appears that D. melanogaster, D. simulans and D. subobscura are specialists on fruit, D. busckii is a specialist on vegetables while D. immigrans and D. hydei are intermediate.

The degrees of specialisation of the species were examined in more detail by computing their niche breadths on breeding sites. The niche breadths were measured using a derivation of Simpson's index (Levins, 1968; Shorrocks, 1974).

$$B_i = 1/n \sum_{n=1}^{n} p_{ih}^2$$

Fig 3.1 Breeding sites clustered according to the percent similarity of Drosophila emerging

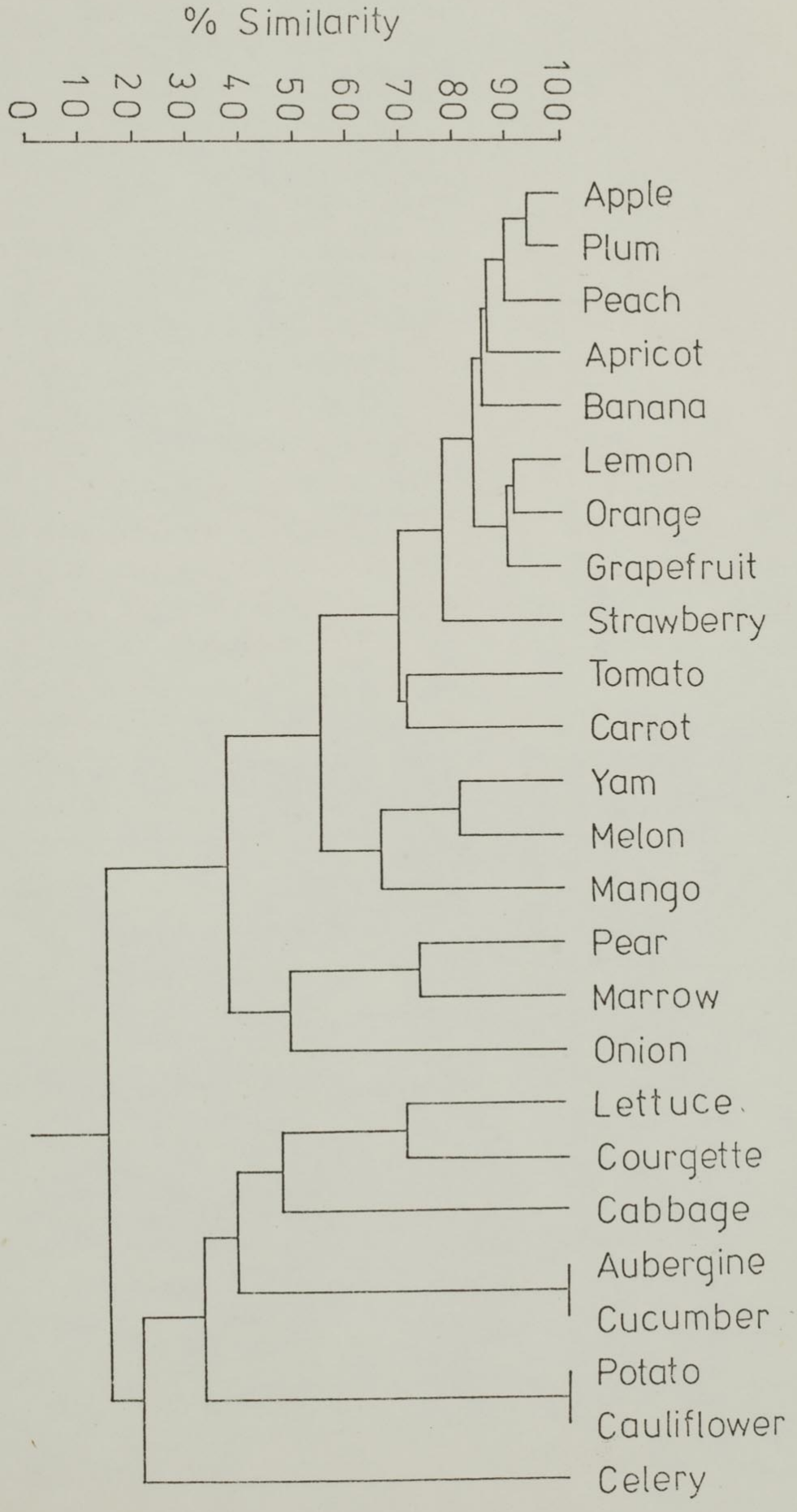
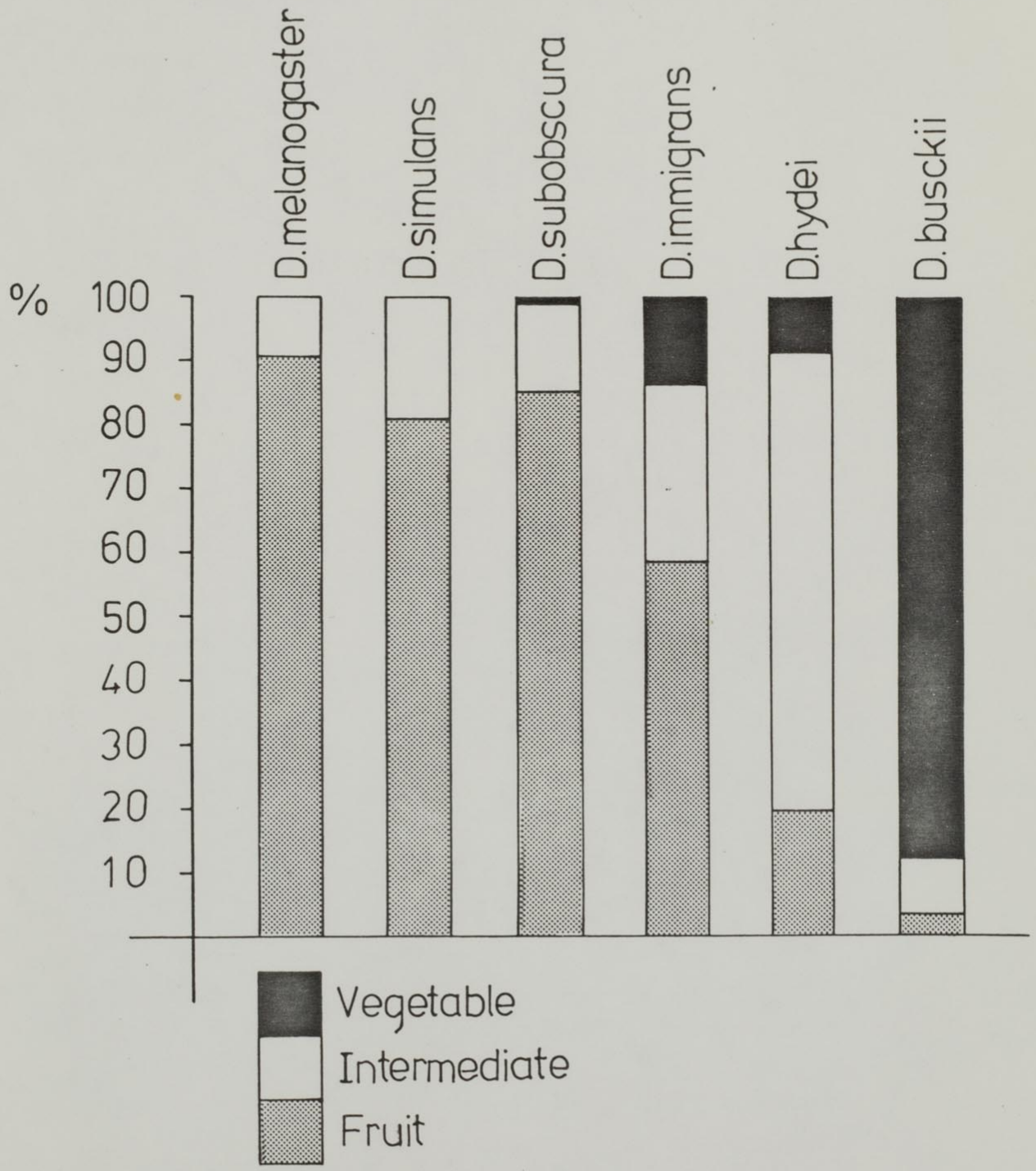


Fig 3.2 Percentage of Drosophila of each species emerging from the three breeding site groups



where p_{ih} is the proportion of species i in category h. The niche breadth was computed for each Drosophila species using breeding site groups, breeding site species and individual breeding site items as categories. A Drosophila species with a narrow niche on breeding site groups has a restricted number of breeding site species available to it and so will have a narrow niche on breeding site species even if it is entirely unselective within a group. In order to investigate the selectivity within groups, the niche breadth across breeding site species was calculated separately for each breeding site group and weighted according to the number of Drosophila individuals of that species emerging from that group. The weighted mean of these niche breadths gives emphasis to the preferred group of that Drosophila species. It is a measure of niche breadth on breeding site species independent of the niche breadth on groups.

Niche breadth across breeding site items is similarly dependent on niche breadth across breeding site species and so the niche breadth on items is calculated separately for each breeding site species and the weighted mean determined. The results are shown in Table 3.4.

The niche breadths may represent selection of breeding sites by the Drosophila or differential survival by the larvae or both. D. immigrans and D. hydei have the broadest niches on breeding site groups reflecting Fig 3.2. On breeding site species D. melanogaster is the least specialised within its preferred group. On the other hand D. hydei, despite being broad niched on groups, is relatively specialised on species. On breeding site items D. hydei and D. busckii are very much broader niched than the other species which may be selecting items for the state of decay or microfloral composition.

The associations between Drosophila species within breeding site items were investigated. The number of flies of each species emerging from each item was transformed to logarithms and the product moment correlation coefficient was calculated between all pairs of species. The species were clustered according to the weighted variable group

Table 3.4 Niche breadths

Categories	D. melanogaster	D. simulans	D. subobscura	D. immigrans	D. hydei	D. buscki
Mean breeding site items	0.14	0.09	0.05	0.14	0.47	0.41
Mean breeding site species	0.53	0.37	0.35	0.36	0.29	0.35
Breeding site groups	0.40	0.48	0.45	0.76	0.60	0.43

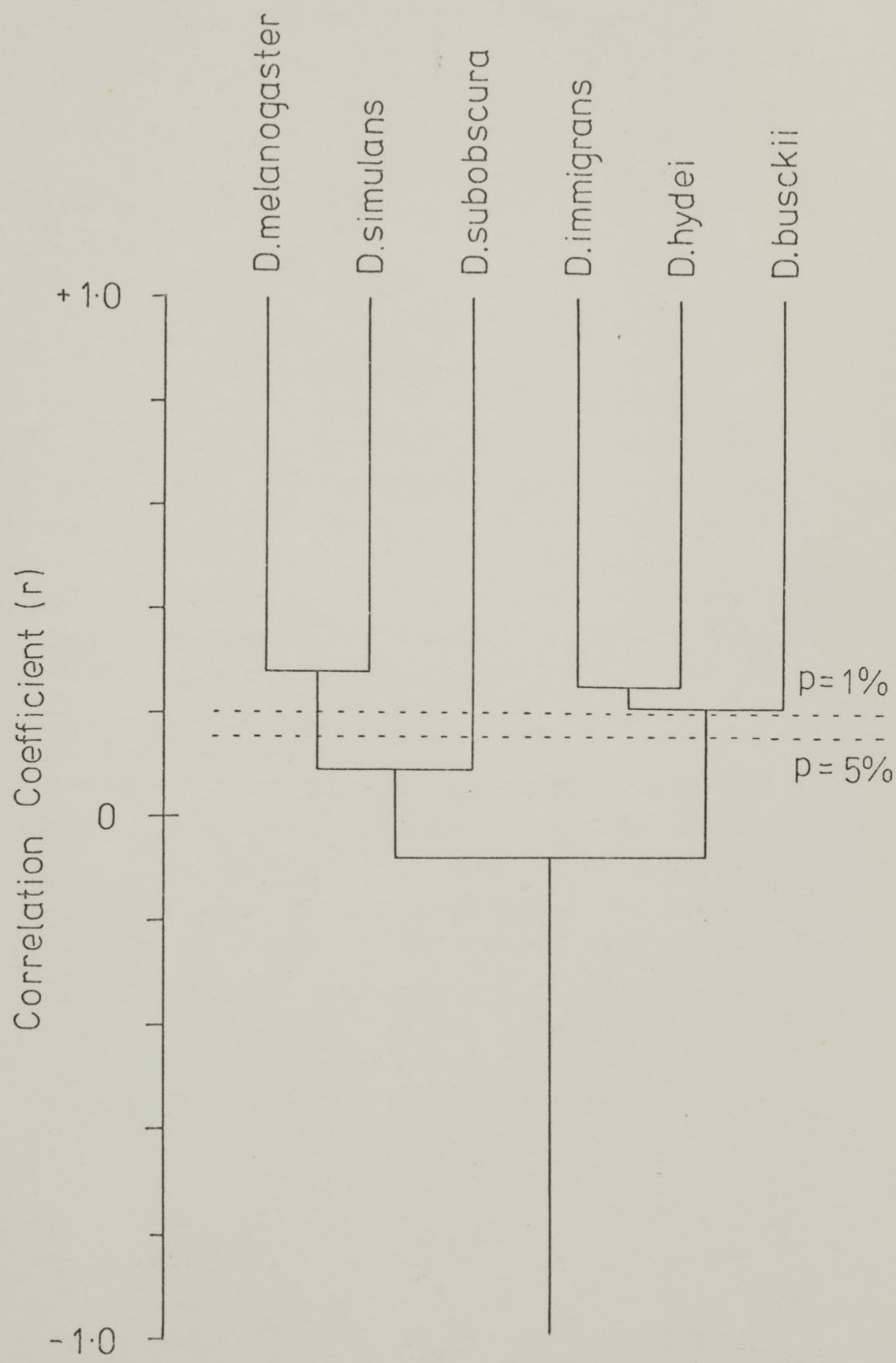
method (Sokal and Sneath, 1963) and the resulting dendrogram is shown in Figure 3.3. There are two significant groups at the 1% level. D. melanogaster and D. simulans are significantly associated and D. immigrans and D. hydei are significantly associated with D. busckii.

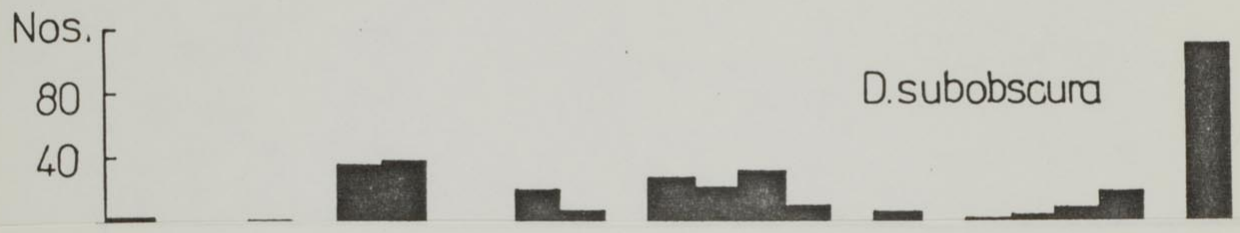
Season

Figure 3.4 shows the maximum and minimum temperatures recorded twice a week throughout the season and, for each species of Drosophila, the number of flies emerging from the breeding sites brought in each week. Drosophila emerging from a breeding site picked up in a given week will not necessarily have come from eggs layed in that week, but allowing for this error and assuming that survival from egg to adult remains constant throughout the season, the emergences in Figure 3.4 reflect the distribution of oviposition through the season. The breeding seasons of the species overlap considerably but there are differences in their time of peak egg laying. D. melanogaster and D. simulans have two peaks, one in mid-June, and the other at the beginning of September. D. hydei and D. immigrans have their peak in mid July, though these peaks may be peculiar to the single season studied.

In order to investigate the relationship between temperature and oviposition the product moment correlation was calculated between mean weekly temperature and the weekly emergences from Figure 3.4, transformed to logarithms. The results are shown in Table 3.5. There is a significant positive correlation for D. melanogaster, D. simulans, D. immigrans and D. hydei suggesting that their breeding is most strictly limited by temperature or another environmental variable correlated with it. McKenzie (1975) has shown that oviposition of D. melanogaster is very slow at 12°C in the laboratory and increases with temperature up to 20°C. He also found that in a field population larvae and pupae are not found at temperatures below 14°C. These temperatures fit the breeding season of D. melanogaster in Leeds quite well. The emergences of D. subobscura in Figure 3.4 remain fairly constant throughout the season and continue into October after the other species have stopped egg laying. This

Fig 3.3 Correlations between the Drosophila species emerging from individual breeding site items.





Despite the limitations of trapping data, it is interesting to compare the numbers of adults captured in Fig. 2.2. with the emergences from breeding sites in Fig. 3.4. The three peaks of trapping occur at more or less the same time as peaks of emergence in Fig. 3.4. It is possible then that the large peaks in Fig. 2.2. indicate genuine increases in the population following emergences from breeding sites.

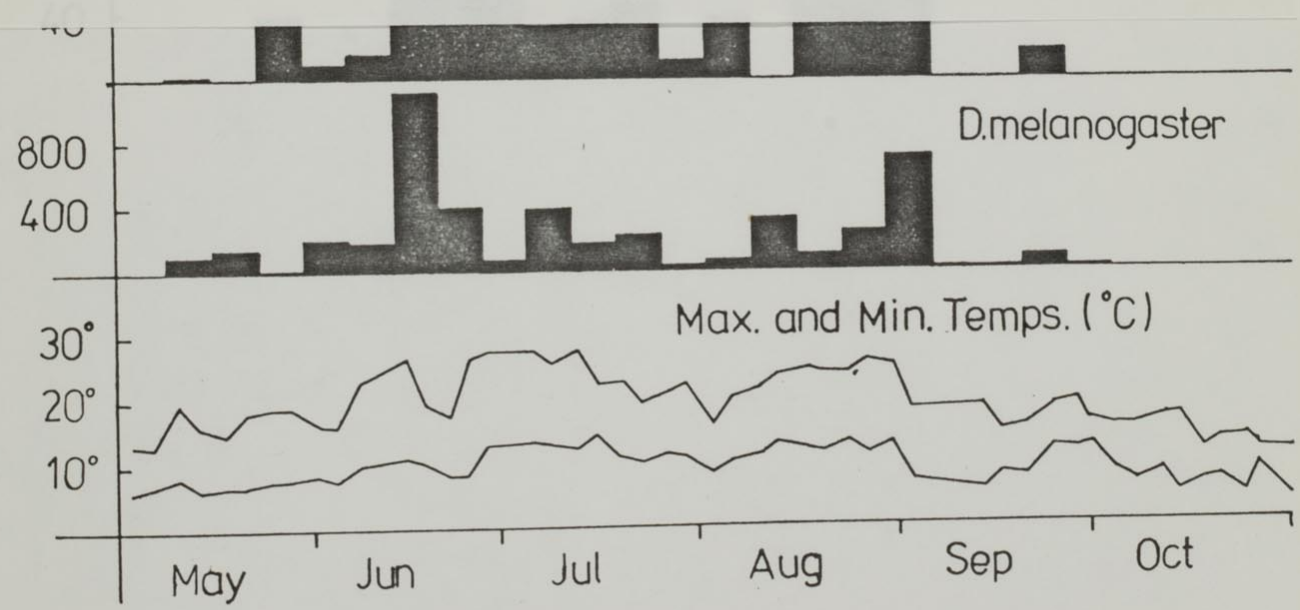


Fig 3.4 Emergences of Drosophila from breeding sites collected each week

Table 3.5 Product moment correlation (r) between mean weekly temperature and oviposition

Drosophila species	r	Significance
D. melanogaster	+ 0.68	$p < .01$
D. simulans	+ 0.77	$p < .01$
D. subobscura	+ 0.12	n.s.
D. immigrans	+ 0.52	$p < .05$
D. hydei	+ 0.57	$p < .01$
D. busckii	+ 0.21	n.s.

species, unlike the others which evolved in various tropical or sub-tropical areas, is a native of Europe. It is less adversely affected by temperatures and less able to exploit high summer temperatures than the cosmopolitan species.

Discussion

Sturtevant in 1921 described the larvae of D. busckii and D. funebris as general scavengers feeding on rotten potatoes, excrement, etc., while most common species prefer decaying fruit. D. hydei is described as intermediate between the two types. Shorrocks (1977) has emphasised the fundamental ecological division in Drosophila between those that use decaying substrates as breeding sites and those that use substrates undergoing alcoholic fermentation. In the domestic habitat fruits undergo alcoholic fermentation but in the vegetables other forms of decay predominate. As we have shown D. melanogaster, D. simulans and D. subobscura are fruit specialists, D. busckii is a vegetable specialist while D. immigrans and D. hydei are able to use both types of breeding site, thus confirming the qualitative statement of Sturtevant.

Despite the partitioning of breeding sites that occurs, the analysis of diversity confirms considerable coexistence of different cosmopolitan Drosophila species within single breeding site items. Budnik and Brncic (1974) suggest that this phenomenon is fairly common in nature. They found D. pavani feeding in the same rotting fruits as some of the domestic species. This coexistence occurs because ovipositing females of domestic species show less selectivity in their choice of breeding sites than many wild species (Pipkin et al, 1966; Heed, 1971). Even at a fruit market the species of fruit available for breeding are fairly unpredictable and in the domestic niche generally, the probability of an ovipositing female finding a breeding site of the same sort as it developed in must be extremely small. Mac Arthur and Pianka (1966) have predicted that low expectation of finding a particular resource and increasing similarity of resource types demands generalisation. Evidently

breeding site species in the domestic niche are similar enough and unpredictable enough to favour generalisation. The difference between fermenting fruits and decaying vegetables, however, is so great that most of the domestic species have specialised on one or the other.

CHAPTER 4

FACTORS AFFECTING BREEDING SITE SPECIFICITY

Introduction

In Chapter 3 it was established that several of the domestic species of Drosophila appear, from their emergences, to specialise either on fermenting fruits or on decaying vegetables as breeding sites. Within these two categories preferences were less marked. The apparent specialisation could be caused by three different factors, alone or in combination. These factors are, differential attraction of the Drosophila species to potential breeding sites, differential oviposition by the Drosophila females, and differential survival of the immature stages. The causes of breeding site specificity are examined in this chapter using field and laboratory results.

Adult Drosophila may be attracted to baits, in the field or in laboratory food preference tests, for the purpose of feeding or for oviposition. Carson and Stalker (1951) and Carson (1951) have discovered that the breeding sites of several species of wild Drosophila are unattractive to the feeding adults. Later studies (Dobzhansky et al, 1956; Carson et al, 1956; Begon, 1975) have shown that the species of yeasts found in the crops of adult flies are often fundamentally different from those found in Drosophila breeding sites. These results have lead to suggestions that there is a clear separation between feeding sites and breeding sites in Drosophila (Carson, 1971). Some results will be presented in this chapter which indicate that the separation is much less evident in domestic species of Drosophila.

Methods

Field Studies

All the field sampling was carried out at Pontefract Lane wholesale fruit and vegetable market.

During the summer of 1975 collections of Drosophila adults were made from different kinds of discarded fruit and vegetables using an aspirator and sweep net.

Between 29.4.76 and 9.12.76 Drosophila were caught in bottle traps as described in Chapter 2. Three different baits, banana, malt bait and tomato were used in each trap unit. After the traps had been exposed for a week the banana and malt bait smelt strongly of alcoholic fermentation and presumably caught flies normally attracted to fermenting fruit; the tomato smelt of other forms of putrefaction and probably caught flies normally attracted to decaying vegetables.

The separation of feeding and breeding sites was investigated during May 1976. The presence or absence of Drosophila adults, on the surface of fruits and vegetables at the market, was noted. These potential breeding sites were taken to the laboratory and placed separately in glass jars with the tops covered with nylon fabric. The jars were placed in an outdoor insectary and emerged flies were removed and identified.

Laboratory Studies

A food preference test was carried out in the laboratory using five species of Drosophila, D. busckii, D. hydei, D. funebris, D. immigrans and D. melanogaster. Five 'foods' were used for the test, two which represented fermenting substrates, banana and orange, and three which represented decaying substrates, tomato, cucumber and melon. Discs 2cm thick were cut from each of these foods and placed in the bottom of 8cm by 3cm plastic tubes. The discs were kept at 20°C for five days and allowed to decay. Five tubes containing the different 'foods' plus a sixth containing 2cm of damp cotton wool were fitted in to the bottom of a perspex population cage (Shorrocks, 1972). Each of these food preference cages was joined by an 8cm long, 3cm wide tube to a similar cage in which one of the Drosophila species was breeding on Drosophila medium (Shorrocks, 1972). The flies were thus able to determine their own density within the food preference cage. For

each run of the test the food preference cage was joined to the population cage and kept undisturbed and lit from above for 4 hours. The number of flies inside each food tube was then counted. Before every run the position of the food tubes was changed according to a regular sequence. All the Drosophila species were tested simultaneously in different pairs of cages. Sixteen runs of the test were carried out.

The survival of the immature stages of five species of Drosophila was tested on foods representing fermenting and decaying substrates. Since temperature might affect the survival of different species on different foods a three way factorial design was chosen for the experiment; Drosophila species by food by temperature. The Drosophila species were D. busckii, D. funebris, D. immigrans, D. melanogaster and D. subobscura. The foods were Drosophila medium (Shorrocks, 1972) and banana, representing fermenting substrates and potato representing decaying substrates. The banana and potato were chopped, allowed to decay at 22°C for 4 days and then homogenised in a blender. Three temperatures, 10°C, 15°C and 20°C were used, chosen as representative temperatures during the breeding season of domestic Drosophila in in Leeds. First instar larvae were obtained by placing tubes of Drosophila medium in population cages, full of flies, for 24 hours. Larvae were transferred with a needle from the surface of the medium to 7cm by 2cm glass tubes containing 10ml of the experimental food. Ten larvae were placed in each tube and five tubes were prepared for each treatment, making 225 tubes in all. The tubes were placed in incubators set at the experimental temperatures and at constant light. The emerging adults were removed daily.

Results

Field Studies

The results of the collections over natural baits are shown in Table 4.1. The baits are classified into two groups, fermenting substrates and decaying substrates (Chapter 3). When calculating χ^2 several of

Table 4.1 Collections over natural baits

Bait	D. melanogaster & simulans	D. subobscura	D. immigrans	D. hydei	D. funebris	D. buscckii	Total
Banana	4	1	2		3	1	11
Pear			1	1			2
Peach	8						8
Grapefruit	9	1					10
Orange	74	8	26	9			117
Total fermenting	95	10	29	10	3	1	148
Melon	71	1	17	23	3	7	122
Tomato	36		3	1			40
Turnip	3					4	7
Total decaying	110	1	20	24	3	11	169
Total	205	11	49	34	6	12	317

the expected frequencies were less than 5, due to the small sample size, and so several categories were combined. The categories which were combined are bracketed off by horizontal or vertical lines in Table 4.1. When the fermenting substrates were compared with decaying substrates there were significant differences in the Drosophila fauna (χ^2 = 11.79, d.f. = 2, $p<0.01$), but there was also significant heterogeneity within the substrate groups (χ^2 = 13.06, d.f. = 4, $p<0.05$). The Drosophila species showed the preferences that would be expected on the basis of their emergences. D. melanogaster and simulans, D. subobscura and D. immigrans had a slightly better than average preference for fermenting substrates, but the biggest contribution to χ^2 came from D. hydei and D. busckii, which showed a marked preference for decaying substrates.

The results of the baited trapping are given in Table 4.2 which gives the mean number of each species of Drosophila per trap for each bait. There are significant differences between the baits (χ^2 = 504.8, d.f. = 12, $p<0.001$). D. melanogaster and D. simulans prefer the fermenting baits, banana and malt, while D. immigrans, D. hydei and D. busckii prefer the decaying substrate, tomato. D. subobscura and D. funebris show no clear preferences.

Table 4.3 shows the potential breeding sites picked up in May 1976 classified according to whether Drosophila were crawling on their surface and whether they subsequently yielded adult flies. The association between the two classifications was very strong (χ^2 = 25.4, d.f. = 1, $p<0.001$). Substrates on which Drosophila were crawling were much more likely to be breeding sites.

Laboratory Studies

Table 4.4 shows the analysis of variance for the food preference test. The numbers of each Drosophila species on each 'food' were transformed to square roots for the analysis. The significant interaction between Drosophila species and food shows that the different species of Drosophila were exhibiting significantly different food preferences in the laboratory. Table 4.5 shows the 'foods' ranked in order of

Table 4.2 Collections from baited traps - mean numbers of *Drosophila* per trap

Bait	*D. melanogaster*	*D. simulans*	*D. immigrans*	*D. hydei*	*D. funebris*	*D. buscki*	*D. subobscura*
Banana	74.7	3.5	9.7	4.2	1.3	0.7	4.5
Malt bait	40.3	1.8	3.5	2.0	0.8	1.3	2.4
Tomato	34.2	1.3	15.8	4.4	1.0	1.9	4.2

Table 4.3 Attractiveness of breeding sites

Adult *Drosophila* emerged	*Drosophila* on surface: +	*Drosophila* on surface: −	
+	10	3	13
−	5	45	50
	15	48	63

Table 4.4 Food preference test - analysis of variance

Source of Variation	SS	d.f	MS	F	
Drosophila species	79.6	4	19.9	339.8	$p < 0.01$
'food'	71.6	5	14.3	244.5	$p < 0.01$
species x 'food'	71.6	29	2.5	42.2	$p < 0.01$
Error	25.8	441	0.06		
Total	248.5	479			

Table 4.5 Food preference test - SNK test

Rank	1	2	3	4	5	6
D. melanogaster	Orange	Melon	Banana	Tomato	Cucumber	Control
D. immigrans	Melon	Tomato	Orange	Banana	Cucumber	Control
D. funebris	Cucumber	Melon	Orange	Tomato	Banana	Control
D. busckii	Melon	Banana	Cucumber	Tomato	Orange	Control
D. hydei	Melon	Banana	Tomato	Cucumber	Orange	Control

preference for each Drosophila species. Student-Newman-Keuls test was applied to each series of 'foods' and those which were not significantly different ($p<0.05$) in attractiveness are bracketed with horizontal lines. The control was the least preferred 'food' in all cases, but for D. funebris it was not significantly different from the 'foods' tomato and banana. This may indicate that the range of 'foods' presented was inappropriate for this species and points out one of the shortcomings of food preference tests. The food preferences show only minor correlation with the breeding site preferences observed in Chapter 3. The fermenting fruit specialist D. melanogaster has two fermenting fruits, orange and banana among its preferred 'foods', but all the other species include one fermenting fruit among their three preferred 'foods'. Cucumber, classified as a decaying vegetable in Chapter 3, was among the preferred 'foods' of the decaying substrate specialists D. busckii and D. funebris. Cucumber is less preferred by all the other species.

Table 4.6 shows the analysis of variance for the factorial survival experiment. The survivals, originally expressed as the number of larvae surviving out of the ten in each replicate, were transformed to arcsines for the analysis. All three main effects, temperature, 'food', and Drosophila species had a significant influence on survival. There is also an effect of temperature that depends on Drosophila species and, more important, an effect of 'food' that depends on the Drosophila species. Since neither the three way interaction nor the two way interaction between 'food' and temperature was significant, we can summarise the results in the form of two tables. Table 4.7 shows the mean survival of each species on each 'food' and Table 4.8 shows the survival of each species at each temperature.

On banana the survival of all the Drosophila species except D. melanogaster was very low. Unlike the Drosophila medium which was a 'killed yeast medium' the banana contained live yeast and would rapidly have built up a high concentration of alcohol in the closed containers. D. melanogaster has been shown to be exceptionally resistant to ethanol (McKenzie and Parsons, 1972; David and Boquet, 1975; David et al, 1974) and this is probably the explanation of its survival

Table 4.6 Factorial survival experiment - analysis of variance

Source of Variation	SS	d.f	MS	F	
Temperature	8645	2	4322	28.43	$p < 0.01$
Food	12659	2	6329	41.64	$p < 0.01$
Drosophila species	27078	4	6769	44.53	$p < 0.01$
Temp x food	910	8	113	0.74	n.s.
Temp x species	10671	14	762	5.01	$p < 0.01$
Food x species	24834	14	1773	11.66	$p < 0.01$
Temp x food x species	5701	44	129	0.85	n.s.
Error	20715	136	152		
Total	111213	224			

Table 4.7 Factorial survival experiment - percent survival on different foods

	D. melanogaster	D. immigrans	D. subobscura	D. funebris	D. busckii
Drosophila medium	74	47	79	5	0
Banana	56	0	7	1	0
Potato	21	44	47	22	26

Table 4.8 Factorial survival experiment - percent survival on different temperatures

	D. melanogaster	D. immigrans	D. subobscura	D. funebris	D. busckii
20°C	76	33	47	16	16
15°C	64	38	46	12	10
10°C	8	21	47	0	0

and the relatively low survival of the other species on bananas. On Drosophila medium the two fermenting fruit specialists, D. melanogaster and D. subobscura showed the highest survival, followed by D. immigrans, the less specialised species. The two decaying vegetable specialists, D. funebris and D. busckii showed almost zero survival. Survival was low for all species on potato, but for the decaying vegetable specialists it was much higher than on the fermenting substrates, banana and Drosophila medium. For the generalist, D. immigrans survival on potato was as high as on Drosophila medium and for the fermenting fruit specialists it was significantly lower.

The survival of D. melanogaster, D. busckii and D. funebris was highest at 20°C, reduced at 15°C and almost zero at 10°C. D. immigrans had its highest survival at 15°C and still showed significant survival at 10°C. This is consistent with the fact that this species continues to emerge from breeding sites later in the year than all the other species apart from D. subobscura. Spencer (1940) describes D. immigrans as being more tolerant of low temperatures than most of the other domestic species. The survival of D. subobscura appeared to be unaffected within the temperature range studied. In Chapter 3 it showed the lowest correlation of its emergences with temperature. Unlike the other species it is a native of Europe and is evidently adapted to lower temperatures.

Discussion

The results presented in Table 4.3 suggest that breeding sites are attractive to feeding domestic Drosophila. If the flies noted on the surface of breeding sites were attracted for the purpose of oviposition we would be left with the problem of discovering the feeding sites of domestic Drosophila. Without an analysis of the crop contents of the adult flies and the yeast flora of the substrates it is impossible to say with certainty what the feeding sites are. However, given the suggestion of Carson (1971) that most Drosophila are highly opportunistic in their feeding sites, and the observation that breeding sites are very attractive, it is likely that there is no separation of breeding and feeding sites in these species. This

accords with the conclusion of Camargo and Phaff (1957) who studied the yeasts of D. melanogaster in tomato fields and concluded that the larval and adult food supply is identical.

Begon (1975) offers two explanations for the separation of feeding and breeding sites in D. obscura and D. subobscura. First, the ovipositing adult which refrains from feeding would benefit its own offspring by increasing their food supply and so this trait could be favoured by kin selection. Second, predators are likely to be attracted to the concentrations of flies at breeding sites and so the ovipositing adult should reduce its time spent in these concentrations by not feeding. The necessary condition for the separation of feeding sites from breeding sites is an adequate alternative food source. Among the 'wild' species of Drosophila the breeding sites have become so specialised (Carson, 1971; Heed, 1968) that they constitute only a proportion of the yeast sources available to the adults. The domestic species, however, are so opportunistic in their use of breeding sites that they probably use most large sources of yeast in the 'domestic' niche leaving no alternative to use as feeding sites.

In the introduction to this chapter it was suggested that three factors could be responsible for the breeding site specificity observed in Chapter 3. These factors were differential attraction, differential oviposition and differential survival. A laboratory test of differential oviposition was not carried out because the texture of the oviposition surface may be more important than its chemical properties (Chiang and Hodson, 1950). Unless the substrates offered to the flies in the laboratory had surfaces of the texture preferred in the field, this would frustrate attempts to detect selection of fermenting or decaying sites.

In this chapter the relative attractiveness of fermenting and decaying substrates to each Drosophila species have tended to mirror the breeding site specialisations observed in Chapter 3. Assuming attraction leads to oviposition as well as to feeding, this could provide the basis for the observed breeding site preferences. The

specificity of attraction, however, is much less strong than the specificity of emergence from breeding sites. Fellows and Heed (1972) obtained very similar results in their study of cactiphilic Drosophila. They suggested that their 'polyphagic species may use passive selection of breeding sites. They oviposit opportunistically on a variety of substrates, their "preferred host plants" merely being those that permit survival with regularity.' In the domestic niche there is a constantly renewed supply of vacant breeding sites and in these circumstances the 'r-selected' attribute of unselective oviposition might be a better strategy than the 'K-selected' attribute of searching out the most suitable breeding sites. The extreme specialist would miss many suboptimal but still usable sites.

Survival is probably important in this case for determining the specialisations. In the factorial survival experiment the survival of each species was the highest on that substrate which represented its preferred breeding sites. In the case of D. busckii and D. funebris their survival was zero on fermenting substrates and this might explain their specialisation on decaying vegetables in nature. In the case of D. melanogaster and D. subobscura which specialise on fermenting breeding sites in nature, their survival on decaying substrates was merely reduced. Their observed specialisation can be explained as the product of differential attraction to fermenting fruits followed by increased survival.

CHAPTER 5

AN ECOLOGICAL INTERACTION BETWEEN D. IMMIGRANS, CITRUS FRUITS AND PENICILLIUM

Introduction

Many species of Drosophila specialise on a narrow range of breeding sites and have adaptations associated with their specialisation. The best known example of this is D. pachea, which breeds in the stems of the senita cactus, Lophocereus schotti. This species of Drosophila requires the sterol schottenol in its diet and this is unique to the senita cactus (Heed and Kircher, 1965). D. pachea is also resistant to an alkaloid, pilocereine, which is poisonous to other Drosophila species and prevents them from breeding in senita cactus (Kircher et al, 1967).

These sorts of adaptations have rarely been associated with the domestic species of Drosophila which have perhaps been regarded as too generalised in their breeding sites to have specialist adaptations. Though relatively unspecialised, the domestic species do have preferences for different breeding sites as in Chapter 3. This chapter describes some preliminary results that reveal adaptations in D. immigrans that might explain the preference this species shows for citrus fruits.

Methods and Results

The fruits of three species of Citrus are used as breeding sites by Drosophila at Pontefract Lane. These are orange (C. sinensis), lemon (C. limon) and grapefruit (C. paradisi).

During the summer of 1976 potential breeding sites were brought back to the laboratory as described in Chapter 3. Table 5.1 shows the percentage of each species of Drosophila emerging from the three species of Citrus. The figures for D. funebris are omitted because only 15 individuals of this species emerged. For each species of Citrus D. immigrans has the highest proportion of emergences from it.

Table 5.1 Percentage of each species of *Drosophila* emerging from citrus fruits

	D. immigrans	*D. melanogaster*	*D. subobscura*	*D. hydei*	*D. simulans*	*D. busckii*
Orange	25.8	17.3	8.3	8.9	10.1	0.6
Lemon	10.2	4.8	3.7	6.6	1.0	2.3
Grapefruit	12.8	10.7	7.5	3.5	0.3	0.0
Total citrus fruit	48.8	32.8	19.5	19.0	11.4	2.9
Other breeding sites	51.2	67.2	80.5	81.0	88.6	97.1

Overall nearly 50% of D. immigrans individuals emerged from citrus fruits. Only D. melanogaster with about 33% of individuals approached this figure, no other species exceeding 20%. D. immigrans is evidently relatively reliant on citrus fruits.

Citrus fruits are among the few species of breeding site which decay in a fairly predictable manner. Their decay is always associated with infections of Penicillium. Two species of Penicillium are characteristic of citrus fruits and are rarely found elsewhere in nature (Raper and Thom, 1949). These are P. digitatum and P. italicum. P. digitatum produces olive green conidia and causes affected fruits to dry up, shrink in size and become hollow mummified shells. P. italicum, on the other hand, produces a blue green conidial mass and causes a soft rot from which the fruit loses shape and becomes a flattened slimy mass. These two moulds are a major cause of loss of citrus fruits in storage.

Since D. immigrans has a marked preference for breeding in citrus fruit it might be expected to have specific adaptations for living in citrus fruits. The two species of Penicillium are so ubiquitous that any adaptations are likely to involve them and so every citrus fruit that was brought back to the laboratory was classified on a scale from 1 to 4 according to how much of the surface was covered with Penicillium conidia. Table 5.2 shows how the fruits were classified. After the fruits were returned to the laboratory the infection always spread and fruits originally classified as stage 1 would often be stage 4 when the Drosophila adults emerged. These adults would, on average, have had less exposure to the effects of Penicillium than those on fruits originally classified as stage 4.

Table 5.3 shows the numbers of Drosophila emerging from citrus fruits at each stage of infection. D. immigrans and D. subobscura show an increase in numbers with stage of infection while D. melanogaster showed a decline. The other species showed no clear pattern. Figure 5.1 is a histogram showing the mean numbers of D. melanogaster and D. immigrans emerging from fruit at each stage of infection. These two species were chosen because they emerged in much larger

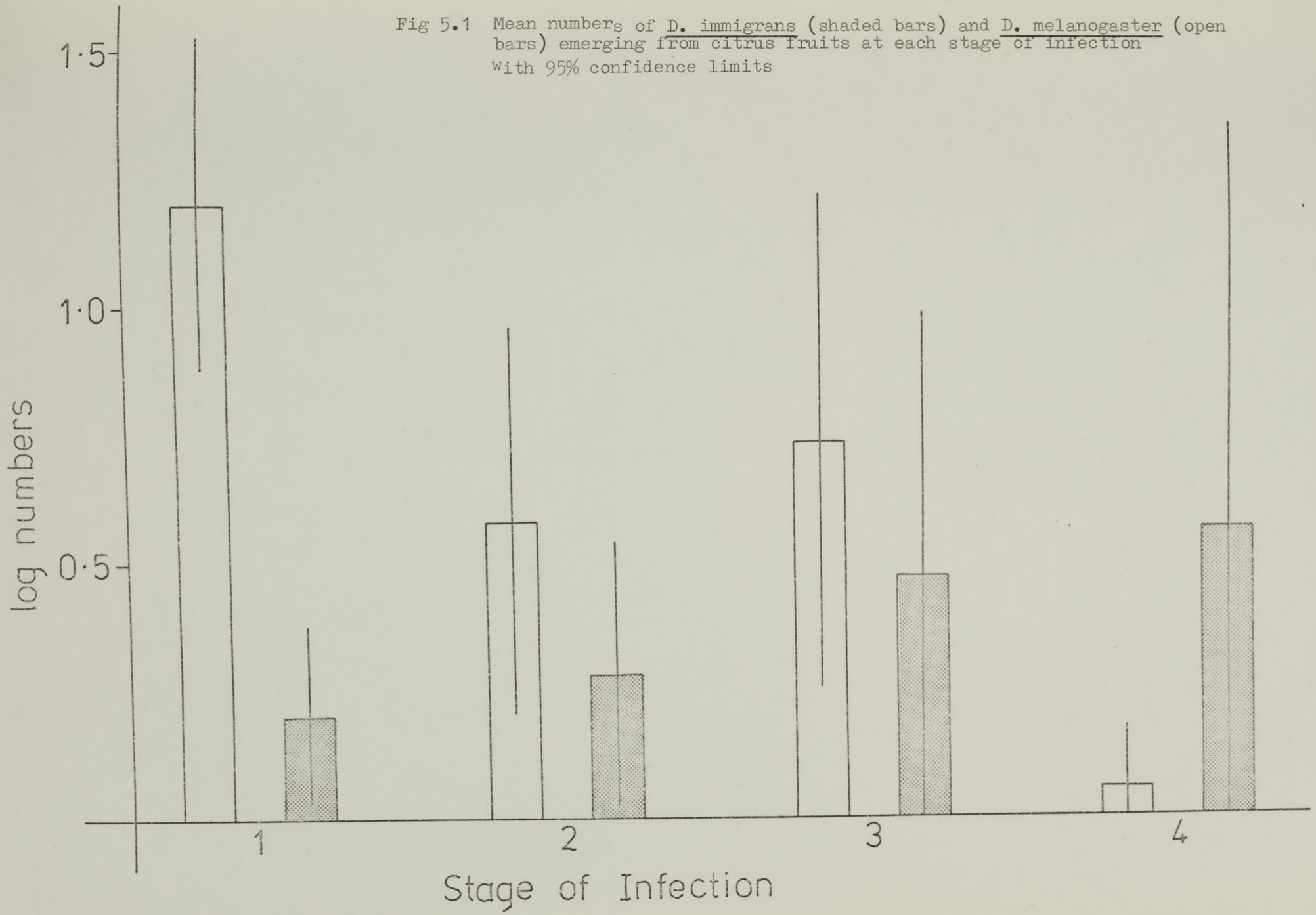
Table 5.2 Classification of citrus fruits

Proportion of surface covered with Penicillium	Stage
0%	1
<50%	2
>50%	3
~100%	4

Table 5.3 Numbers of Drosophila emerging from citrus fruits at each stage of infection

Stage	1	2	3	4	Total
Number of fruits	51	21	19	19	110
D. immigrans	45	39	94	115	293
D. subobscura	3	6	26	37	72
D. melanogaster	1208	177	113	1	1499
D. simulans	38	42	1	1	82
D. hydei	45	12	14	4	75

Fig 5.1 Mean numbers of D. immigrans (shaded bars) and D. melanogaster (open bars) emerging from citrus fruits at each stage of infection with 95% confidence limits



numbers from citrus fruits than the other species. The trends are obvious but the standard errors are large. Neither species showed significant heterogeneity in numbers emerging among infection stages in one-way analyses of variance. The mean numbers emerging from uninfected stage 1 fruits were compared with the mean numbers from all infected fruits combined. The numbers were transformed to logarithms for the analysis. D. immigrans showed a significant excess on infected fruits ($t = 2.1$, $p < 0.05$) while D. melanogaster showed a a significant excess on uninfected citrus fruits ($t = 2.26$, $p < 0.05$). Even these results are close to the borderline of significance but they do suggest that there is an interaction between Penicillium and these two species of Drosophila.

The spread of the Penicillium infection is progressive and so the amount of mould on the surface is correlated with the age of the fruit. The results above would be obtained if both species oviposited in uninfected fruit but D. melanogaster developed much faster than D. immigrans. Citrus fruits brought back to the laboratory at stages 3 or 4 might already have been left by the emerging D. melanogaster while D. immigrans had still to complete its development.

A laboratory experiment was set up to test whether D. melanogaster and D. immigrans larvae survived differently on Penicillium infected citrus fruits. The survival experiment was conducted using slices of lemon 1cm thick and between 4cm and 5cm in diameter. Before the slices were cut the surface of the lemon was washed in a solution of the fungicide benomyl and the knife was heat sterilised to try to prevent accidental infection of the lemon slices. Sixty slices were prepared and each was placed in a sterile plastic petri dish. Half of the slices were inoculated with spores of P. italicum obtained from a lemon found at Pontefract Lane. A few spores were smeared on each slice using a loop. Both the control and infected lemon slices were incubated at 20°C for three days. At the end of this period the infected slices were all completely covered with Penicillium conidia. Drosophila eggs were obtained from population cages and ten eggs were placed on each lemon slice. On 20 of the slices, 10 infected and 10 control, the eggs were all D. immigrans; another 20 slices had

D. melanogaster only while the last 20 slices each had five D. immigrans and five D. melanogaster eggs. The lemon slices were again incubated at 20°C. In spite of the use of sterile equipment the control slices gradually became infected with Penicillium. This is probably unavoidable without sterilising the lemon slices and the Drosophila eggs. By the end of the experiment few control slices had developed a complete covering of mould but all were affected to some degree. The control slices, therefore, represent a much less severe infection rather than a complete absence of infection. As adult Drosophila emerged from the lemon slices they were removed and identified.

A three way analysis of variance was performed on the results. The three main effects were 'Species' (D. immigrans or D. melanogaster), 'Infection' (infected or control) and 'Combination' (species alone or together). The survivorships were expressed as the proportion of eggs in each replicate surviving to adult. The proportions were transformed to arcsines for the analysis which is presented in Table 5.4. Only one of the main effects, 'Infection', contributes a significant amount to the variation showing that overall survival is significantly higher on the infected lemons than on the controls. The largest contribution to the variation is provided by the interaction between 'Species' and 'Infection'. This shows that the two species are affected differently by the state of infection. D. immigrans has its highest survival on infected lemon while D. melanogaster survives better on the controls. The main effect 'Combination' does not make a significant contribution to the variation, either on its own or in interaction with other effects. This means that the two species have the same survivorship when reared together as when reared apart. At these densities there is no evidence of facilitation or competition.

The mean survivorships with 95% confidence limits are presented in Table 5.5 with the 'Combination' results pooled. The results are as expected from the emergences in the field though the reduction in survival of D. melanogaster due to the effect of Penicillium is much less than the increase in survival of D. immigrans. The survival of D. melanogaster is only reduced from 55% to 45% by the infected lemon,

Table 5.4 Survivorships of *Drosophila* - Analysis of variance

Source of variation	SS	d.f.	MS	F	
Species	677.3	1	677.3	2.1	n.s.
Infection	2056.9	1	2056.9	6.2	$p < 0.05$
Combination	171.8	1	171.8	<1	n.s.
Species x Infection	5079.0	1	5079.0	15.4	$p < 0.01$
Species x Combination	3.2	1	3.2	<1	n.s.
Infection x Combination	0.9	1	0.9	<1	n.s.
Species x Infection x Combination	1.3	1	1.3	<1	n.s.
Error	23784.9	72	330.3		
Total	31775.3	79			

Table 5.5 Mean survivorships with 95% confidence limits

	Infected	Control
D. melanogaster	$45.5\ ^{58.4}_{32.8}$ %	$55.6\ ^{69.8}_{40.9}$ %
D. immigrans	$81.1\ ^{90.3}_{69.6}$ %	$38.0\ ^{54.9}_{22.5}$ %

Table 5.6 Preferences of Drosophila for infected and uninfected lemon slices

	Infected	Control
D. immigrans	2	35
D. melanogaster	5	42

while the survival of D. immigrans is significantly increased from 38% to 81%. The field results are almost certainly explained by the presence of Penicillium rather than by the age of the fruit.

It might be expected that D. immigrans would select fruit infected with Penicillium for oviposition, while these should be rejected by D. melanogaster. A food preference test was set up in the laboratory using infected and uninfected lemon slices prepared as for the survival experiment. Population cages (Shorrocks, 1972) were set up with two tubes containing an uninfected lemon slice each and two containing infected slices. Each tube was fitted with a bottle trap top (Chapter 2) so that Drosophila could enter the tubes but not leave. Fifty D. immigrans, 25 females and 25 males were introduced into one cage and 50 D. melanogaster into another. The cages were kept in an incubator, lit from all sides for 24 hours. At the end of this time nearly all the flies had entered one of the tubes. The results are presented in Table 5.6. In both species there is a significant excess on the uninfected lemon slices. There is no suggestion that D. immigrans adults find lemon infected with Penicillium attractive. It is possible, of course, that females would be attracted for oviposition, but since both sexes are alike in their rejection of infected lemon this is unlikely.

Discussion

The results presented above show that D. immigrans emerges more often from Citrus fruit when it is infected with Penicillium while D. melanogaster emerges less often. The laboratory experiments indicate that this is probably due to differential survival of the larvae and not to the preferences of ovipositing females. Further experimental work is required to establish the reasons for this effect, but some speculations at this point might be useful.

In the survival experiment the survival of D. melanogaster was reduced on Penicillium while infected fruit from Pontefract Lane certainly produce significantly fewer D. melanogaster. Hanssen (1969) has shown that P. digitatum isolated from lemons produces aflatoxin B1, a

mycotoxin to which D. melanogaster adults are very sensitive (Matsumura and Knight, 1967). This provides a plausible reason for the reduced survival of D. melanogaster on Penicillium infected citrus fruits. The fact that D. immigrans' survival is increased on Penicillium suggests that this species must be resistant to aflatoxin B1. This would be a desirable adaptation for any Drosophila species whose preferences was for citrus fruits.

It is not clear why the survival of both species was so low on uninfected lemon in experimental conditions. These lemons are evidently unsuitable in some way; perhaps the lemons have chemical defences against insect larvae (Janzen, 1977) which are otherwise rendered harmless for D. immigrans by Penicillium.

In Chapter 3 it was established that D. immigrans is fairly catholic in its choice of breeding sites. It is not confined to either one of the breeding site groups, fruit or vegetables, and in this sense is more of a generalist than D. melanogaster. The adaptations this species has for breeding in citrus fruits, however, are the sorts of adaptations normally associated with specialists such as D. pachea. This paradox might be explained if D. immigrans was originally a specialist on citrus fruits.

The different species of Citrus are native in southern China (Hume, 1957) while the immigrans group of the subgenus Drosophila have mostly been reported from the Oriental region (Patterson and Stone, 1952). It is quite conceivable, then, that D. immigrans itself was originally native in southern China breeding in citrus fruits. Since P. digitatum and P. italicum are so specialised on citrus they must have a long association with these fruits going back to their origins in China. Successful breeding on citrus fruits would therefore involve adaptations to the effects of the Penicillium species. As citrus fruits have been spread round the world the Penicillium species and perhaps D. immigrans have gone with them. This process would be similar to the case of D. buzzatii which has become almost cosmopolitan due to the accidental human transport of its breeding sites, weed cacti of the genus Opuntia (Carson, 1965). In D. buzzatii there is no evidence

that it can depart from its cactus niche, whereas if D. immigrans is primititively a citrus specialist it has broadened its niche considerably since then. In Chapter 3, however, I argued that there must be considerable selection pressure for generalisation of breeding sites in the domestic refuse niche.

Obviously this discussion has been extremely speculative but it suggests specific questions, the answers to which may help to explain the origins of the domestic species in general.

CHAPTER 6

A FIELD INVESTIGATION OF LARVAL COMPETITION IN DROSOPHILA

Introduction

In field studies of *Drosophila* the occurrence of competition has often been inferred when two species are exploiting the same resource, even when there is no evidence that this resource is in short supply (Carson, 1951; Sokoloff, 1955; Ayala, 1970; McKenzie and Parsons, 1972). Reynoldson (1964) has condemned the uncritical use of evidence to demonstrate competition. 'Many examples of so-called competition do little else but offer the obvious explanation based on superficial data.' Reynoldson and Bellamy (1970) have drawn attention to the general lack of well-established cases of competition in the field. They have proposed five criteria which together would establish competition beyond reasonable doubt. This chapter reports an attempt to discover whether competition is occurring among the domestic species of *Drosophila* at Pontefract Lane. It concentrates on Reynoldson and Bellamy's third criterion:

> 'There should be evidence from the performance of the particular species populations in the field that intraspecific competition is occurring. This may relate to fecundity, growth rate of individuals or some other appropriate parameter. This criterion assumes that if persistent interspecific competition is occurring then intraspecific competition must also be taking place.'

In this chapter changes in adult body size were used as evidence of intraspecific competition in the larvae. There are two main environmental factors on which a *Drosophila* larva's subsequent adult body size depends. These are the larval food supply and its temperature of development. Increased temperature or larval density reduces the ultimate body size of the adults (Chiang and Hodson, 1950; Sokoloff, 1955; Tantawy and Mallah, 1961).

Body size has been investigated in field populations by several authors, but evidence for competition in wild Drosophila is equivocal. Sokoloff (1957, 1966) found that D. pseudoobscura and D. persimilis, trapped in the wild, were of comparable size to flies reared under near optimal conditions in the laboratory. He concluded that these species do not experience intense competition. In Egypt, Tantawy (1964) found that the wing length of D. melanogaster and D. simulans declined in summer but stated that this was mainly due to high temperature, as food resources are abundant. Similar results were obtained by Stalker and Carson (1947) in D. robusta from North America. McFarquhar and Robertson (1963), in contrast, considered that competition was occurring in their populations of D. subobscura in Scotland. Flies caught in the wild were extremely variable in size, indicating great variation in larval nutrition. Fellows and Heed (1972), in their study of desert Drosophila found that the inferior competitor D. mojavensis was 'stunted' when emerging from the same breeding sites as D. nigrospiracula.

In Chapter 3 it was shown that there is considerable coexistence of different domestic Drosophila species in the same breeding sites. This suggests that interspecific larval competition is possible. This chapter examines seasonal changes in adult body size and the effect of larval competition on body size in the field.

Methods

Wing length was used as an index of adult body size because it is the easiest body dimension to measure on large numbers of flies. The wing length was measured along vein 3 from the anterior cross vein to the wing tip, as shown in Figure 6.1. Wing length is highly correlated with body size (Sokoloff, 1966) but is more sensitive to temperature than thorax length (Stalker and Carson, 1947; Tantawy and Mallah, 1961). Changes in wing length will therefore overestimate the effects of temperature.

The wing lengths of samples of Drosophila from open traps at Kirkgate and Pontefract Lane in 1975 and from bottle traps at Pontefract Lane

Wing of D. melanogaster

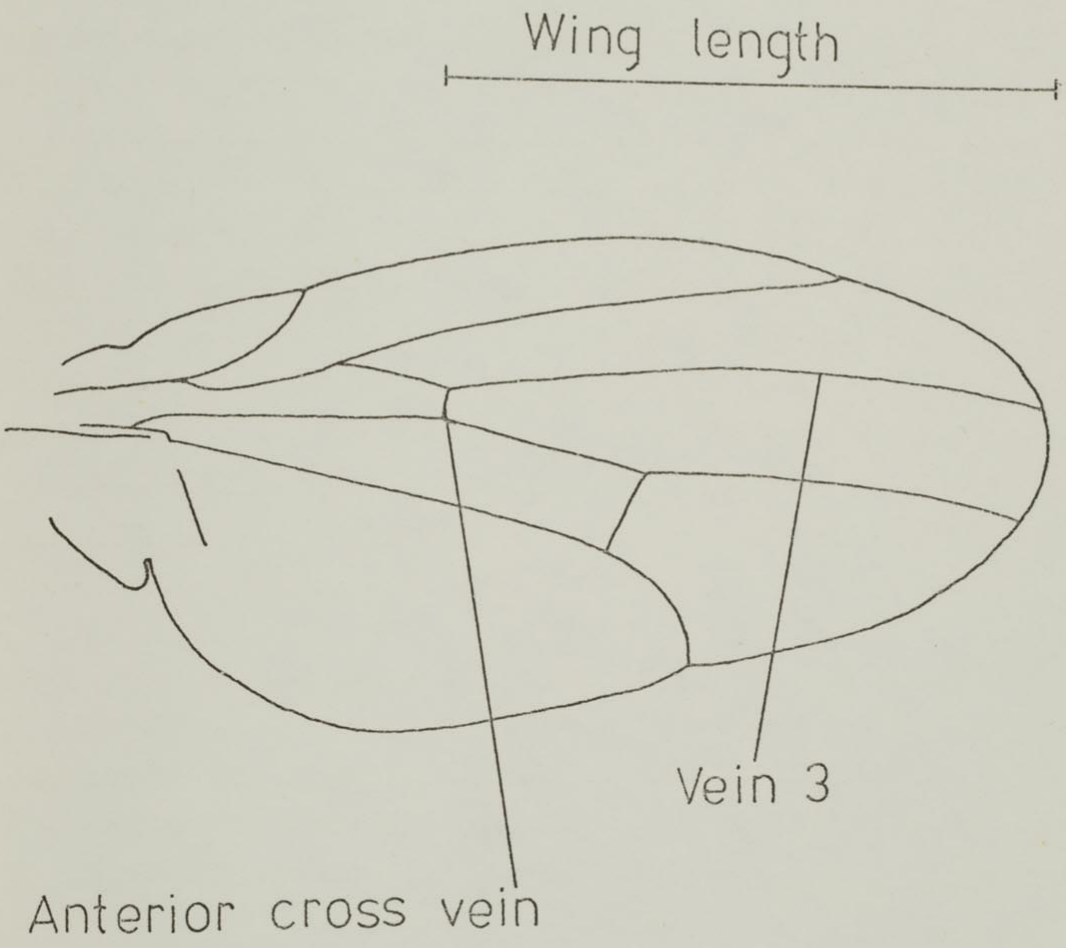


Fig 6.1

in 1976 were measured (Chapter 2). During 1976 breeding sites from Pontefract Lane were brought back to the laboratory (Chapter 3). On every day on which a breeding site yielded adult flies, the wing lengths of a sample of those flies were measured. The environmental conditions, under which those Drosophila had developed, were known in some detail and could be used to interpret the body sizes.

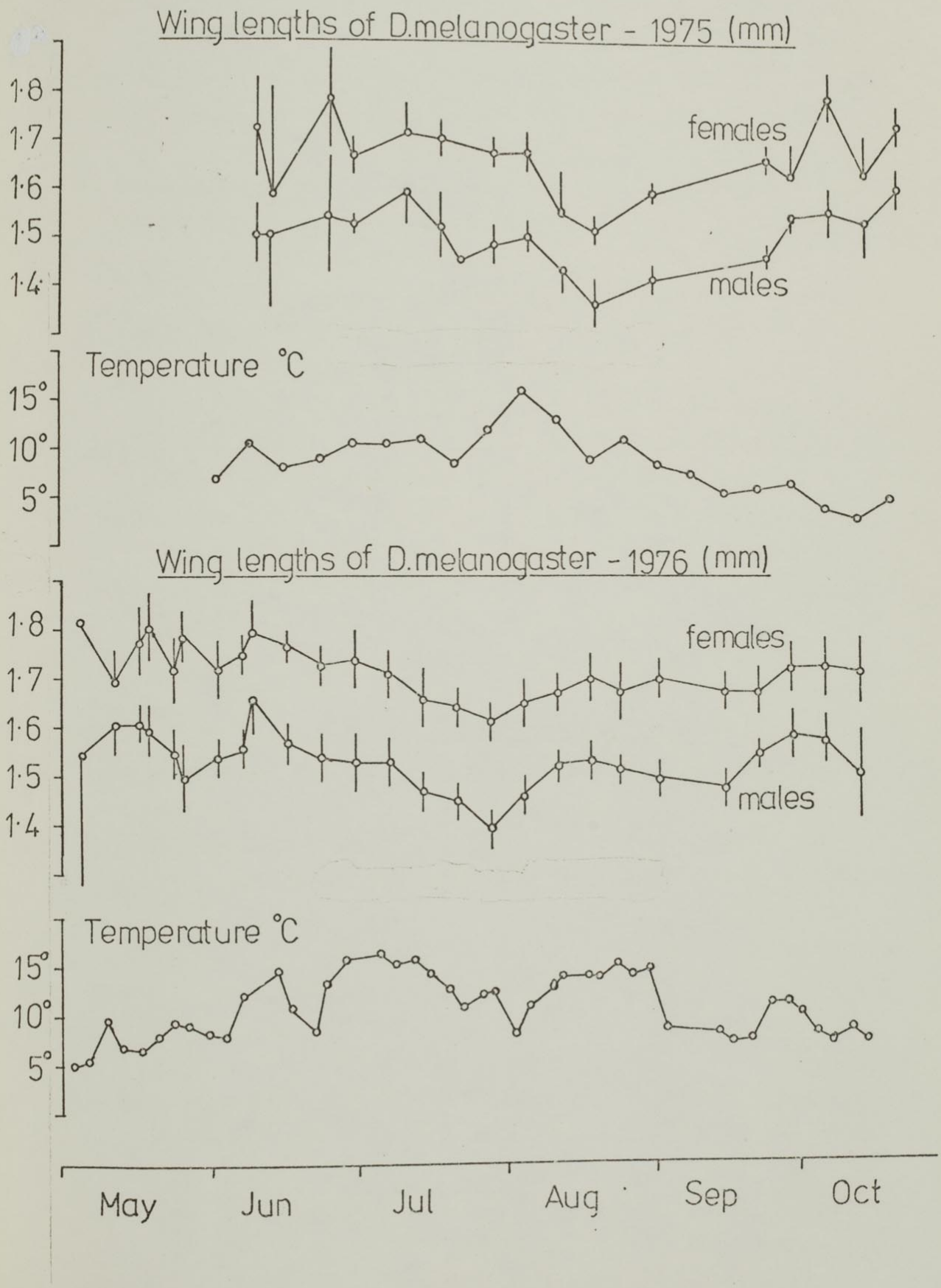
Reeve and Robertson, (1953), have shown that the heritability of wing length in D. melanogaster in their laboratory conditions was about 30%. If heritability in the field is of this order then any seasonal changes in wing length might as well be the results of natural selection as of environmental effects. In order to estimate heritability in the field, mated female D. melanogaster were captured by sweep netting at Pontefract Lane. They were allowed to lay eggs for 24 hours and 10 eggs from each female were transferred to a tube containing 10ml of malt culture medium (Lakovaara, 1969). The tubes were incubated at 18°C until adults emerged. The wing lengths of mothers and offspring were measured and the heritability was estimated from the daughter-mother regression (Falconer, 1964).

Results

Figure 6.2 shows the changes in wing length of D. melanogaster during the summers of 1975 and 1976, together with mean temperatures. In both years the wing length declined towards the middle of the season and then increased. The changes in both sexes corresponded to each other. In 1975 the wing lengths reached their minimum in mid August, whereas in 1976 the minimum was at the end of July. This difference seems to reflect a difference between the temperatures of the two years. In both years the minimum wing length occurred two to three weeks after the maximum mean temperature of that summer.

Temperature may exert a direct physiological effect on body size, but it may also have a secondary influence through its connection with the population dynamics of Drosophila. In Chapter 3 it was shown that the numbers of D. melanogaster emerging from breeding sites is positively

Fig 6.2


Wing lengths of D.melanogaster - 1975 (mm)
1·8
1·7
1·6
1·5
1·4
females
males
Temperature °C
15°
10°
5°
Wing lengths of D.melanogaster - 1976 (mm)
1·8
1·7
1·6
1·5
1·4
females
males
Temperature °C
15°
10°
5°
May
Jun
Jul
Aug
Sep
Oct

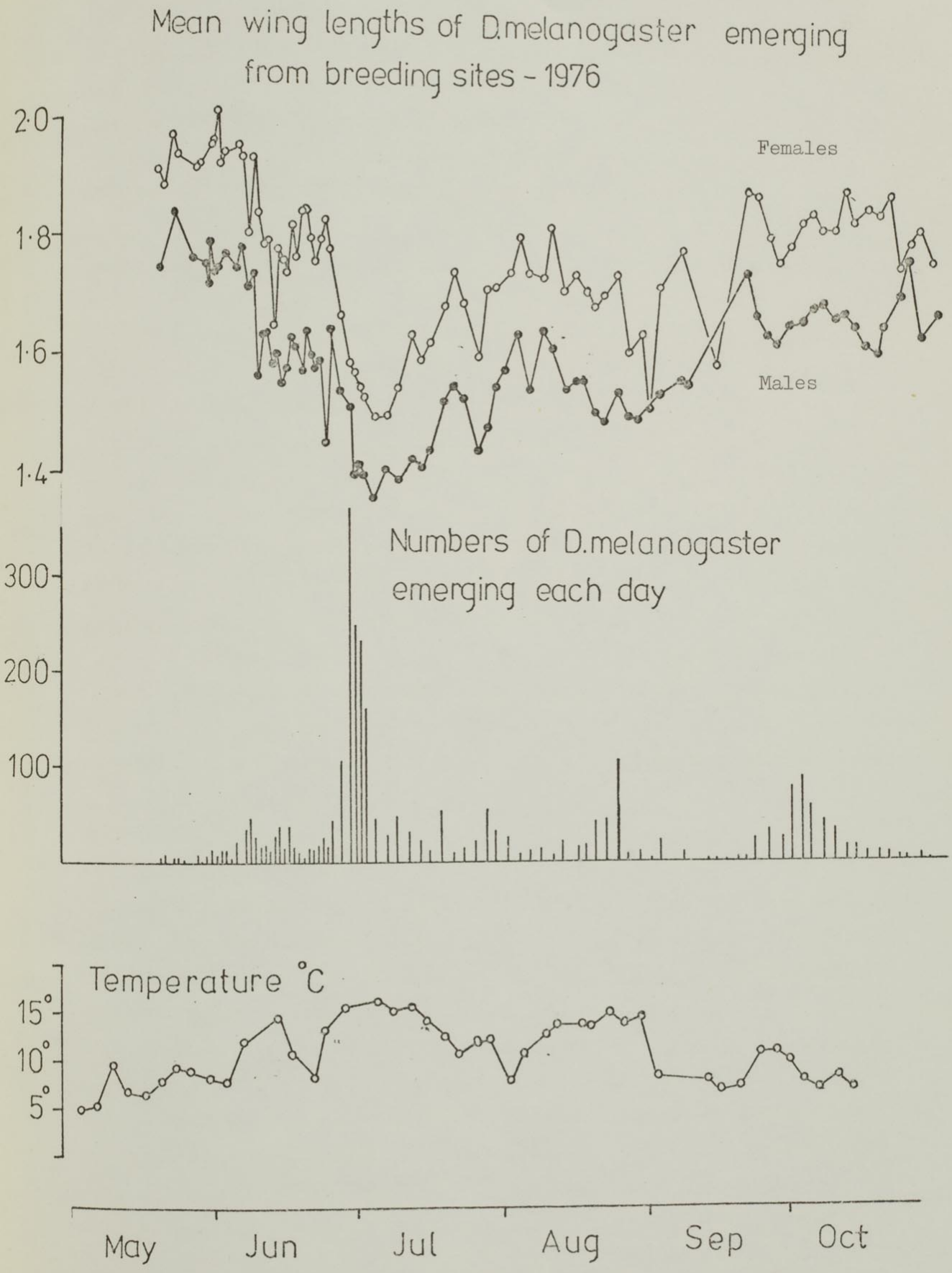
correlated with temperature. Larvae developing at higher temperatures are therefore more likely to be crowded and so have reduced body size. Buzzati-Traverso (1955) found that in crowded conditions D. melanogaster were selected for increased body size. He suggested that those genotypes were favoured that exploited the food most efficiently, thereby reaching a greater weight. This effect seems to be swamped in the wild by the influence of environmental factors.

The heritability of wing length, estimated from the daughter-mother regression was 24%. This is less than the laboratory estimate of Reeve and Robertson (1953) because the mothers developed in the wild where environmental influences are stronger. The true heritabilty in the field could only be obtained if the offspring were allowed to develop in the wild, in the breeding sites chosen by the mother. Also, the father should be known because otherwise maternal effects may increase the apparent heritability. For these reasons the figure of 24% is very much an upper estimate and it seems unlikely that genetic changes in the wing length during the season would be detectable in the phenotypes of flies caught in the wild.

Figure 6.3 shows the mean wing lengths of the D. melanogaster emerging from all the breeding sites brought back to the laboratory, recorded each day. Also shown are the number of D. melanogaster emerging each day and the mean temperature.

At the end of June, 1976 there was a peak in the number of flies emerging and the temperature reached a maximum. These events were reflected in the wing lengths which declined to a minimum. Other smaller peaks in the number of flies emerging were also associated with a rise in temperature and a decline in wing length. There seems to be a cause-effect relationship between temperature and the numbers of D. melanogaster emerging. This may be due to high temperatures speeding up pupal development and so concentrating emergences which would have taken place over a period into one or two days. Larval crowding need not, then, be important even at periods with large numbers of emergences. Reeve and Robertson (1953) have shown that wing lengths

Fig 6.3


Mean wing lengths of D.melanogaster emerging from breeding sites - 1976
2·0
1·8
1·6
1·4
Females
Males
Numbers of D.melanogaster emerging each day
300
200
100
Temperature °C
15°
10°
5°
May
Jun
Jul
Aug
Sep
Oct

are most sensitive to temperatures in the pupal stage and so the temperature during pupation may explain both the number of Drosophila emerging and their wing lengths. One piece of evidence that throws doubt on this is the fact that in 1976 there were two temperature peaks of about the same size; the first, at the end of June, was accompanied by emergences of several hundred D. melanogaster per day and a very large reduction in wing length, while during the second peak at the end of August the number of flies emerging was much less, as was the reduction in wing length.

Effect of temperature and larval crowding.

Multiple regression analysis was used to try to establish the relative magnitude of the effects of temperature and larval crowding on body size. The data used was that obtained from the breeding sites brought back to the laboratory and kept in natural conditions. For each breeding site three parameters were determined; the mean wing length of all the adult male D. melanogaster emerging, the number of D. melanogaster emerging per gram of breeding site ('numbers'), and the mean temperature, from the date on which the breeding site was picked up to the date on which the last Drosophila emerged ('temperature').

Multiple regression must be interpreted with great caution when it is being used to determine the causal factors in a relationship. Gilbert (1973) nevertheless states that if it were known in advance that a given set of xs determines y, multiple regression might be used to assess the relative importance of those xs. There are three provisos; errors of measurement of x dilute the size of the functional relationship, all the important xs must be included in the analysis, and the effect of the xs must be linear and additive. In this analysis it is difficult to assess the effect of errors of measurement. It is likely, however, that the measure of temperature is a better measure of the true temperature than the number of D. melanogaster per gram of breeding site is, of the larval food supply. The multiple regression will therefore underestimate the effect of larval food on wing length. It is fairly certain that all the important xs are included in this

analysis. Bishop et al (1975) have criticised the use of multiple regression where it is possible that an unidentified factor is an important variable. In the Drosophila literature no environmental factors apart from temperature and larval food supply are regarded as important in determining the adult body size. Additivity and linearity were tested for by putting three extra variables into the regression equation. The extra regression accounted for by each of the main variables squared is a measure of the departure of the relationship from linearity. The extra regression on the product of the two variables is correspondingly a measure of the departure from additivity.

Table 6.1 shows the results of the multiple regression analysis. The regression of wing length on the two main variables was calculated first and the derived variables were put into the equation later. The regression equation accounts for a significant amount of the variation in wing length. The coefficient of multiple determination (R^2) equals 59%. The two main variables together account for most of the variation (R^2=54%). Each, on its own, is significant ($p < 0.01$) when the other is taken into account. Of the derived variables, the product of 'numbers' and 'temperature', and 'temperature' squared are on the borderline of significance ($0.01 < p < 0.05$) while 'numbers' squared is non significant. The indication is that in the relationship between 'temperature' and wing length there is a slight departure from linearity. There is also a small multiplicative effect of 'numbers' and 'temperature' on wing length. These departures, however, are not regarded as great enough to seriously affect the interpretation of the analysis. Evidently both 'temperature' and 'numbers' are influential in determining body size, but 'temperature' accounts for much more of the variation than 'numbers' and seems to be the more important variable.

One reason why the number of D. melanogaster per gram of breeding site is less important may be that breeding sites are very variable. A gram of apple must be very different nutritionally from a gram of tomato for example. For this reason the multiple regression analysis was carried out separately for each species of breeding site; this

Table 6.1 Regression of male wing length on numbers of *D. melanogaster* and temperature - analysis of variance

y = mean wing length of D. melanogaster males
x_1 = numbers emerging per gram of breeding site ('numbers')
x_2 = mean temperature ('temperature')

Source of variation	SS	df	MS	F	
Regression	4.152	5	0.830	27.02	$p < 0.01$
x_1 alone	0.366	1	0.366	11.91	$p < 0.01$
x_2 alone	3.443	1	3.443	112.08	$p < 0.01$
$x_1 \cdot x_2$	0.157	1	0.157	5.12	$p < 0.05$
x_2^2	0.181	1	0.181	5.89	$p < 0.05$
x_1^2	0.006	1	0.006	0.18	n.s.
Residual	2.918	95	0.031		
Total	7.070	100			

Table 6.2 Regression performed separately on each species of breeding site - analysis of variance of pooled results

Source of variation	SS	df	MS	F	
Regression	3.568	18	0.198	9.91	$p < 0.01$
x_1 alone	1.299	9	0.144	7.25	$p < 0.01$
x_2 alone	2.269	9	0.252	12.67	$p < 0.01$
Residual	1.373	69	0.020		
Total	4.941	87			

reduced the effect of differences between the species. Only the two main variables 'numbers' and 'temperature' were put into the equation, but much more of the variance in wing length was accounted for in this analysis. The mean R^2 was 86.3%. Table 6.2 gives the results; the sums of squares were obtained by adding up the sums of squares for each breeding site. The total sum of squares is less than that obtained in Table 6.1 because the analysis could not be performed on breeding site species represented by only one individual. Both main variables again accounted for a significant amount of the variation in wing length but 'temperature' was only slightly more important than 'numbers' when the breeding site species were considered separately. If it were possible to consider breeding sites in different states of decay separately more of the variation in wing length might be accounted for by 'numbers'. The problem is in determining the intensity of competition without knowing precisely what the larvae are competing for and how to measure it.

The evidence is, however, that numbers of D. melanogaster per gram of breeding site is an important determinant of wing length. The larvae are evidently short of some resource, a sufficiency of which would enable them to grow to a size determined only by temperature. In other words they must be competing.

Interspecific Competition

In Chapter 3 it was demonstrated that several other species of domestic Drosophila coexist with D. melanogaster in the same breeding sites. Since there is evidence of intraspecific competition in D. melanogaster, interspecific competition might also be occurring if the coexisting species are exploiting the same resource within the breeding sites. A negative correlation between the wing lengths of one species and the numbers of another, emerging from the same breeding site may indicate the occurrence of competition between the two. Such an interpretation must be made with care, however, because the numbers of one species may be correlated with conditions which adversely affect the other, independently of any competition.

Regression analyses were performed, of the wing lengths of the males of each species on the numbers of every other species, per gram of breeding site. The amount of variation in each species' wing length accounted for by the numbers of every other species is given in Table 6.3 in the form of F ratios. Spaces in the table occur where two species coexisted too infrequently for the analysis to be performed. Among the 22 F tests shown in Table 6.3, there is a probability of 68% that one will be significant by chance. The results of the individual analyses are not, therefore, important. The interesting fact is that the numbers of D. melanogaster account for a significant amount of the variation in wing length of three species, including itself. The other species are, on the whole, at a competitive disadvantage to D. melanogaster, which is also the only species in which intraspecific competition is important.

Discussion

It has been shown that body size in D. melanogaster is partly determined by the level of intraspecific competition. Previous studies (Sokoloff, 1957, 1966; Tantawy, 1964; Stalker and Carson, 1947; McFarquhar and Robertson, 1963) have not attempted to separate the effect of temperature from food shortage. They have explained changes in body size with whichever of the factors seemed, superficially, to be important. Intraspecific competition in Drosophila may, therefore, be much commoner than these studies suggest.

Studies of crowding on Diptera in the laboratory have shown that reduced body size due to competition is associated with reduced survival (Sokoloff, 1955; Miller, 1964; Sullivan and Sokal, 1963). It can be assumed, then, that D. melanogaster do suffer some density dependent mortality in the field. Table 6.3 also suggests that this species is dominant competitively at Pontefract Lane. The coexistence of seven common species of Drosophila therefore needs some explanation.

The two species suffering in competition seem to be D. immigrans and D. hydei. These species, however, are generalists (Chapter 3); they have an ecological refuge in vegetable breeding sites not exploited

Table 6.3 Effect of numbers of each species on the body size of every other. F-tests give the significance of the proportion of variation in wing length accounted for by 'numbers'

	Numbers of Drosophila per gram of breeding site					
	D. melanogaster	D. simulans	D. immigrans	D. hydei	D. busckii	D. subobscura
D melanogaster	F=5.72 $p < 0.05$	F=0.14 n.s	F=0.00 n.s	F=0.79 n.s	F=0.00 n.s	F=0.00 n.s
D simulans	F=3.68 n.s	F=2.10 n.s	F=7.77 $p < 0.05$			F=2.01 n.s
D immigrans	F=12.55 $p < 0.01$	F=0.07 n.s	F=0.93 n.s	F=0.60 n.s		F=0.68 n.s
D hydei	F=5.35 $p < 0.05$		F=0.54	F=3.11 n.s		
D busckii					F=0.63 n.s	
D subobscura	F=0.15 n.s	F=0.96 n.s				F=0.01 n.s

by D. melanogaster. The other fruit specialists, D. simulans and D. subobscura, which have no refuge in different breeding sites, may avoid competition by behavioural adaptations. For instance, Barker (1971) has shown that D. simulans larvae burrow deeper into laboratory medium than D. melanogaster.

There is some evidence, also, that the population of D. melanogaster, despite the density dependent mortality, never reaches carrying capacity. Even at the end of June when emergences were at their peak many breeding sites remained unused and others produced very few flies. Birch and Battaglia (1957) found a similar situation in D. willistoni. When breeding sites were brought in from the wild far fewer flies were reared from them than the fruits could sustain in the laboratory, despite the fact that the population size seemed to be limited by the amount of fruit available. The unused sites at Pontefract Lane similarly, appeared suitable for breeding.

In traditional mathematical and laboratory models of competition the environment is homogeneous and the intensity of competition is the same throughout. Wild Drosophila, however, live in a heterogeneous environment. The larvae live in discrete breeding sites and competition in one has no direct effect on other sites, the larvae usually being unable to migrate between them. If adult females find breeding sites with a given probability, then many sites may not be found while a few are found by several females. In these few larval competition may be intense. As population density increases to carrying capacity even the empty sites will be found. Unused breeding sites are therefore a sign that mortality, not associated with competition, is keeping the population size down.

The cause of this mortality is not known for certain. Subjective evidence suggests that there is little predation of Drosophila at Pontefract Lane. Insect predators are rarely found in or around traps and no parasitoids were reared from breeding sites. Abiotic factors are required to explain the comparatively low population size. The likely explanation is that many adult Drosophila lay eggs on fruit and vegetables which are subsequently swept up and removed from the market

(Chapter 1). To the population at Pontefract Lane removal of immature stages is equivalent to a high level of density independent mortality. This, coupled with massive winter mortality must effectively limit the population size and will ensure that the community never reaches an ecological equilibrium.

To many ecologists this will seem a controversial finding. Clark et al (1967) have reviewed the controversy between those biologists who believe that populations are controlled by density dependent mortality and those who believe density independent mortality is more important. Williamson (1972) considers that the argument is settled. Following the logic of Moran (1962) he states that unless populations were limited by density they would inevitably decline to extinction, and so all populations, with the possible exception of temporary populations, must be limited by density dependent factors. In the real world, however, as opposed to the homogeneous theoretical world of Moran, there is no reason to suppose that any population is permanent. Especially in the temperate regions populations may commonly suffer local extinctions followed by recolonisation. The necessary condition for density independent factors to control the population is that the environment must be heterogeneous enough to always allow some individuals to survive any density independent catastrophe. At Pontefract Lane the domestic Drosophila must be at or near extinction during the winter. The population is reconstituted in spring from neighbouring populations or from flies imported with the fruit. There is no reason, then, given the evidence of this chapter, to doubt that density independent factors limit the population.

CHAPTER 7

REPRODUCTIVE STRATEGIES AND DOMESTIC SPECIES OF DROSOPHILA

Introduction

Much of the current interest in reproductive strategies is centred on r- and K- selection theory (Mac Arthur and Wilson, 1967). This is an attractive theory because it seeks to explain the evolution of several components of fitness using only one variable, whether the population is (K-selected) or is not (r-selected) at carrying capacity. Pianka (1970) has published a table of the characters which should be favoured by the two types of selection. r-selection favours rapid development, high r-max, early reproduction, small body size, semelparity, and short life. K-selection favours slower development, greater competitive ability, lower resource thresholds, delayed reproduction and longer life. Barbosa (1977) has supplemented this list with many other characteristics attributed to either r- or K-strategists.

An obvious prediction of the theory is that the characters should be correlated (Stearns, 1976); a species should possess either r-characters or K-characters but not both. Wilbur et al (1974), however, cite the example of the green sea turtle in which extremely long adult life is associated with high fecundity and small offspring. They also give examples of several other species in which the life history characteristics are not necessarily the result of r- and K-selection. They suggest that additional ecological dimensions such as environmental predictability and the effects of predation are also important in the evolution of reproductive strategies.

Several theoretical papers have examined the effect of environmental fluctuations on life histories. Some authors (MacArthur, 1960; Pianka, 1970; Southwood, et al, 1974) have assumed that environmental fluctuations, because they reduce the population below carrying capacity, should result in r-selection. Murphy (1968) and Schaffer

(1974), however, have shown that if the fluctuating environment has a greater effect on juvenile than on adult mortality, then increased adult longevity and reduced reproductive effort will be selected for. The pattern of mortality in the life history of a species has been shown to be important in several other theoretical models (Williams, 1966; Emlen, 1970; Gadgil and Bossert, 1970; Hirshfield and Tinkle, 1975; Pianka and Parker, 1975) and so the effects of predation and environmental fluctuations may be just as important as population density (r- and K- selection) in the evolution of reproductive strategies.

Stearns (1976) has severely criticised the field evidence that has been gathered to test the theories. Most of this evidence consists of correlations between environmental patterns and reproductive characters. Stearns dismisses the need for further evidence of this kind and says "In order to make progress at this point, we need carefully controlled field experiments on a short lived plant or animal." It must be said, however, that experimental tests of theoretical models with the theoretical assumptions built into the experimental design nearly always yield the 'desired' result, and so are not always very valuable. Although the correlative field evidence cannot be regarded as tests of the theories, they have yielded much information about the predominant selective forces affecting the reproductive strategies of different species.

Many field studies have attempted to explain observed reproductive strategies in terms of r- and K-selection theory. Unfortunately it is very difficult to establish whether a population is at carrying capacity or not, so this is rarely attempted. Environmental disturbance is often used as an indication that r-selection is occurring. The pattern of mortality in the life history of a species will also be affected by environmental disturbance, however, and the effects of this cannot be separated from the effects of r- and K- selection. A study of this type is that of Gadgil and Solbrig (1972) who showed that dandelions from disturbed sites showed increased reproductive effort. Similar results were achieved by Abrahamson and Gadgil (1973) in goldenrods, Abrahamson (1975) in dewberries, Gaines et al (1974)

in sunflowers, and Schlosser and Buffington (1977) in Aedes aegypti. Some studies have assumed that northern species or races should have more r-characters than southern ones. McNaughton (1975) in his study of Typha found that the northern species had the highest reproductive effort, while the southern species had greater competitive ability. High reproductive effort has often been used as an indicator of an r-selected species, though it could also indicate greater unpredictable mortality of adults than of juveniles (Murphy, 1968). Force (1972) found that among the hymenopterous parasitoids of gall forming midges, those with highest reproductive effort were the poorest competitors. Grahame (1977) was able to explain the life history characters of two species of Lacuna after classifying them as r- or K- species on the basis of their reproductive effort. Forsyth and Robertson (1975) found that the characteristics of a sarcophagid fly were consistent with it being a K-species. Loya (1976) correlated the characters of a coral species with a supposed r-strategy. All the above field studies have suffered from an uncritical assumption that r- and K-selection, that is population density, was the dominant force affecting life history strategies.

Other authors have been forced to look for different selective forces. Menge (1974) in a seastar, Leptasterias, found that density independent mortality caused by wave action resulted in decreased reproduction, contrary to r- and K- theory. He explained this as the result of high juvenile mortality selecting for increased adult longevity and reduced reproductive effort. Dearn (1977) explained the reproductive effort of grasshoppers by altitudinal changes in the predictability of the growing season. Crovello and Hacker (1972) used environmental unpredictability to explain the greater reproductive effort of urban strains of Aedes aegypti when compared to rural strains. Effects of predation were used to explain aspects of the life histories of amphipods by Strong (1972) and of lizards by Derickson (1976). Price (1973) used availability of hosts to explain the strategies of parasitoid wasps, while Schaffer and Elson (1975) considered the lengths of rivers were important for populations of salmon.

Reproductive effort has been an important concept in life history

theory, but its measurement in practice has proved very difficult. Hirshfield and Tinkle (1975) defined reproductive effort as the proportion of total energy that an organism devotes to reproduction. They criticised the use of simple measurements of phenotypic characteristics which have a presumed, but unknown relationship to reproductive effort. Tinkle and Hadley (1975) obtained estimates of reproductive effort in lizard species based on a knowledge of the energy budgets, but such estimates are rare. Grahame (1977) has defended the simple measures such as the ratio of reproductive to somatic biomass on the grounds that they have given interpretable results.

This chapter describes a study of the reproductive strategies of the domestic species of Drosophila. Drosophila are potentially excellent subjects for studies of reproductive strategies because their short generation time enables the genetic basis of any character to be easily established (Stearns, 1976). Unfortunately the only major study of the reproductive strategies of Drosophila in the field is that of Kambysellis and Heed (1971). They concluded that the reproductive physiology of the Hawaiian Drosophilidae had been adapted to the carrying capacity of the larval niches. In species breeding in abundant or nutritionally rich breeding sites evolution favoured increased family size. In species using poorer sites evolution favoured efficiency of conversion of food into offspring by lowering family size. The domestic species provide an interesting contrast to the Hawaiian Drosophila. They are well known for their colonising ability (Carson, 1965; Dobzhansky, 1965) and should therefore be at the r-end of an r-K continuum.

Methods

Three categories of information were sought about the Drosophila species; first, a simple measure of reproductive effort, second, how this effort was allocated between egg size and egg number, and third, details of the life history such as age at first reproduction and investment in adult food reserves.

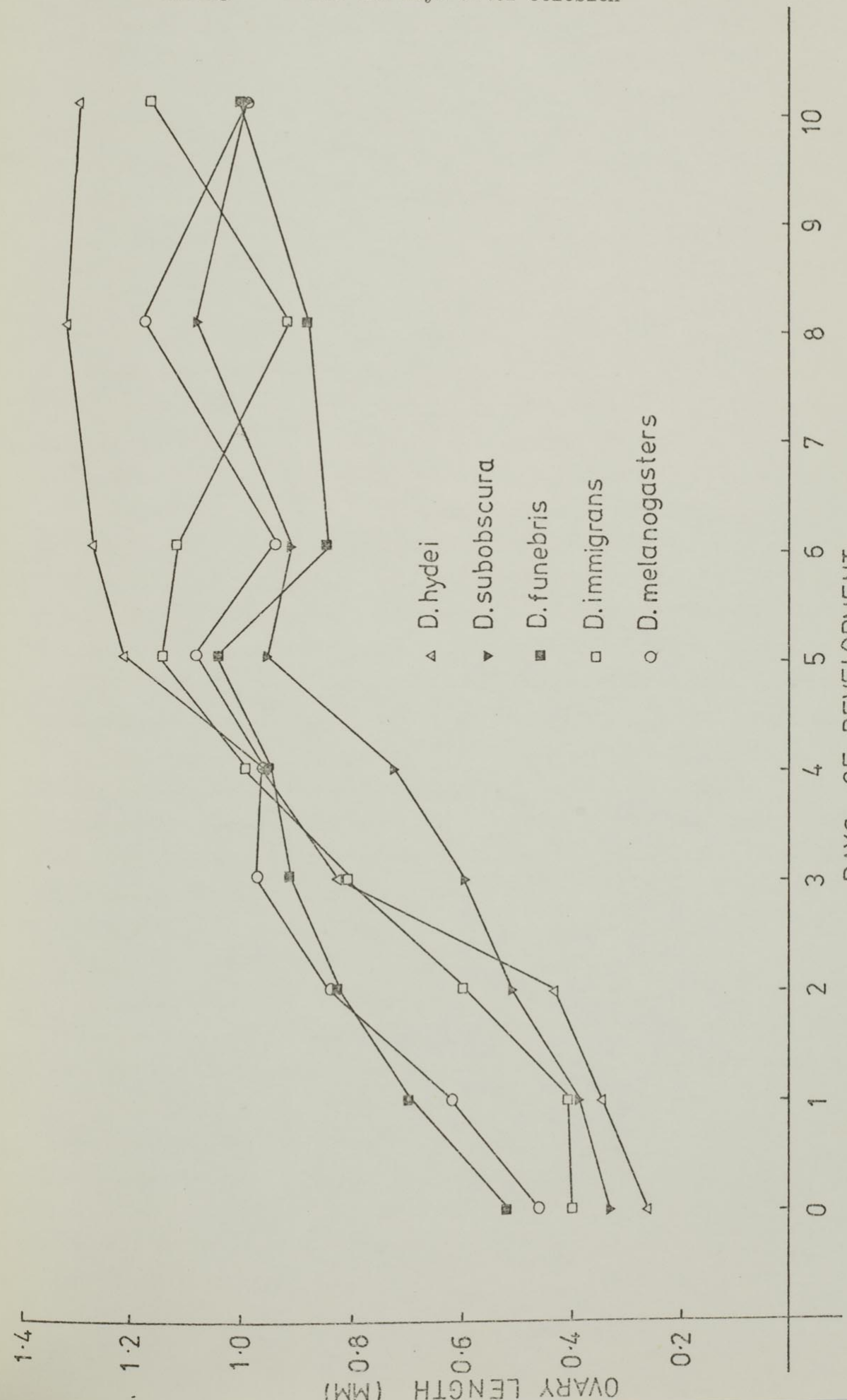
Reproductive Effort

In this study reproductive effort was measured as the ratio of the reproductive to the somatic biomass. Several assumptions have to be made if this measure is to be used as an estimator of the real reproductive effort. It must be assumed that the turnover of reproductive tissue goes on at the same rate in all the species, that the energy demands for growth and maintenance are the same for equal weights of reproductive and somatic tissue, and that the animal expends little energy in searching for mates or breeding sites. Many studies have also assumed that the effect of the environment on reproductive effort is negligible and that observed reproductive efforts have an entirely genetic basis. In this study the reproductive effort was not measured on Drosophila obtained in the wild, but on their F_1 offspring which were reared in conditions of constant food and temperature. This ensures that any differences between the species were genetic.

Since adult Drosophila mature for several days after eclosion it was necessary to make sure that reproductive effort was measured on mature flies, preferably of the same age. A preliminary study was set up to establish the rate of ovary maturation in the different species. Adults of all the species except D. simulans and D. busckii were reared in population cages and allowed to lay eggs in bottles of Drosophila medium (Shorrocks, 1972) for 24 hours. The bottles were incubated at 18°C and inspected every morning. When adults emerged they were put into 75mm by 25mm glass vials containing Drosophila medium and kept at 18°C. Every day after eclosion, for ten days, 12 females of each species were dissected. The lengths of the ovaries were measured. Mature eggs can be recognised by the presence of chorionic filaments. The number of mature eggs in each ovary was counted. The results are presented in Figure 7.1. The ovaries of all species contained mature eggs after four days and had reached more or less their maximum length after five days. In the study of reproductive effort the females were allowed to mature their ovaries for ten days to ensure complete development.

Adult flies for the determination of reproductive effort were obtained

Fig 7.1 Changes in mean ovary length of each species of Drosophila during the first few days after eclosion



from Pontefract Lane. On eight occasions, between May and July 1976, adult flies were collected by sweep netting over discarded fruits and vegetables. A total of 137 flies were investigated. The wild adult females were put individually onto 75mm by 25mm glass vials containing malt culture medium (Lakovaara, 1969), which was prepared with carefully weighed quantities of the ingredients. The live yeast supplement was omitted from Lakovaara's recipe, but twice the recommended quantity of killed yeast was used. The medium was made up in only two batches to increase the uniformity of the food. 10ml of medium were measured into each vial, the tops were covered with plastic film and the malt vials were stored in a refrigerator until required. The wild females were allowed to lay eggs for 24 hours. Most females laid fertile eggs, having been inseminated in the field. After laying eggs the wild females were dissected, the wing length and ovary length was measured and the ovarioles and mature eggs counted. This was to discover if any of these simple phenotypic traits were correlated with reproductive effort. Ten eggs from each wild female were transferred to another malt vial so that the food supply for each larva was the same. The eggs were incubated at 18°C and inspected every day. When adult females emerged they were put individually onto new malt vials and allowed to mature for ten days at 18°C. These flies were unfertilised, so few eggs were laid (Mohan, 1971). After the ten days the flies were dissected in a weighed foil tray. The ovaries were removed and placed in another weighed foil tray. Both trays with their contents were dried and reweighed. Reproductive effort was calculated as the dry weight of the ovaries divided by the total dry weight. The total time to maturity for each species was obtained in this study as the sum of the time from egg to eclosion of the F_1 females and the time from eclosion to maturity in the preliminary study.

Allocation of Resources

There is quite a considerable body of theory dealing with the allocation of resources to clutch size and egg number (Cody, 1966; Price, 1974; Wilbur, 1977). Presumably when *Drosophila* find a suitable breeding site in the wild they usually lay several eggs and so can be thought of as laying the eggs in clutches. Unfortunately it is

impossible to obtain information about clutch sizes in the field directly. When eggs are found on a breeding site it is not known how many individuals laid them, while laboratory experiments are also informative, because so little is known about factors such as substrate texture and state of decomposition, which might influence clutch size. The problem of clutch size might be approached indirectly, however. Kambysellis and Heed (1971) found that in species of Drosophila which deposit numerous eggs simultaneously, the ovariole number was increased. Clutch size seems, therefore, to be related to ovariole number. D. melanogaster can only mature three eggs per ovariole per day (King et al, 1966), so ovariole number effectively sets an upper limit on clutch size, unless, of course, laying opportunities are so infrequent that several mature eggs are accumulated in each ovariole. In this study ovariole number and number of eggs per ovary were used as an indication of clutch size.

Drosophila were obtained from the bottle traps at Pontefract Lane each week (Chapter 2) and a sample of the flies were dissected. The thorax and one ovary were measured and the ovarioles and mature eggs were counted. A total of 555 Drosophila were dissected.

The egg volume characteristic of each species was determined as a comparative measure of the parental investment in each offspring. Eggs were obtained by putting vials of malt medium into population cages and allowing the Drosophila to lay. The lengths and maximum widths of 25 eggs of each species of Drosophila were measured. Assuming each egg is a regular ellipsoid its volume could be calculated from the formula:-

$$\text{Volume} = \pi LW^2/6$$

where L = maximum length and W = maximum width (King et al, 1966).

Parental investment in its own future survival was investigated in the laboratory, resistance to starvation being used as a measure of an adult's food reserves. Adults of each species of Drosophila were fed for 24 hours on malt medium liberally supplemented with live yeast.

75mm by 25mm vials were prepared containing 5ml of agar jelly, but no food. Ten flies were introduced into each vial and for each species six vials were set up. The vials were kept at 18°C and any dead flies were removed daily. For each species of Drosophila the cumulative adult survival, transformed to probits, was plotted against hours of starvation, transformed to logarithms. In all cases a straight line could be accurately fitted to the points by eye and adult survival was expressed as the LD50 of hours to starvation.

Results

Reproductive Effort

Table 7.1 shows the reproductive effort of each species of Drosophila expressed as the mean of all the F_1 daughters. A one way analysis of variance was performed. The data was not transformed because the reproductive efforts of D. melanogaster were normally distributed (χ^2=2.72, df=8, p≃0.95) and the species' variances were homogeneous (Bartlett's test, χ^2=6.31, df=5, p>0.20). The analysis revealed significant heterogeneity among the Drosophila species for reproductive effort. A comparison among the means was carried out using Student-Newman-Keul's test. In Table 7.1 the Drosophila species are ranked in order of their reproductive efforts. Groups of species not significantly (p=0.05) different from one another are underlined. Species in non-significant groups are not always adjacent, due to different sample sizes, and here double headed arrows join the non significant pairs. D. simulans, D. melanogaster and D. subobscura all have significantly greater reproductive effort than D. immigrans. D. melanogaster also showed greater reproductive effort than D. hydei. All other differences were non-significant.

Table 7.2 shows the results of regression analyses of daughter's reproductive effort on mother's ovary length and on mother's ovariole number. These were carried out for D. melanogaster, the species for which most data were available. There is significant heterogeneity among mothers in their daughter's reproductive effort, but neither the linear regression on ovary length or on ovariole number accounted

Table 7.1 Mean reproductive effort with 95% confidence intervals

	Reproductive effort (%)
D. melanogaster	26.0 ± 1.87
D. simulans	30.7 ± 17.44
D. subobscura	22.9 ± 3.07
D. immigrans	16.4 ± 2.76
D. hydei	16.2 ± 2.68
D. funebris	19.6 ± 7.65

One-way analysis of variance

Source of variation	SS	df	MS	F	
Among species	2273.2	6	378.9	6.45	$p < 0.001$
Residual	7278.8	124	58.7		
Total	9552.0	130			

Comparison among means - SNK test (p=0.05)

Rank	1	2	3	4	5	6
Species	D. simulans	D. melanogaster	D. subobscura	D. funebris	D. immigrans	D. hydei

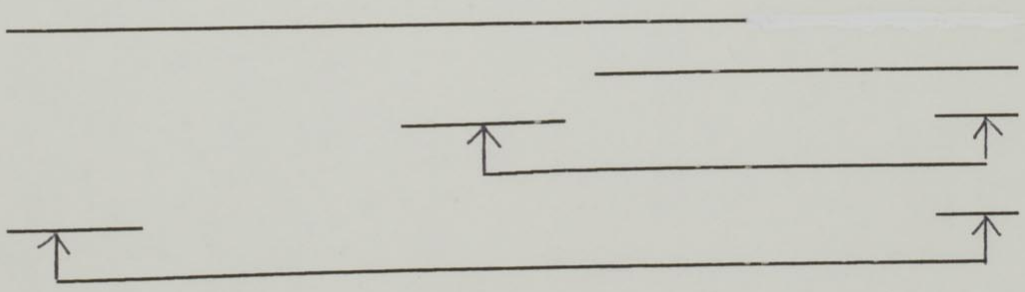


Table 7.2 Regression analyses of reproductive effort on two simple phenotypic traits

1. Regression of reproductive effort on mother's ovary length

Source of Variation	SS	df	MS	F	
Among mothers	2926.6	25	117.1	2.55	$p < 0.01$
Linear regression	19.7	1	19.7	0.43	n.s.
Deviation from regression	2906.9	24	121.1	2.64	$p < 0.01$
Residual	2616.3	57	45.8		
Total	5575.9	82			

2. Regression of reproductive effort on mother's ovariole number

Source of Variation	SS	df	MS	F	
Among mothers	2012.9	23	87.5	1.82	$p < 0.05$
Linear regression	64.3	1	64.3	1.33	n.s.
Deviation from regression	1948.6	22	88.6	1.84	$p < 0.05$
Residual	2217.7	46	48.2		
Total	4230.6	70			

for a significant amount of this variation. As expected environmental effects were very strong. The two phenotypic measures, ovary length and ovary number cannot, then, be used as indices of reproductive effort.

Allocation of Resources

Table 7.3 gives the thorax lengths and measurements of ovaries made on wild flies. Thorax length was measured as an indication of body size. In intraspecific comparisons thorax length cubed is often taken as being directly proportional to body size (Robertson, 1957). In interspecific comparisons, where body shape as well as size is different then this may not be the case. Linear regressions of mean species body weight on mean species thorax length and on mean species thorax length cubed were carried out. The total sum of squares was 3.75 (df=5), the sum of squares explained by thorax length was 1.20 (df=1, F=1.88, n.s.) and by thorax length cubed was 0.23 (df=1, F=0.26, n.s.). The body weights were determined on small samples and so the means are much less reliable than the mean thorax lengths. Though neither thorax length nor its cube explained significant amount of the interspecific variation in body weight, the evidence is that thorax length is the better linear estimator.

In all the species the mean number of mature eggs was over 40% of the mean ovariole number. To test whether mature egg number was associated with ovariole number, the correlation coefficient between the two variables was computed, for each species. All the correlations were positive and all were significant at the 1% level except those for D. simulans and D. funebris which were non significant. The number of mature eggs in an ovary seems to be related to ovariole number. This gives further credence to ovariole number as a measure of clutch size.

Table 7.4 gives mean egg volumes for each species of Drosophila with 95% confidence limits. We now have information for each species on its allocation of reproductive effort to clutch size (ovariole number) and to egg size. Depending on its body size each species has a

Table 7.3 Measurements of wild Drosophila with 95% confidence intervals

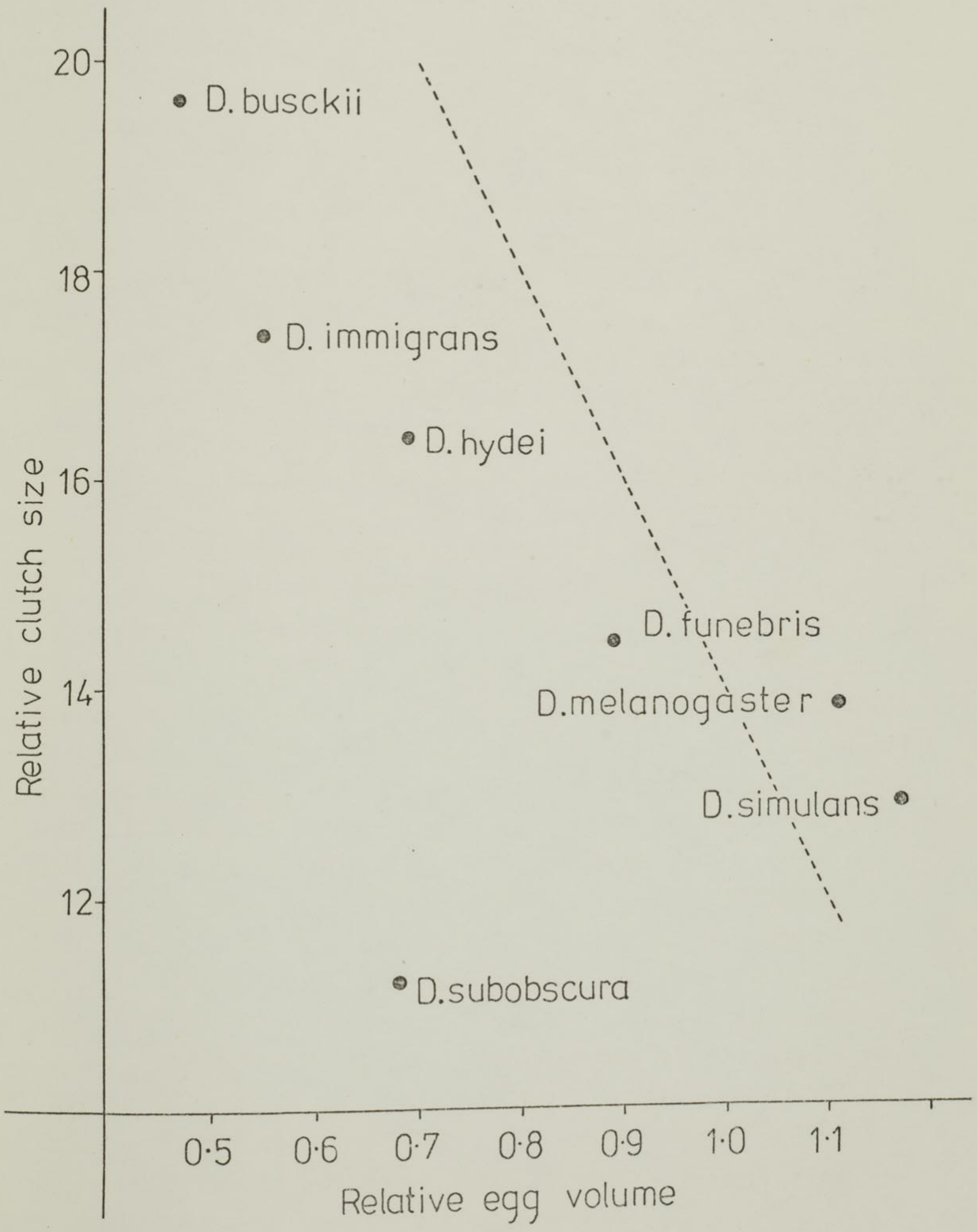
Species	n	Thorax length (mm)	Ovary length (mm)	Ovariole number	Mature eggs per ovary
D. melanogaster	252	1.11±0.01	1.12±0.03	15.4±0.4	7.2±0.7
D. simulans	33	1.02±0.03	0.93±0.07	13.2±1.2	5.6±1.9
D. subobscura	86	1.24±0.02	1.07±0.04	13.9±0.8	9.7±1.7
D. immigrans	57	1.59±0.04	1.30±0.08	27.6±2.1	16.1±4.6
D. hydei	70	1.51±0.02	1.33±0.08	24.8±1.3	22.1±3.7
D. busckii	22	1.05±0.03	1.10±0.08	20.6±3.1	10.9±3.1
D. funebris	31	1.41±0.01	1.21±0.10	20.4±2.0	12.5±3.5

Table 7.4 Egg volume with 95% confidence intervals

	Mean egg volume ($mm^3 x10^{-2}$)
D. melanogaster	1.23±0.03
D. simulans	1.19±0.04
D. subobscura	0.84±0.03
D. immigrans	0.88±0.03
D. hydei	1.04±0.04
D. busckii	0.49±0.02
D. funebris	1.26±0.06

different quantity of resource to allocate. In order to correct for this the ovariole number and egg volume were divided by thorax length to give respectively the relative clutch size and relative egg volume. The product of these two values is the relative clutch volume, a measure of the investment in the whole clutch (Wilbur, 1977). Figure 7.2 shows, for the seven species of Drosophila, their relative clutch sizes plotted against the relative egg sizes. Among the cosmopolitan species there is a remarkably linear inverse relationship between relative clutch size and relative egg volume. Only D. subobscura fails to conform to this pattern. Superficially this relationship suggests that the cosmopolitan species are all devoting the same proportion of their resources to reproduction, but allocating it to large clutches or large eggs. The relative clutch volumes are, however, different in the different species. The broken line in Figure 7.2 is the line of equal relative clutch volumes. It has a much steeper slope than the line on which the Drosophila species fall. Relative clutch volume is a similar measure of reproductive effort to the ratio of reproductive to somatic biomass. For the cosmopolitan species Spearman's rank correlation between the two measures is +0.80 ($p \simeq 0.05$). Perhaps the line on which the Drosophila species fall in Figure 7.2 is a line of equal reproductive effort. The assumptions which lead to the use of the biomass ratio or relative clutch volume as measures of reproductive effort might then be usefully questioned. One of the major assumptions was that the turnover of reproductive tissue was the same in all species. It is quite possible, however, that the time it takes for a fly to mature and lay an egg depends on the species' relative egg volume. The mean ovary size of a species would then be proportional to the relative egg volume as well as to the energy devoted to reproduction. Species with small eggs would have a greater reproductive effort than indicated by the relative clutch volume or by the biomass ratio. If this latest assumption were correct then in Figure 7.2 the true line of equal reproductive effort would be less steep than the line of equal relative clutch volumes, and so despite the evidence of the biomass ratio the cosmopolitan domestic species of Drosophila might have equal reproductive efforts. A new, equally plausible assumption has lead to a different conclusion about the reproductive efforts. This confirms the opinion of Hirshfield and

Fig 7.2 Relative clutch size plotted against relative egg volume. The broken line indicates equal relative clutch volumes.



Tinkle (1975), that real measures of reproductive effort can only be obtained through detailed studies of energy budgets.

Table 7.5 gives the adult survivals of each species of Drosophila expressed as the LD50 of hours to starvation. The LD50 was determined separately for each sex and then combined to give an overall figure, assuming a 1:1 sex ratio. Males were significantly more susceptible to starvation than females in all the species except D. hydei. Trivers (1972) has shown that where there is little male parental investment selection favours adaptations in males that lead to high reproductive success at the cost of increased mortality. Adult males should then invest less in their own food reserves than females.

Table 7.6 gives for each species the time from egg to eclosion, measured during the determination of reproductive effort, and the time from eclosion to maturity, measured during the preliminary study. The sum of the two gives the time to maturity.

Discussion

Many different characters have been measured which might be influenced by the reproductive strategies of the different species of Drosophila. The rank correlations between the characters were calculated in order to uncover any pattern among the species. The characters chosen were the biomass ratio, the relative clutch volume, the ovariole number, the number of mature eggs per ovary, egg volume, thorax length, time from egg to eclosion and LD50 of adult survival. The species were ranked according to their scores for each character and Spearman's rank correlation coefficient was calculated between all pairs of characters. The characters were clustered using the weighted variable group method (Sokal and Sneath, 1963) and the resulting dendrogram is shown in Figure 7.3. Overall the characters fall into two groups negatively correlated with one another. One group includes thorax length, ovariole number and number of eggs per ovary (clutch size), time to eclosion, and adult survival. The other group contains egg volume, the biomass ratio and relative clutch volume. In general, then, large species of Drosophila have large clutches of small eggs,

Table 7.5 Adult survival

	LD50 of hours to starvation with 95% confidence intervals		
	Males	Females	Total
D. melanogaster	38.5±2.2	49.6±2.6	41.7±2.6
D. simulans	50.7±2.6	63.1±2.4	56.5±2.6
D. subobscura	43.8±2.4	53.7±2.4	48.5±2.4
D. immigrans	75.6±2.5	83.4±2.4	78.7±2.4
D. hydei	72.0±2.6	53.8±2.4	63.3±2.6
D. funebris	81.2±3.0	91.0±2.6	86.2±2.8
D. busckii	62.1±2.6	92.5±2.6	78.2±2.8

Table 7.6 Time from egg to maturity (means with 95% confidence intervals)

	Egg to eclosion (days)	Eclosion to maturity (days)	Egg to maturity (days)
D. melanogaster	19.1±0.4	2.3±0.3	21.4
D. simulans	17.9±1.8	-	-
D. subobscura	21.1±0.3	4.3±0.3	25.4
D. immigrans	20.0±0.5	4.0±0.5	24.0
D. hydei	24.0±1.4	3.8±0.4	27.8
D. funebris	26.2±1.3	2.6±0.5	28.8
D. busckii	25.4±2.3	-	-

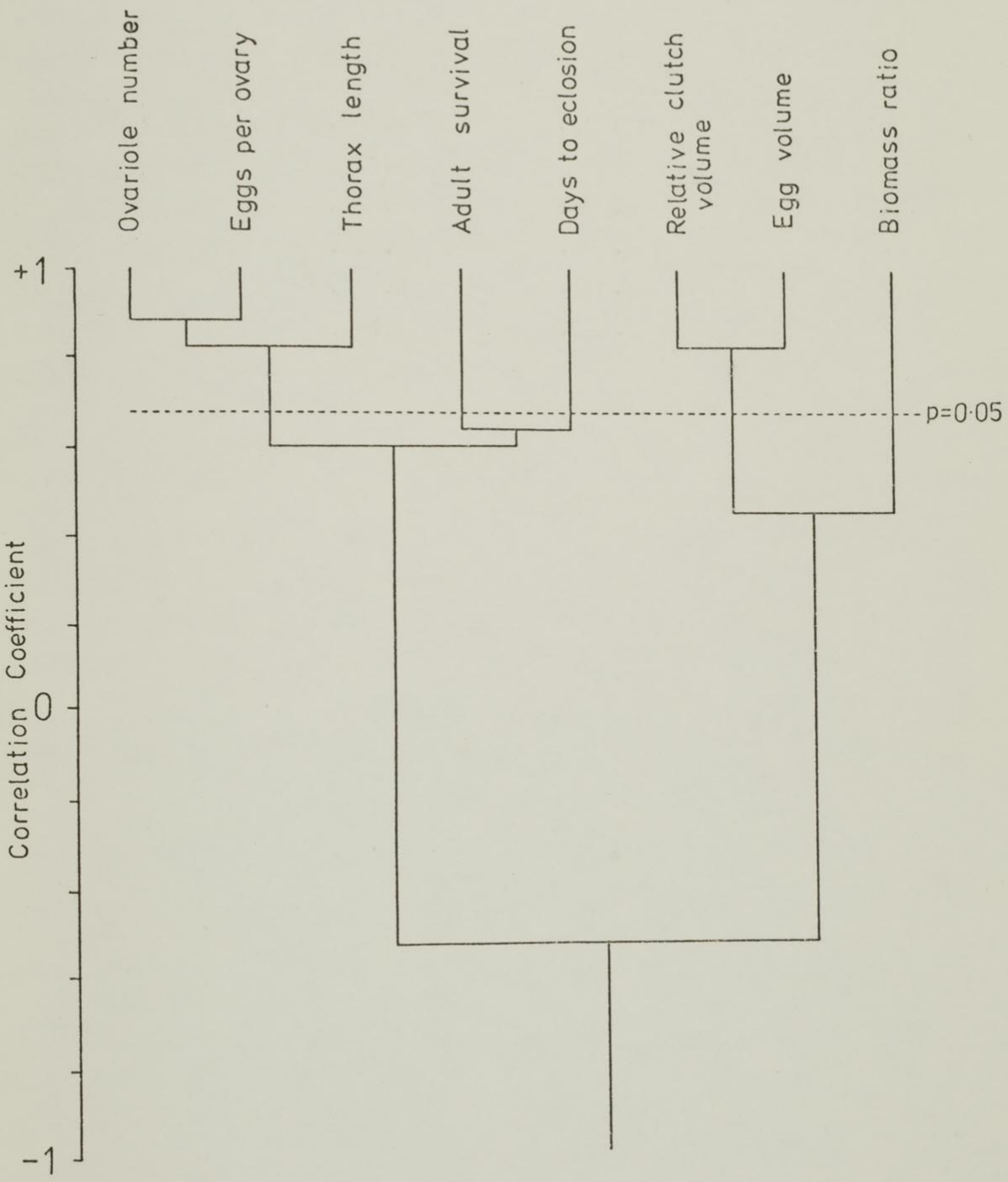


Fig 7.3 Clustering of reproductive characters

slow larval development and good adult survival. Small species have the oppostive characteristics. Only D. busckii conspicuously fails to fit these stereotypes, being small but having all the characteristics of a large species.

The Drosophila species were clustered in the same way as the reproductive characters. First, the characters were transformed to standard deviates so that the characters of each species could be ranked. Spearman's rank correlation was calculated between all pairs of species, the species were clustered using the weighted variable group method, and the resulting dendrogram is presented in Figure 7.4. The groupings tend to link species with the same breeding site preferences. D. melanogaster and D. simulans, both of which breed almost exclusively on fermenting fruit (Chapter 3) form a significant group based on their reproductive characters. The two generalists, D. hydei and D. immigrans form another significant group, while the vegetable specialists D. busckii and D. funebris have positively correlated reproductive characters, though the correlation is not significant. D. subobscura is a fermenting fruit specialist but does not form a group with any other species, probably because its reproductive strategy is modified for woodland habitats.

These results confirm the finding of Kambysellis and Heed (1971), that there is a relationship between a species' preferred breeding sites and its reproductive strategy. Kambysellis and Heed have suggested that the production of large clutches of small eggs is associated with productive yet infrequent breeding sites. Wilbur (1977) has shown that if environmental catastrophes destroy all the eggs in a nest then the variance in the number of survivors is directly proportional to the number of eggs per nest. Species with large clutches would then have more unpredictable juvenile survivorship and this would select for increased investment in the mature adult (Murphy, 1968). If the survival of individual offspring is unpredictable selection should favour reduced parental investment in each individual; egg volume would be reduced and consequently larval development time would increase. This whole suite of characters is possessed by the generalists, D. immigrans and D. hydei and by the vegetable

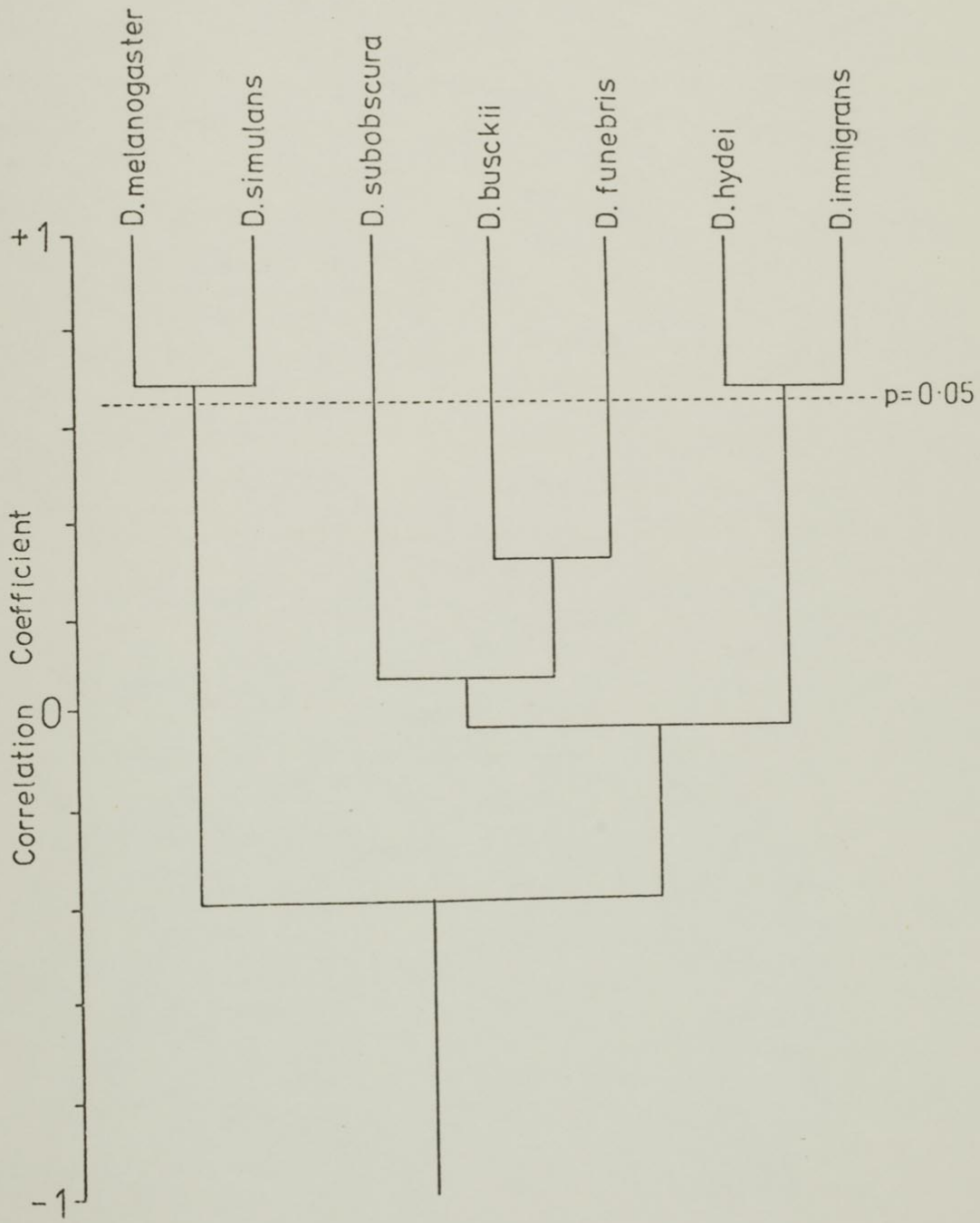


Fig 7.4 Drosophila species clustered according to their reproductive characters

specialists D. funebris and D. busckii and this can all be explained as a result of breeding on infrequent breeding sites.

This suite of characters is clearly inconsistent with an explanation based on r- and K- selection, which would predict that small species such as D. melanogaster and D. simulans would have large clutches of small eggs (Pianka, 1970). There is, however, no evidence to support the alternative explanation because no information is yet available on the frequency of the breeding sites of different Drosophila species. Without this information it would clearly be absurd to infer from their reproductive strategies that D. melanogaster and D. simulans have more frequent breeding sites than the other species, yet this sort of inference is often made in studies of r- and K- selection. If an organism has a reproductive strategy consistent with r- and K- theory it is often described as an r- or K- strategist, with no regard to whether its population is usually at carrying capacity or not (Forsyth and Robertson, 1975; Loya, 1976). Swingland's (1977) study of reproductive strategies in the Aldabran giant tortoise is one of the few to consider population density at all. Field evidence relating to strategies is, then, clearly incomplete unless it includes information about all the environmental variables which might be selecting for the different characters. The information presented in this chapter should be the prelude to a study of the frequency with which Drosophila find breeding sites. Until this is done one can merely say that the evidence is consistent with the statement of Kambysellis and Heed (1971), that the larval niches of Drosophila are a major factor in establishing the diversity of female reproductive systems.

CHAPTER 8

GENERAL DISCUSSION

This thesis is a preliminary survey of the ecology of the domestic species of Drosophila at Pontefract Lane. I have not, therefore, attempted to pursue a single line of research throughout, but have worked on interesting problems as they occurred. The chapters of this thesis describe pieces of work which are fairly complete in themselves, and which have been discussed fully within the relevant chapters. A general discussion which attempted to draw this work together into a complete picture of the ecology of the domestic species of Drosophila at Pontefract Lane would have to be highly speculative because much work remains to be done. I have therefore limited this chapter to a short discussion of how the properties of this community of Drosophila accord with modern ecological theory.

In Chapter 6 it was noted that populations are usually regarded as being controlled by density dependent factors (Williamson, 1972). This view, suggesting that populations and communities must have inherent stability in order to persist, has greatly influenced the way the science of ecology is practised. Mathematical ecology has perhaps been most affected. Most recent mathematical descriptions of the interactions between species have been largely concerned with a search for the stable points in the system (Mac Arthur, 1970; May, 1973; Usher and Williamson, 1974). This is partly because of the prevalent view of population control and partly because there are well known mathematical techniques for dealing with the stability properties of systems. Field studies in ecology also reflect this bias. They often start with the assumption that closely related species are potential competitors for a resource that is in short supply, and then are content to confirm this with observational evidence of differences between species which might be evidence of resource partitioning (Schoener, 1974).

One might expect, then, that there is overwhelming evidence for self

regulation in most natural populations or communities. There are, of course, some good examples. Broadhead and Wapshere (1966), for instance, found that the populations of two species of Mesopsocus were separately governed by competition for oviposition sites. Good examples of competition occurring in the field are, however, rare (Elton and Miller, 1954; Reynoldson, 1964; Reynoldson and Bellamy, 1971). Most examples in the literature infer competition when two species are exploiting the same resource even when there is no evidence that the resource is in short supply. Miller (1967) in his review of evidence for competition in nature considered that the populations of most terrestrial insects are normally underclimatic control. One of the most detailed studies of insect population dynamics is that of Varley and Gradwell (1968) on the winter moth. They found that density dependent pupal mortality occurred but was not strong enough to regulate the population. The most important source of mortality was density independent mortality of eggs and larvae.

In Chapter 6 it was suggested that density independent factors are most important in the ecology of domestic Drosophila at Pontefract Lane. It might be argued that this is wholly a result of their living in a man-modified habitat. They are, however, adapted to living in such a habitat and are rarely found elsewhere (Dobzhansky, 1965). Despite the fact that they must usually coexist with the same group of domestic species they do not seem to show much coadaptation in the form of resource partitioning. It was demonstrated in Chapter 3 that the larvae show some partitioning of the breeding sites and to a lesser extent of the season but on the whole they tend to share the same breeding sites with one or more other species. It was suggested that partitioning of the breeding sites would be difficult because of their unpredictability. Assuming resources were limited, conventional theory (MacArthur, 1972) would predict a reduced number of species due to competitive interactions. In fact, as noted in Chapter 6, several species can coexist because interspecific competition is negligible and intraspecific competition has some importance only For D. melanogaster. In Chapter 5 a situation was described which might be consistent with resource partitioning between D. melanogaster and D. immigrans. D. immigrans tends to emerge from citrus fruits infected

with Penicillium, while D. melanogaster emerges from uninfected fruit. This difference is, however, based on survival of the larvae, not on selection of the fruit by the adults and so is unlikely to have evolved by ecological displacement. In the study of reproductive strategies in Chapter 7, none of the strategies displayed by the domestic species was consistent with a K-strategy, evolved as a result of competitive interactions.

The community of Drosophila seems to be a community only in the sense that the species share the same habitat. It is futile to continue the old controversy between the proponents of density dependent and independent mortality. It is obviously absurd to suggest that all populations are controlled by density independent factors just as density dependent control is unlikely to be universal. There is a danger, however, that ecological theory, in particular, is so much concerned with the consequences of density dependent control, that field ecologists tend to look for these consequences without asking whether density independent factors might be important.

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