

A FIELD INVESTIGATION OF LARVAL COMPETITION IN DOMESTIC *DROSOPHILA*

By W. D. ATKINSON*

Department of Pure and Applied Zoology, The University, Leeds LS2 9JT

SUMMARY

(1) This paper investigates the occurrence of larval competition in several domestic species of *Drosophila* in a fruit and vegetable market.

(2) Regular seasonal changes in body size were demonstrated in *D. melanogaster* Meigen.

(3) The heritability of body size in the field was negligible and so the seasonal changes must have been due to the environmental effects of temperature and larval density.

(4) Multiple regression analysis was used to separate the effects of temperature from the effects of larval density. Density was found to account for a significant amount of the variation in body size in *D. melanogaster*. This is evidence of intraspecific competition.

(5) Interspecific competition was demonstrated by the fact that the density of *D. melanogaster* was found to affect the body size of several other species.

(6) The coexistence of seven species of *Drosophila* in the fruit and vegetable market was explained by the partitioning of breeding sites and by the fact that the community may never reach equilibrium.

INTRODUCTION

It was established by Atkinson & Shorrocks (1977) that the species of *Drosophila* living in a fruit and vegetable market partition the breeding sites to some extent, but that coexistence of several species in the same sites still takes place. In this paper two questions were asked. Does intraspecific larval competition occur within any of the *Drosophila* species, and is there interspecific competition among the species that do coexist?

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 reason to believe that this resource is in short supply (Carson 1951; McKenzie & Parsons 1972; Budnik & Brncic 1974). Reynoldson (1964) has condemned the uncritical use of evidence to demonstrate competition and Reynoldson & Bellamy (1971) have drawn attention to the general lack of well established cases of competition in the field. In *Drosophila* a direct measure of competition is available in the body size of the adults. There are two important variables, the larval food supply and the temperature of development, on which the ultimate adult body size of a *Drosophila* larva depends. Increased temperature or larval density reduces the subsequent size of the adults (Chiang & Hodson 1950; Sokoloff 1955; Tantaway & Mallah 1961).

Body size has been investigated in field populations of *Drosophila* by several authors, but evidence for competition is equivocal. Sokoloff (1957, 1966) found that *D. pseudoobscura* and *D. persimilis*, trapped in the wild, were of comparable size to flies reared

*Present address: Department of Zoology, University of Edinburgh, West Mains Road, Edinburgh 9, U.K.

under near optimal conditions in the laboratory. He concluded that his populations did not experience intense competition. In Egypt, Tantawy (1964) found that the wing lengths of *D. melanogaster* and *D. simulans* declined in summer, but he decided that this was mainly due to high temperature, as food resources were abundant. Similar results were obtained by Stalker & Carson (1947) in *D. robusta* from North America. McFarquhar & 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 & 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*.

The field work described in this paper was carried out in a fruit and vegetable market 4 km south-east of Leeds. Atkinson & Shorrocks (1977) found six cosmopolitan domestic species of *Drosophila* breeding on discarded fruits and vegetables in the market; *D. funebris* (Fabricius) was very uncommon, *D. busckii* Coquillett specialized on decaying vegetable breeding sites, *D. hydei* Sturtevant and *D. immigrans* Sturtevant were generalists, while *D. melanogaster* Meigen and *D. simulans* Sturtevant specialized on fermenting fruits. A seventh species, *D. subobscura* Collin was also present though it is not a cosmopolitan domestic species, but a native of Europe commonly found in woodlands (Shorrocks 1975). This species specialized on fruits as breeding sites. Of the seven species *D. melanogaster* was the most common, comprising 67% of the *Drosophila* emerging from breeding sites in the study of Atkinson & Shorrocks (1977).

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. Wing length is highly correlated with body size in *Drosophila* but is influenced more by temperature than are other body dimensions such as thorax length (Stalker & Carson 1947; Tantawy & Mallah 1961).

During the summers of 1975 and 1976 seasonal changes in the body size of adult *Drosophila* were investigated. Adult flies were trapped at the fruit and vegetable market using a variety of baits and the wing lengths of samples of these flies were measured. Temperature was recorded each week using maximum and minimum thermometers.

In order to determine the effects of different components of the environment, during the summer of 1976 potential breeding sites were brought back from the market, weighed, and kept in jars in an outdoor insectary. At least three times per week the emerged adults were removed and the wings of a sample of them were measured. For each adult *Drosophila* its body size was known as well as the density of larvae sharing the same breeding site and the temperature during its larval development. Many breeding sites yielded more than one species of *Drosophila* which enabled the effects of interspecific competition to be investigated.

Reeve & Robertson (1953) showed 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 result of natural selection as of environmental effects. In order to estimate the heritability of wing length in the field, inseminated female *D. melanogaster* were captured by sweep netting at the fruit and vegetable market. They were allowed to lay eggs for 24 h and ten eggs from each female were transferred to a tube containing 10 ml 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

Genetic factors

The heritability of wing length estimated from the daughter-mother regression was 24% and was non-significant. The mothers had developed in the wild in a variable environment and so the estimate was less than that of Reeve & Robertson (1953) who used laboratory reared *Drosophila*. The true heritability in the field could only have been obtained, however, if the offspring had been allowed to develop in the field in breeding sites chosen by the mother. The wing length of the father should also have been known because otherwise maternal effects might increase the apparent heritability. For these reasons even the non-significant figure of 24% is very much an upper estimate, and it seems unlikely that genetic changes in wing length during a season would be detectable in the phenotypes of flies caught in the wild. It was assumed, therefore, that any observed variation in wing length could be explained by the effects of temperature and larval crowding alone.

Seasonal changes in body size

The most common species at the fruit and vegetable market was *D. melanogaster* and so most of the following results refer to this species. Figure 1 shows the changes in mean wing length of *D. melanogaster* trapped in the market 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. Parallel changes occurred in the two sexes. Differences in the time of minimum wing length between the two years may reflect differences in temperature. In 1975 the wing lengths reached their minimum in mid-August, whereas in 1976 the minimum was at the end of July. In both years the minimum wing length occurred 2 to 3 weeks after the maximum mean temperature for that summer. Superficially the changes in wing length seem to be readily explicable in terms of the physiological effect of temperature on body size. Temperature, however, also has an effect on the population dynamics of *Drosophila*. Atkinson & Shorrocks (1977) showed that there was a significant correlation between the numbers of *D. melanogaster* emerging from breeding sites returned to the laboratory in a particular week and the mean weekly temperature. Larvae developing at higher temperatures are therefore more likely to be crowded, and so the seasonal changes in body size might be due to larval competition as well as to the physiological effects of temperature.

Figure 2 gives the changes in mean wing length of the *D. melanogaster* emerging from all the breeding sites brought back to the laboratory during 1976. Also shown are the numbers of *D. melanogaster* emerging 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 small peaks in the number of flies emerging were also associated with a rise in temperature and a decline in wing length.

The wing lengths of *Drosophila* trapped during 1976 show some differences from the wing lengths of flies emerging from breeding sites in the same year. In particular, the minimum wing length of trapped flies occurred at the end of July while in the flies emerging from breeding sites the minimum occurred at the beginning of July, about 3

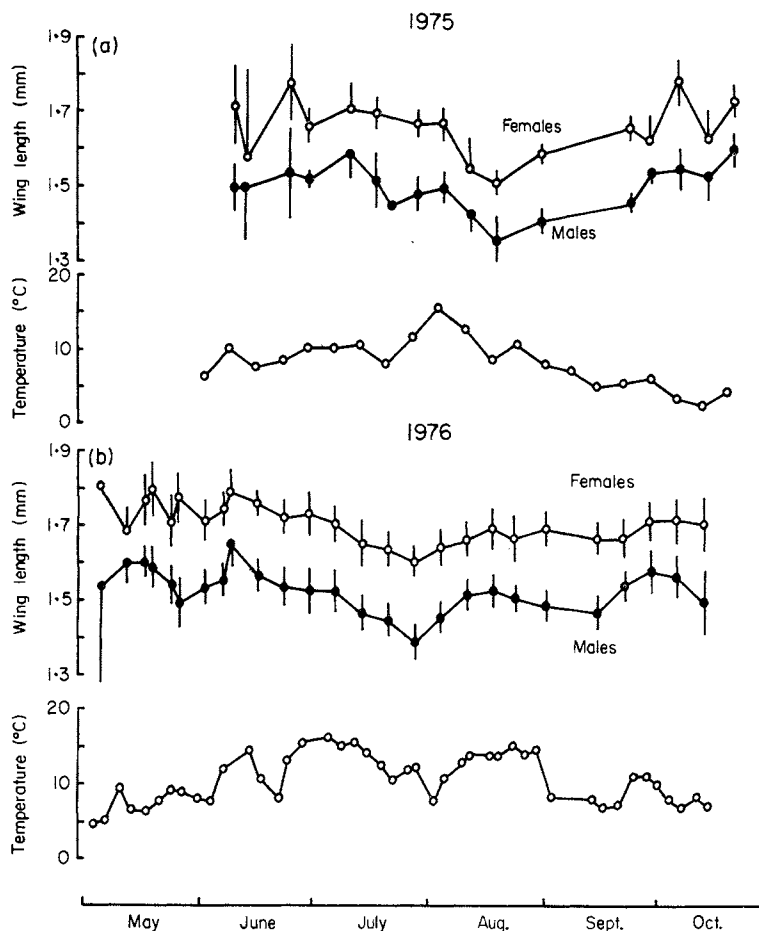


FIG. 1. Seasonal changes in the wing lengths of *D. melanogaster* trapped during 1975(a) and 1976(b) together with mean temperatures. Mean wing lengths are shown with 95% confidence limits.

weeks earlier. This difference can probably be accounted for because, unlike the emerging *Drosophila*, the trapped flies are of all ages and some may be several weeks old.

Effect of temperature and larval density

From the data obtained from the breeding sites brought back to the laboratory three parameters were determined for each site: the mean wing length of all the adult male *D. melanogaster* emerging, the density of larvae estimated from the number of adults emerging, and the mean temperature from the date on which the breeding site was discovered to the date on which the last *Drosophila* emerged. Figure 3 shows the regressions of wing length on temperature and on larval density. As expected there is a significant negative correlation between wing length and temperature ($r = -0.67$, $P < 0.01$). The relationship between wing length and density is, however, much less clear, although there is a small negative correlation ($r = -0.23$, $P < 0.05$). A multiple regression analysis was carried out to discover whether larval density was really as unimportant as the simple regressions suggest, or whether its effects are masked by the effect of temperature.

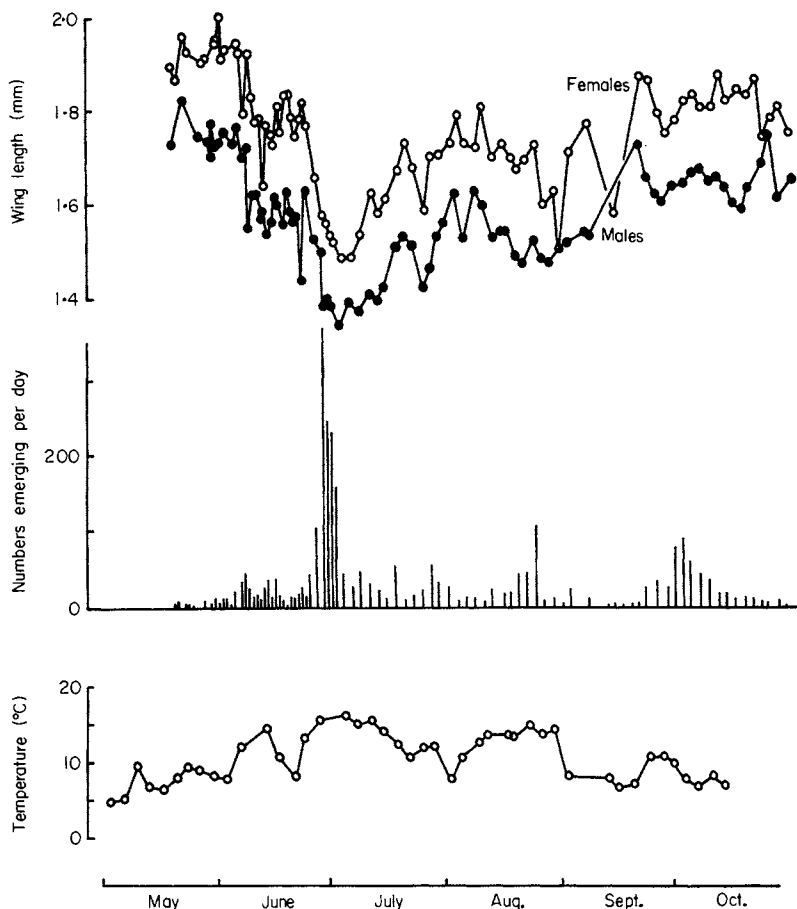


FIG. 2. Seasonal changes in the wing lengths and numbers of *D. melanogaster* emerging from breeding sites during 1976. Also shown are mean temperatures.

In the *Drosophila* literature no environmental factors apart from temperature and larval food supply are regarded as important in determining the adult body size. It seems reasonable to suppose, therefore, that in the multiple regression of wing length on temperature and density, no important variable has been left out which might affect the results. In order for multiple regression to identify the most important variable it is imperative that the main variables, density and temperature, have a linear and additive effect on body size (Gilbert 1973). 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, density and temperature, squared is a measure of the departure of the relationship from linearity. The extra regression on the product of the two main variables is correspondingly a measure of the departure of the relationship from additivity.

Table 1 shows the results of the multiple regression analysis presented as an analysis of variance. The regression of wing length on the two main variables was calculated first and then the derived variables, density squared, temperature squared, and the product of density and temperature, were entered into the equation. The regression equation accounts for a significant amount of the variation in wing length. The coefficient of multiple

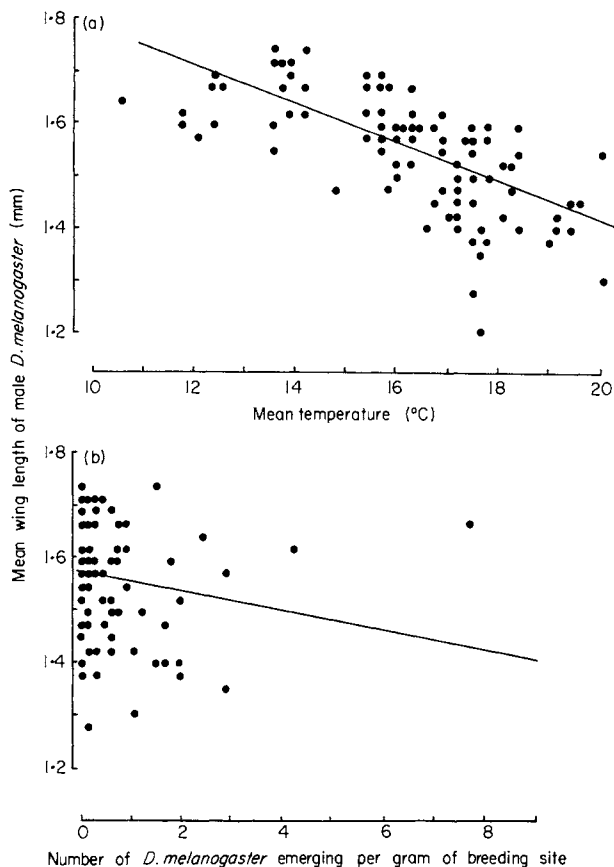


FIG. 3. The wing lengths of *D. melanogaster* emerging from breeding sites (a) as a function of temperature ($y = 2.13 - 0.035 \pm 0.008x$), and (b) as a function of the density emerging ($y = 1.57 - 0.018 \pm 0.016x$).

determination (r^2) equals 59%. The two main variables, density and temperature, together account for nearly all the explained variation ($r^2 = 54\%$) and each is significant ($P < 0.01$) on its own. Of the derived variables, the product of density and temperature, and temperature squared are on the borderline of significance ($0.01 < P < 0.05$), while density squared is non-significant. In the relationship between temperature and wing length there is, then, a slight departure from linearity. There is also a small multiplicative effect of density and temperature on wing length. These departures from linearity and additivity are not, however, severe enough to affect seriously the broad conclusion that both density and temperature are influential in determining body size.

In the above analysis temperature ($F = 112.08$) accounts for much more of the variation in wing length than density ($F = 11.91$) and seems to be the most important variable. However, errors of measurement of either of the two main variables would reduce its contribution to the regression (Gilbert 1973). The temperatures experienced by the *Drosophila* larvae, the internal temperatures in the breeding sites, might have been different from the measured air temperature in the outdoor insectary. Microbial action in the breeding sites might create such a discrepancy, but since all the breeding sites were

TABLE 1. Regression of male wing length on density of *D. melanogaster* and temperature. Analysis of variance

Source of variation	SS	d.f.	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_1^2	0.006	1	0.006	0.18	NS
x_2^2	0.181	1	0.181	5.89	$P < 0.05$
Residual	2.918	95	0.031		
Total	7.070	100			

y = mean wing length of *D. melanogaster* males.

x_1 = numbers emerging per gram of breeding site.

x_2 = mean temperature.

stored in the same way this source of error should not significantly reduce the regression due to temperature. Density, however, may well be a very poor estimator of the larval food supply. The same density recorded in, for example, apple and tomato, may imply very different levels of larval nutrition. In order to reduce the effect of differences between species of breeding site the multiple regression analysis was carried out separately for each breeding site species. Only the two main variables, density and temperature, were put into the equation. Table 2 gives the results of all the separate multiple regression analyses

TABLE 2. Regression of male wing length on density of *D. melanogaster* and temperature, performed separately on each species of breeding site. Analysis of variance with the individual species' sums of squares pooled

Source of variation	SS	d.f.	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			

x_1 = numbers emerging per gram of breeding site.

x_2 = mean temperature.

combined in an analysis of variance. The table was obtained by adding up the sums of squares calculated in the separate analyses. The total sum of squares in Table 2 is not the same as in Table 1 because some of the breeding site species, such as mango and yam, were only represented by one item and the analysis in Table 2 could not be performed on these. Much more of the variation in wing length was explained with the breeding sites analysed separately. The average coefficient of multiple determination (r^2) was 86.3%. Again each of the main variables accounted for a significant amount of the variation in wing length, but this time temperature ($F = 12.67$) was only slightly more important than density ($F = 7.25$). Evidently density within each breeding site species more accurately reflected larval nutrition than density recorded irrespective of breeding site. Even within a species of breeding site there may be differences in the nutrition provided by different items due to factors such as state of decay. If it were possible to correct for this as for differences between species it might be possible to account for even more of the variation in wing length by density. The problem is in determining the intensity of

competition without knowing precisely what the larvae are competing for and how to measure it.

If an observed reduction in body size has a component associated with competition it would be expected that at low mean levels of crowding all the flies would have enough food to develop to a size determined by temperature. At higher mean levels of crowding some larvae would develop in conditions of intense competition while others would still be in relatively empty breeding sites. The variation in wing length should, therefore, increase with the level of crowding. This prediction was tested on the flies emerging from breeding sites during 1976. Figure 4 shows the relationship between the logarithm of the number of *D. melanogaster* emerging per day and the standard deviation of their wing lengths. The correlation is positive ($r = +0.40$) and significant ($P < 0.01$).

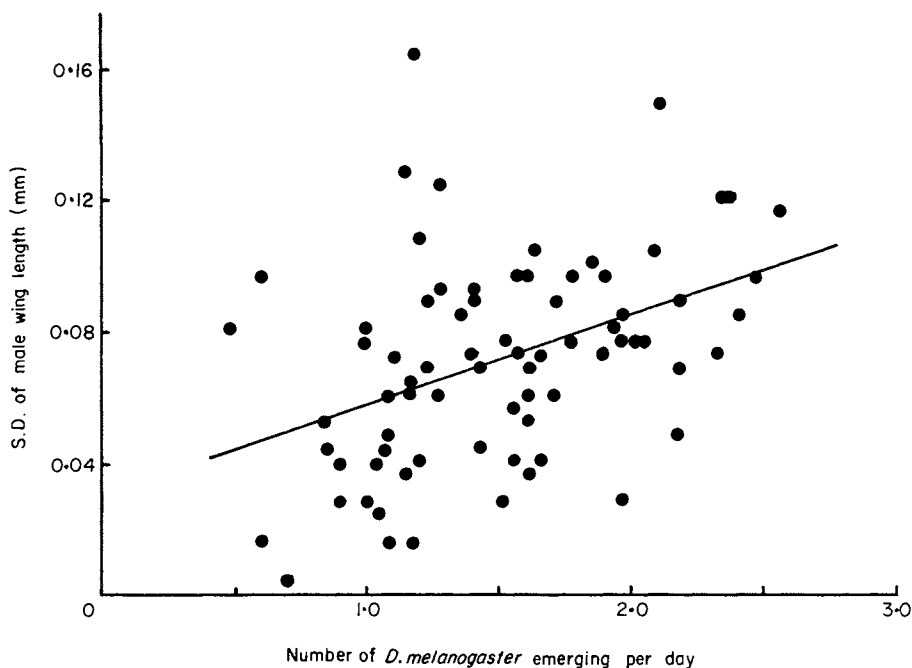


FIG. 4. The relationship of the log of the number of *D. melanogaster* emerging from breeding sites per day, and the standard deviation of the male wing lengths ($y = 0.031 + 0.026 \pm 0.014x$).

The evidence is, then, that the number 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 short, they must be competing.

Interspecific competition

Atkinson & Shorrocks (1977) showed that several species of domestic *Drosophila* share the same breeding sites as *D. melanogaster*. Since there is evidence of intraspecific competition in *D. melanogaster* interspecific competition might also be occurring if the coexisting species exploit the same resource within the breeding sites. A negative correlation between the wing lengths of one species and the numbers of another, when they emerge from

the same breeding sites, might indicate the occurrence of competition between the two species. Some care must be made with such an interpretation, however, because the numbers of one species may be enhanced by conditions which adversely affect the body size of the other, independent of any competition. *D. immigrans* larvae, for instance, survive much better on citrus fruits infected with the mould *Penicillium italicum* than on uninfected fruit, while *D. melanogaster* larvae survive very poorly on infected citrus fruit (W. D. Atkinson, unpublished). Such a situation might give results which suggested that *D. immigrans* was competitively superior to *D. melanogaster*. On the other hand, it is equally possible that the conditions of the breeding site would lead to a positive correlation between the numbers of one species and the wing lengths of another, especially where the two species have similar requirements. There is no reason to suppose, therefore, that in the absence of competition interspecific correlations between wing length and density would be more often negative than positive. Table 3 gives the partial correlation coefficients between each species' wing length and the density of every species, controlling for temperature. Spaces in Table 3 occur where two species coexisted in the same breeding sites too infrequently for the analysis to be performed. Of the twenty-six partial correlations in Table 3 only eight are positive. It seems likely, then, that interspecific competition is the dominant factor affecting the relationship between wing length and density. Among the twenty-six tests of significance in Table 3 there is a probability of 74% that one will be positive at the 5% level by chance. The results of individual analyses may not, then, be important. The interesting fact is that the density of *D. melanogaster* is significantly negatively correlated with the wing lengths of three other species. The coexisting species are, on the whole, at a competitive disadvantage to *D. melanogaster*, the most common species.

DISCUSSION

It has been shown that body size in *D. melanogaster* is partly determined by the level of intraspecific competition. Previous studies on body size in *Drosophila* (Sokoloff 1957, 1966; Stalker & Carson 1947; Tantawy 1964; McFarquhar & Robertson 1963) have not attempted to separate the effects of temperature from the effects of food shortage. They explained changes in body size with whichever of the environmental factors seemed, superficially, to be important. Most of these studies concluded that temperature was the main influence on body size, but the results presented in this paper show that there may be a correlation between temperature and larval crowding which tends to conceal the effects of larval competition. Competition in *Drosophila* may, therefore, be much commoner than previous studies have suggested.

A reduction in body size due to larval crowding does not necessarily imply that density dependent mortality is occurring. If, when starved, the larvae could compensate entirely by reducing their size then no mortality need take place. Studies of crowding on Diptera in the laboratory, however, have shown that, in practice, reduction in body size due to larval crowding is always associated with reduced survival (Sokoloff 1955; Sullivan & Sokal 1963; Miller 1964). It can be assumed, then, that *D. melanogaster* does suffer some density dependent mortality in the field. Table 3 suggests that, where they share the same breeding sites, the other domestic species of *Drosophila* must also suffer density dependent mortality through interspecific competition with *D. melanogaster*. In view of this the coexistence of seven species of *Drosophila* in the fruit and vegetable market needs some explanation.

TABLE 3. Effect of density of each species on the body size of the other species.
Partial correlation coefficients controlling for temperature

Wing length	Numbers of <i>Drosophila</i> per gram of breeding site					
	<i>D. melanogaster</i>	<i>D. simulans</i>	<i>D. subobscura</i>	<i>D. immigrans</i>	<i>D. hydei</i>	<i>D. busckii</i>
<i>D. melanogaster</i>	-0.25 ***	+0.02 NS	+0.29 NS	-0.11 NS	-0.41 NS	+0.02 NS
<i>D. simulans</i>	-0.43 ***	-0.16 NS	-0.35 NS	-0.26 NS		
<i>D. subobscura</i>	-0.38 NS	+0.69 NS	-0.01 NS	-0.65 NS		
<i>D. immigrans</i>	-0.80 ***	-0.23 NS	+0.02 NS	-0.15 NS	+0.06 NS	-0.68 NS
<i>D. hydei</i>	-0.64 *			+0.04 NS	-0.50 *	-0.83 NS
<i>D. busckii</i>				-0.86 NS		+0.45 NS

One-tailed significance test; *** $P < 0.01$, * $P < 0.05$.

There are two possible reasons for the coexistence. The first is that the partitioning of the breeding sites observed by Atkinson & Shorrocks (1977) is efficient enough to allow refuges for species competitively inferior to *D. melanogaster*. It may be significant that in Table 3 the two species which appear to suffer most in competition with *D. melanogaster* are the breeding site generalists, *D. hydei* and *D. immigrans*. Atkinson & Shorrocks (1977) found that, whereas *D. melanogaster* was confined to fermenting fruits, the two generalists could exploit decaying vegetables. It is possible that the evolution of generalization has been stimulated by the need to find a refuge from competition with *D. melanogaster*. The other fermenting fruit specialists, *D. simulans* and *D. subobscura*, which have no refuge in alternative breeding sites may avoid such intense competition by their behaviour. Barker (1971) has shown, for instance, that *D. simulans* larvae burrow deeper into laboratory medium than *D. melanogaster*. As Pianka (1974) has pointed out, the effects of interspecific competition on niche-breadth are complex and under different conditions may favour niche contraction or expansion. It is possible that both processes have been involved in the breeding site partitioning of the domestic species of *Drosophila*. *D. immigrans* and *D. hydei* have expanded their niches onto vegetable breeding sites which may be suboptimal, while *D. simulans* and *D. subobscura* have perhaps contracted their niches to exploit only a part of each fermenting fruit breeding site.

The foregoing explanation of the coexistence of several species assumes that the community of *Drosophila* is in equilibrium. An alternative explanation for the persistence of the community would be that it is never in equilibrium. Hutchinson (1961) has suggested that equilibrium would never be expected in nature where organisms have a reproductive rate such that the time for competitive replacement is of the same order as the time taken for a significant seasonal change in the environment. Most of the cosmopolitan species of *Drosophila* are tropical in origin (Patterson & Stone 1952; Throckmorton 1975) and must suffer considerable density independent mortality during every temperate winter. The breeding season in Leeds is from May to September and is probably too short for competitive exclusion to take place. This is the likely explanation for the coexistence of seven species of *Drosophila* in the fruit and vegetable market. The partitioning of breeding sites observed by Atkinson & Shorrocks (1977) is unlikely to have evolved in such circumstances but must be evidence of more prolonged competitive interactions in less severe climates.

ACKNOWLEDGMENTS

I would like to thank Dr B. Shorrocks for his help and advice, Dr E. Broadhead and Dr S. L. Sutton who made helpful comments on the manuscript, and Professor R. McN. Alexander for the provision of laboratory facilities. This work was supported by a Natural Environment Research Council grant.

REFERENCES

- Atkinson, W. D. & Shorrocks, B. (1977). Breeding site specificity in the domestic species of *Drosophila*. *Oecologia, Berlin*, **29**, 223–232.
- Barker, J. S. F. (1971). Ecological differences and competitive interaction between *Drosophila melanogaster* and *Drosophila simulans* in small laboratory populations. *Oecologia, Berlin* **8**, 139–156.
- Budnik, M. & Brncic, D. (1974). Preadult competition between *Drosophila pavani* and *Drosophila melanogaster*, *Drosophila simulans* and *Drosophila willistoni*. *Ecology*, **55**, 657–661.

- Carson, H. L. (1951). Breeding sites of *Drosophila pseudoobscura* and *Drosophila persimilis* in the transition zone of the Sierra Nevada. *Evolution*, **5**, 91–96.
- Chiang, H. C. & Hodson, A. C. (1950). An analytical study of population growth in *Drosophila melanogaster*. *Ecological Monographs*, **20**, 173–206.
- Falconer, D. S. (1964). *Introduction to Quantitative Genetics*. Oliver and Boyd, Edinburgh.
- Fellows, D. P. & Heed, W. B. (1972). Factors affecting host plant selection in desert-adapted cactophilic *Drosophila*. *Ecology*, **53**, 850–858.
- Gilbert, N. (1973). *Biometrical Interpretation*. Clarendon Press, Oxford.
- Hutchinson, G. E. (1961). The paradox of the plankton. *American Naturalist*, **95**, 137–145.
- Lakovaara, S. (1969). Malt as a culture medium for *Drosophila* species. *Drosophila Information Service*, **44**, 128.
- McFarquhar, A. M. & Robertson, F. W. (1963). The lack of evidence for coadaptation in crosses between geographical races of *Drosophila subobscura* (Coll.). *Genetical Research*, **4**, 104–131.
- McKenzie, J. A. & Parsons, P. A. (1972). Alcohol tolerance: an ecological parameter in the relative success of *Drosophila melanogaster* and *Drosophila simulans*. *Oecologia, Berlin*, **10**, 373–388.
- Miller, R. S. (1964). Larval competition in *Drosophila melanogaster* and *D. simulans*. *Ecology*, **45**, 132–148.
- Patterson, J. T. & Stone, W. S. (1952). *Evolution in the Genus Drosophila*. Macmillan, New York.
- Pianka, E. R. (1974). *Evolutionary Ecology*. Harper and Row, New York.
- Reeve, E. C. R. & Robertson, F. W. (1953). Studies in quantitative inheritance. II. Analysis of a strain of *Drosophila melanogaster* selected for long wings. *Journal of Genetics*, **51**, 276–316.
- Reynoldson, T. B. (1964). Evidence for intra-specific competition in field populations of triclads. *Journal of Animal Ecology (Jubilee Symposium Supplement)*, **33**, 187–201.
- Reynoldson, T. B. & Bellamy, L. S. (1971). The establishment of interspecific competition in field populations with an example of competition in action between *Polycelis nigra* (Mull.) and *P. tenuis* (Ijima) (Turbellaria, Tricladida). *Dynamics of Populations* (Ed. by P. J. den Boer and G. R. Gradwell), pp. 282–297. Centre for Agricultural Publishing and Documentation, Washington.
- Shorrocks, B. (1975). The distribution and abundance of woodland species of British *Drosophila* (Diptera: Drosophilidae). *Journal of Animal Ecology*, **44**, 851–864.
- Sokoloff, A. (1955). Competition between sibling species of the pseudoobscura subgroup of *Drosophila*. *Ecological Monographs*, **25**, 387–409.
- Sokoloff, A. (1957). Comment on A. Milne—Theories of natural control of insect populations. *Cold Spring Harbour Symposium on Quantitative Biology*, **22**, 253–271.
- Sokoloff, A. (1966). Morphological variation in natural and experimental populations of *Drosophila pseudoobscura* and *Drosophila persimilis*. *Evolution*, **20**, 49–71.
- Stalker, H. D. & Carson, H. L. (1947). Morphological variation in natural populations of *Drosophila robusta* Sturtevant. *Evolution*, **2**, 295–305.
- Sullivan, R. L. & Sokal, R. R. (1963). The effects of larval density on several strains of the house fly. *Ecology*, **44**, 120–130.
- Tantawy, A. O. (1964). Studies on natural populations of *Drosophila*. III Morphological and genetic differences of wing length in *Drosophila melanogaster* and *D. simulans* in relation to season. *Evolution*, **18**, 560–570.
- Tantawy, A. O. & Mallah, G. S. (1961). Studies on natural populations of *Drosophila*. I. Heat resistance and geographical variation in *Drosophila melanogaster* and *D. simulans*. *Evolution*, **15**, 132–144.
- Throckmorton, L. H. (1975). The phylogeny, ecology and geography of *Drosophila*. *Handbook of Genetics*, vol. 3. (Ed. by R. C. King), pp. 421–469. Plenum, New York.

(Received 10 March 1978)