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The Evolutionary Ecology of *Drosophila*

LAURENCE D. MUELLER

INTRODUCTION

In this review I have attempted to summarize a number of topics with which I am familiar that have significance for the field of evolutionary ecology. Since a good deal of this work includes laboratory studies, the following section provides a detailed description of the ecology of *Drosophila* (usually *melanogaster*) in the laboratory environment. This is followed by a section on the population dynamics of *Drosophila*, with particular attention paid to sources of bias that are inherent in certain experimental techniques. The next section considers the mechanisms and evolution of intra- and interspecific competition. This is followed by a section examining tradeoffs and correlations in *Drosophila* life-history traits and the consequences of density-dependent natural selection. The last section summarizes a rapidly growing literature on the habitat and oviposition preference of *Drosophila*. Several recent reviews touch upon areas of the ecology and evolution of *Drosophila* that I will not address (Parsons, 1980, 1981; Barker and Starmer, 1982). In this review I have attempted to develop a critical review of certain major topics and, I hope, unify certain disparate observations rather than be comprehensive in my citations. To all those whose work I have failed to cite I offer my apologies.

Often in the halls of academia or occasionally in print (King and Dawson, 1983) the relevance of laboratory research with *Drosophila* to the understanding of the natural ecology or evolution in this genus is

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questioned. Although it is perhaps ovbious to many, it may be worth emphasizing the role of controlled experiments on laboratory organisms. Laboratory studies of evolution tell us what the possible responses of a species may be; they do not necessarily tell us what has happened in nature or what will happen—only what is possible. This is not to say that trying to understand why *D. melanogaster* prefers to live in one garbage can over another is not a worthwhile endeavor; it should not be considered the *only* worthwhile endeavor. The obvious benefits of conducting laboratory experiments with *Drosophila* are that the evolutionary process can be examined in much finer detail than is possible "out of doors" and causation can be inferred since the experimenter is free to control all variables of interest.

It is true that the results obtained from any study of a "model" organism may have limited generality. This will probably be the case more often in studies of the evolution of *Drosophila* than with studies of its molecular genetics. As discussed in the section on life-history evolution, the evolution of density-dependent rates of population growth differ substantially between *D. melangaster* (Mueller and Ayala, 1981*d*) and *Escherichia coli* (Luckinbill, 1978). Despite these problems, the wealth of knowledge on the laboratory ecology of *Drosophila* and the facility of doing genetic experiments make species of this genus especially useful for experimental evolutionary ecology.

THE LABORATORY ECOLOGY OF *DROSOPHILA*

Since a large number of studies on the evolutionary biology of *Drosophila* are conducted in the laboratory environment, it is clearly of interest to understand the details of *Drosophila* ecology in these environments. Almost all detailed studies of *Drosophila* laboratory ecology have utilized *D. melanogaster*. Thus in this section references will be limited to *D. melanogaster* unless mentioned otherwise.

The laboratory environment may range from a small 1-oz. vial to large plexiglass cages of 6–8 ft^3, although the traditional culture consists of a ½-pint milk bottle. In the vial and bottle cultures measured amounts of food are deposited on the bottom, while population cages often have several removable food cups, which can be changed at regular intervals. The food medium generally consists of sugars (sucrose, dextrose, molasses), carbohydrates (corn meal, flour), dead yeast, a mold inhibitor (propionic acid, tegosept), and agar to solidify the medium. In addition, the larvae and adults gain substantial nutrition from a growing yeast pop-

ulation. Because the yeast are growing during most experiments and the depth of the medium utilized is variable, it is hard to quantify the amount of food available for larvae and adults. Sang *et al.* (1949) have shown that the yeast population in *Drosophila* cultures where *Drosophila* are omitted increases exponentially for 5–8 days before reaching a maximum. There is a substantial decrease in the maximum yeast biomass when flies are added to these cultures and the decrease is roughly proportional to the number of files added. However, there is still substantial temporal variation in the biomass of live yeast in *Drosophila* cultures.

Simply increasing the volume of the food medium can increase larval survival (Sang, 1949*a*) and the number of adults produced (Sang, 1949*c*), although increases in the surface area are more effective than increases in the depth of the medium. In addition, cultures with live yeast are substantially more productive than cultures with dead yeast only (Sang, 1949*c*).

Mold can be a substantial problem in some *Drosophila* cultures. For instance, in the study by Mueller and Ayala (1981*a*) the density-dependent rates of population growth were estimated for 25 lines of *D. melanogaster* isogenic for different second chromosomes. One line (number 30) was so unproductive at the lowest density examined that many cultures were overgrown with mold before the end of the experiment. This resulted in an actual decline in the per-capita rate of population growth relative to higher densities. This "Allee effect" was not seen in other cultures unaffected by mold. Antimold agents can affect population dynamics. Sang (1949*c*) reports that the antimold agent nipagin added to *Drosophila* cultures results in a significant decline in productivity relative to cultures without nipagin.

Methods of maintaining populations will be discussed more fully in the next section. Briefly, most techniques involve moving adults to a fresh food source, since manipulation of eggs, larvae, or pupae is much more cumbersome. In some population cages adults are kept indefinitely in a single cage and food cups are changed at periodic intervals. The exact method of population maintenance is quite important if one is interested in modeling population dynamics. This will be discussed further in the following section.

The remainder of this section on *Drosophila* laboratory ecology will examine the egg, larval, pupal, and adult life stages, respectively.

Eggs

In studies of life-history evolution a distinction is usually made between the number of eggs an organism produces and the energy invested

in these eggs. This distinction is especially important in species where the nutritional content of eggs may vary and this variation can translate into differential survival. In Bakker's (1961) study of larval competition he compared the average egg weight of a wild-type stock to a Bar-eyed stock. No significant differences were found. It should be noted that under competitive conditions the probability of survival and the final adult size of these two stocks can differ substantially. These differences are not due to an initial difference in the eggs. Prout (1985) has also shown that the viability of eggs is not dependent on their mothers' past history. Thus, even though factors such as larval density can affect female adult size and fecundity, they do not seem to affect egg viability. Although more data would be welcome, it seems reasonable to consider a *Drosophila* egg as being a standard unit of reproductive investment.

At 25°C eggs will hatch about 20 h after fertilization. However, the average time of egg hatch may depend on genotype. Bakker (1961) found a 45-min difference between his wild and Bar stocks.

Female *D. melanogaster* will lay unfertilized eggs, although at a much reduced rate (Alvarez and Fontdevila, 1981). Alvarez and Fontdevila (1981) also present data that indicate that for some female genotypes the proportion of unfertilized eggs they lay may increase with the age of the female.

Eggs may also fail to hatch due to the feeding activity of larvae. Larvae may bury eggs while feeding and the probability of this will depend on the density and age of the larvae. With day-old larvae less than 25% of all eggs are buried (Chiang and Hodson, 1950). However, with a dense culture of 5-day-old larvae nearly 100% of all eggs were buried (Chiang and Hodson, 1950). Chiang and Hodson further demonstrated that buried eggs rarely hatch. In both an agar medium and a yeast–water mixture fewer than 20% of buried eggs hatch, while controls showed 90% hatchability. This frequency increased to 50% if the egg was within a few hours of hatching when it was buried.

Larvae

The larval life stage is quite important in the laboratory ecology of *Drosophila* for a number of reasons. Although the effect is difficult to quantify, the larvae probably experience the most severe viability effects of crowded cultures (Sang, 1949*b*). In addition, the final size of the adult flies will be determined by the amount of food consumed by the larvae prior to pupation. Since female size is correlated with fecundity, nutrition of larvae has an important impact on this component of fitness. In crowded

cultures *Drosophila* must cope with limited pupation sites, waste accumulation, and, perhaps most importantly, limited food. Several studies have looked specifically at the effect of limited food on larval survival (Chiang and Hodson, 1950; Bakker, 1961, 1969; Nunney, 1983). The difficulty in regulating the amount of food available in standard cultures has been overcome by using nonnutritive agar cultures onto which measured amounts of a yeast paste have been added. Since the yeast do not grow in such cultures, the food available for larvae can be determined accurately.

The process of larval competition for limited food will be described first with a model proposed by Nunney (1983) and then by experimental data that support the basic tenets of the model. Suppose a population consists of n competitive types with frequencies p_i $i = 1, \ldots, n$. These types can be different sexes and genotypes. These types can differ with respect to the minimum amount of food needed for pupation m_i, the relative feeding rate α_i, or the variance in feeding rate σ_i^2. Thus it is assumed that when food is limiting, the superior competitor will be the one that consumes food at the fastest rate (largest α_i) or is most efficient in turning food into biomass (smallest m_i). Interference between types is assumed to be unimportant in larval competition for food. In a population with limited food this model assumes that the amount of food that has been consumed by individuals of a given type by the time no food is left has a normal distribution with mean $\alpha_i Y/\bar{\alpha}$ and variance $(\sigma_i \alpha_i Y/\bar{\alpha})^2$, where $\bar{\alpha} = \sum p_i \alpha_i$ and Y is the initial amount of food per larva in the environment. Figure 1 shows the distribution of food consumed by individuals of competitive type i. Only those individuals that have consumed more than m_i grams of food will survive. Thus the probability of survival for type i competitors W_i is given by the shaded area in Fig. 1. If the population consists entirely of type i individuals, then $\alpha_i = \bar{\alpha}$ and W_i is independent of α. If a large number of inferior competitors, type j, are added to a pure population of type i individuals and Y is kept constant, then $\alpha_i/\bar{\alpha} > 1$ and W_i will increase. In a pure population each type i individual consumes Y grams of food on average. When types i and j compete for this same limited amount of food type, the faster rate of consumption of type i will allow them to consume more than Y grams of food on average by the time the food runs out. Similarly, type j individuals will have received less than Y grams of food on average. The opposite effect is also possible. If the amount of food per larva is kept the same but superior competitors are added to a population of type i individuals, W_i will decrease.

It is also obvious from Fig. 1 that if m_i is decreased and all other parameters are kept the same, then W_i will increase. The effect of σ_i on viability is more complicated. If m_i is less than the mean amount of food

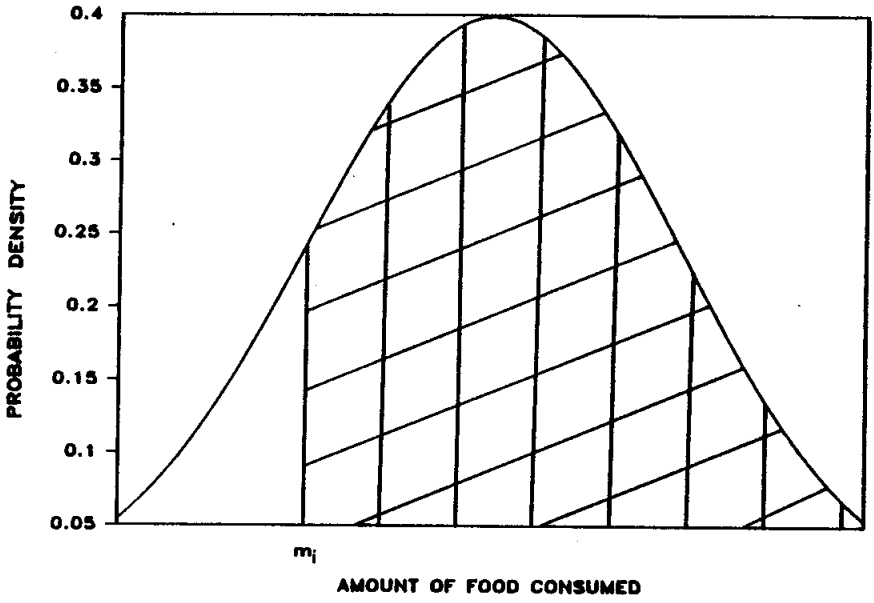


FIG. 1. A normal distribution describing the probability that a larva of competitive type i has consumed a certain amount of food in a population with n competitive types. The mean of the distribution is $\alpha_i Y/\bar{\alpha}$ and m_i is the minimum amount of food necessary for successful pupation by type i larva. The cross-hatched region represents the probability of a type i larva successfully pupating.

consumed, as shown in Fig. 1, then increasing σ_i will increase the area to the left of m_i and hence decrease W_i. However, when $m_i > \alpha_i Y/\bar{\alpha}$, σ_i will increase the area to the right of m_i and thus increase W_i. These conditions can be qualitatively interpreted as follows: when the average amount of food per larva is greater than the minimum needed for successful pupation, reducing the variance in food consumed by different individuals will ensure that all individuals consume more than the minimum amount. However, when the average amount of food per individual is less than the minimum amount, the only way to ensure some pupation is to have a few individuals consume much more than the average available and others consume much less, resulting in an increase in individual variation.

Figure 2 shows Bakker's (1961) data on the percent emergence of wild-type and Bar-eye flies as a function of food availability. These experiments all started with 200 first-instar larvae and the amount of food

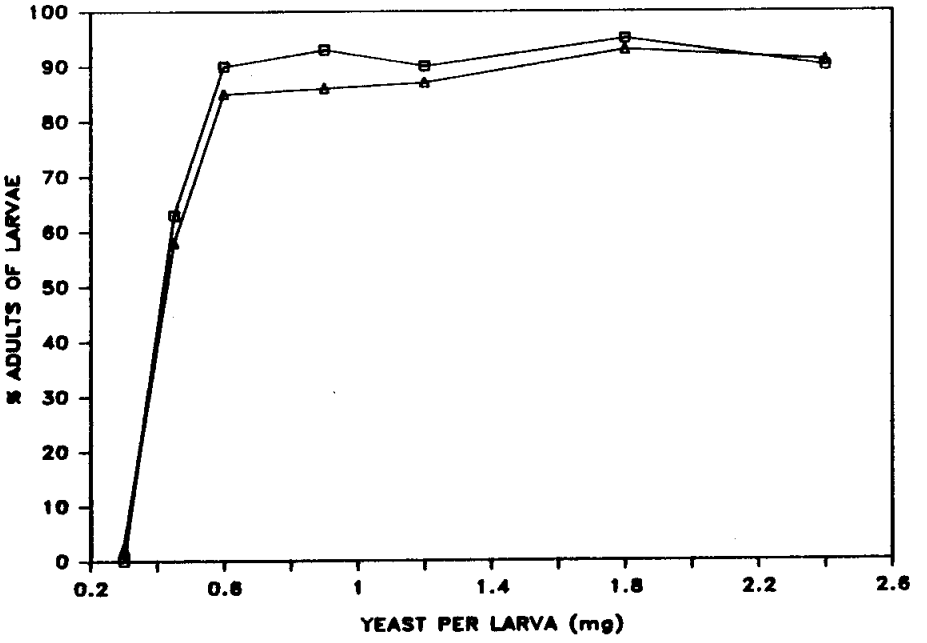


FIG. 2. The percent of all larvae that successfully pupate as a function of different food levels. The data are from Bakker (1961): (□) wild-type larvae, (△) Bar larvae.

used varied. Figure 3 gives the adult weights of males and females from each stock. Several results are immediately apparent: first, there is a minimum weight that males and females reach at about the same level of food availability; second, even after the maximum emergence rate has been recorded, the adult size continues to increase. These results alone do not eliminate the possibility that the competitive effects are due to interference rather than a simple scramble for the limited amounts of food. To test this possibility, Chiang and Hodson (1950) and Bakker (1961) looked at the percent emergence and adult weight by varying both the amount of food per larva and the density of larvae. In the range of densities examined in these experiments it was seen that the amount of food per larva was the most important determinant of percent emergence and adult weight. There was no increase noted in competitive effects by simply increasing the density while keeping the amount of food per larva constant.

If the above basic assumptions of larval competition are correct, we should be able to detect differential rates of growth for larvae with dif-

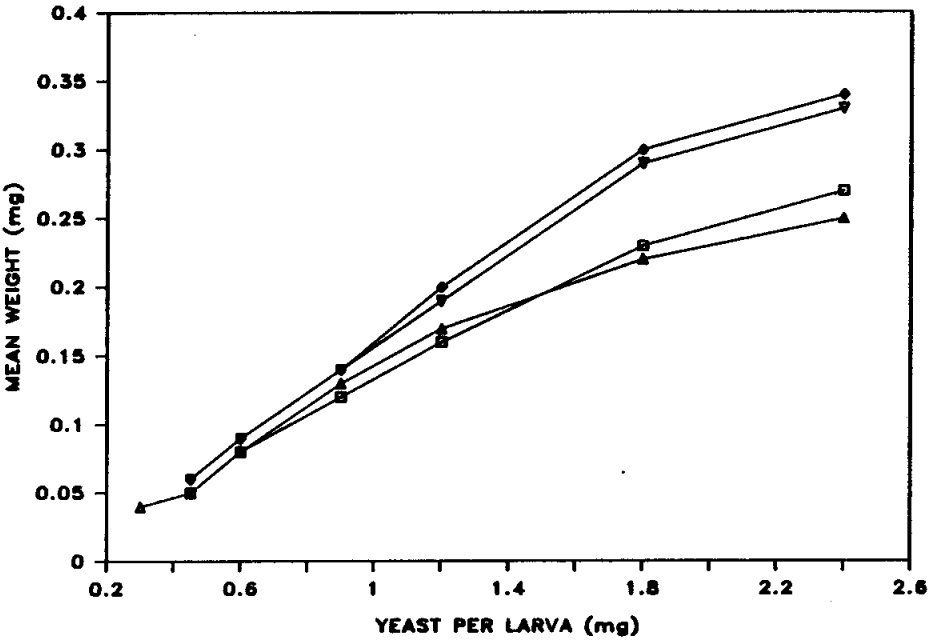


FIG. 3. Mean dry weight of adults as a function of different food levels. The data are from Bakker (1961): (◇) wild-type females, (▽) Bar females, (□) wild-type males, (△) Bar males.

ferent α_i. Bakker (1961) let larvae feed with unlimited food for periods of 39–60 h. At various times the larvae were transferred to nonnutritive medium; a portion of these were weighed and another portion were allowed to pupate. Limiting the length of feeding time produces similar effects as limiting the total amount of food. In Fig. 4 the difference between the wild and Bar populations in percent pupation is shown. Figure 5 shows the difference in larval weight for the same two populations as a function of feeding time. If the data in these two figures are reanalyzed, it turns out that the percent pupation is approximately the same for each population, given that larvae have achieved the same size. Since the results in Fig. 3 indicate that wild and Bar flies have approximately the same efficiency of converting food into *Drosophila* biomass, we can interpret the size differences in Fig. 5 as indicating a difference in the rate at which food is changed into biomass. From Fig. 5 it appears that Bar flies require approximately 3 h longer to reach the same larval size as a wild fly.

According to the model of larval competition, we would expect the

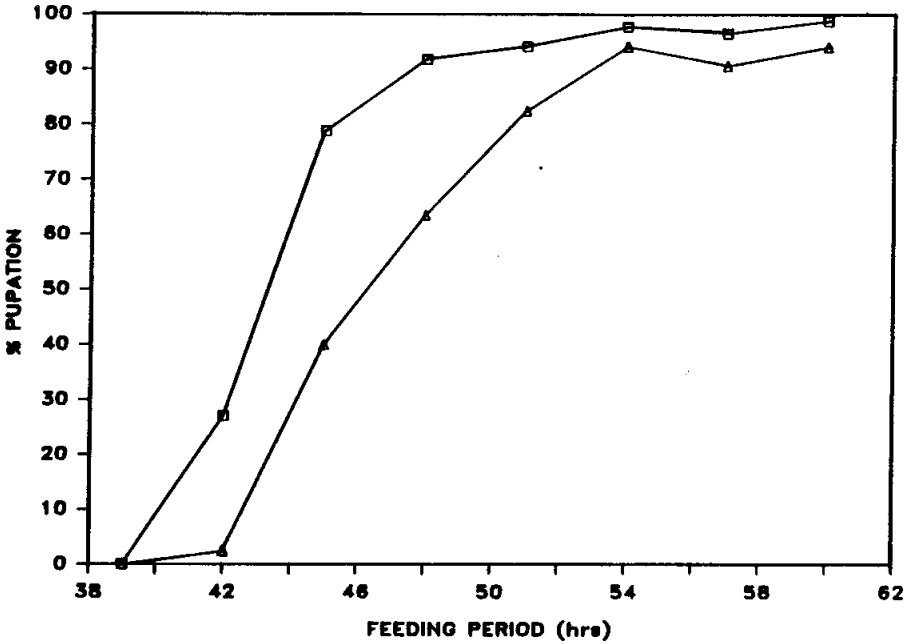


FIG. 4. The percent of all larvae that successfully pupate as a function of different feeding times. The data are from Bakker (1961); the symbols are the same as in Fig. 2.

wild flies to have a substantial competitive advantage relative to Bar flies due to their higher feeding rates. Bakker (1961) conducted larval viability experiments similar to those described previously with 100 wild larvae and 100 Bar larvae placed in vials with 0.42 mg yeast per larva. Only 40% of the larvae reached the adult stage, and of these, 85% were wild and 15% were Bar. It would seem reasonable that if differential feeding rates were the major reason for the differential competitive abilities, then this competitive difference could be eliminated by providing Bar larvae a slight headstart in feeding. As shown in Fig. 5, the Bar larvae generally lag 3 h behind the wild larvae in reaching a given weight. If Bar larvae are given a 3-h headstart, then by the time that the food is exhausted both larvae should be approximately the same size and hence have the same probability of successfully pupating. Bakker (1961) performed this experiment and found that among the emerging adults 59% were Bar.

Nunney (1983) has examined differential competitive abilities of males and females of the same population. Figure 6 shows Nunney's (1983) viability results as a function of food availability in addition to the

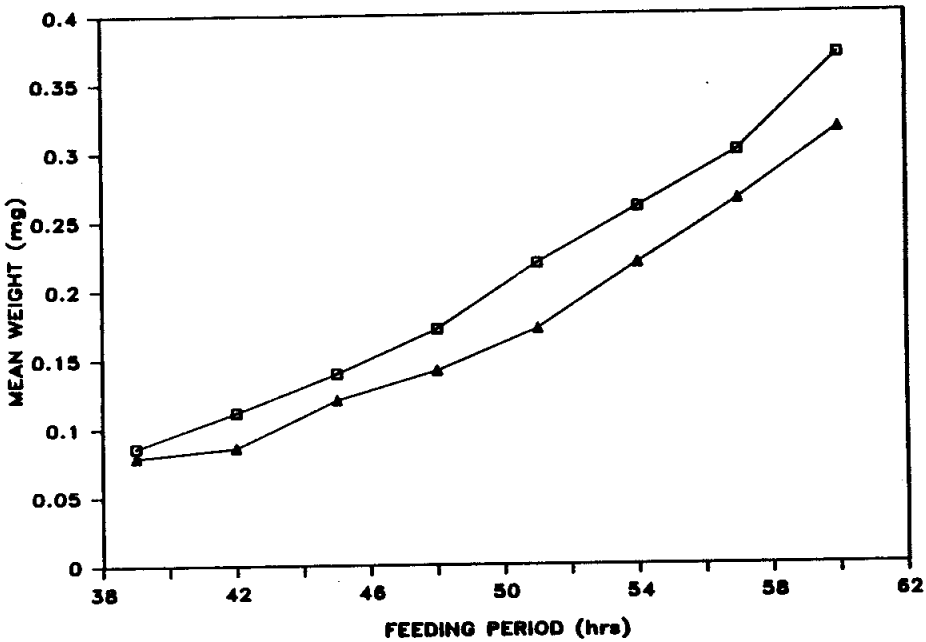


FIG. 5. The weight of larvae as a function of different feeding times. The data are from Bakker (1961); the symbols are the same as in Fig. 2.

least squares fit to the competition model outlined previously. Clearly, the fit is quite good. De Jong (1976) has examined a model similar to Nunney's (1983) in which she assumes that the amount of food consumed has a binomial distribution. Nunney (1983) demonstrates that his empirical results do not fit this model with the same degree of accuracy as the normal distribution model.

Pupae

Just as larval crowding and limited food will affect the final size of adults, they will also affect the size of pupae. Chiang and Hodson (1950) present data that show that pupal length declines with increasing larval density. There is an approximately linear relationship between pupal length and adult size as measured by wing length. Although not discussed by Chiang and Hodson, their data on adult wing length and pupal length show a clear difference between the male and female populations. The

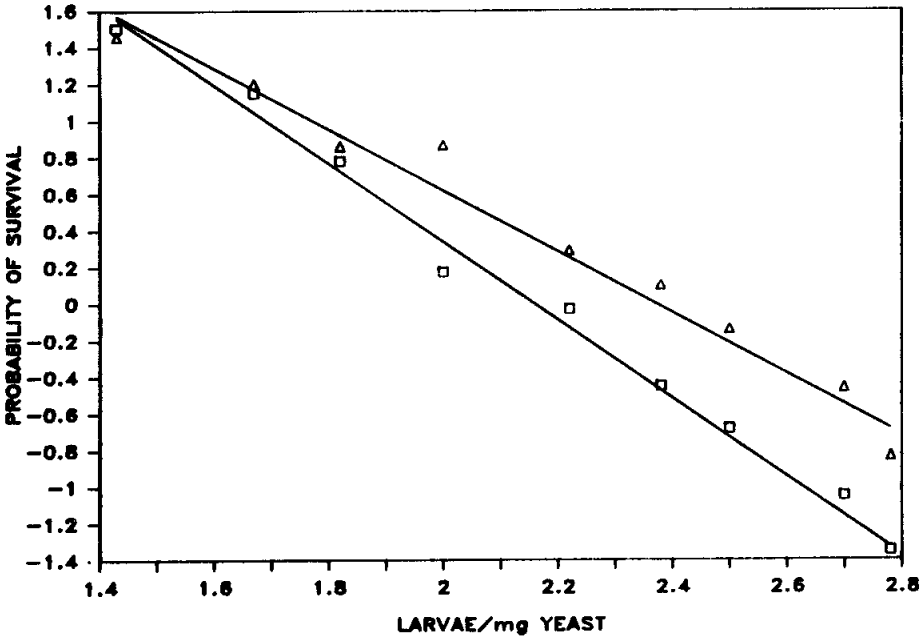


FIG. 6. The probability of survival, measured in standard normal deviates, versus food level. The lines are least squares estimate from the model described in the text. The data are from Nunney (1983): (△) Barton males, (□) Barton females.

relationship between wing length and pupal length is linear for males and females; however, there appear to be different parallel lines for each sex. Thus, females with the identical pupal length as males will develop into adults with longer wings.

Chiang and Hodson (1950) note two main sources of pupal mortality: first, drowning in the medium, and second, inadequate larval size leading to incomplete development. Pupation will often occur on the walls of the culture. In populations yielding large numbers of larvae, early-pupating individuals can become dislodged by larvae crawling up the sides of the culture to pupate. These dislodged pupae will often drown in the medium. In very crowded or old cultures food may be quite limiting and many pupae may fail to develop due to inadequate nutrition.

Adults

The ecological properties of most interest in adults are survival rates and female fecundity. Pearl *et al.* (1927) studied the density-dependent

survivorship of an inbred line. Sex differences were not taken into consideration. Because these studies involved following the number of survivors from an initial cohort, the density of these populations decreased over time. Consequently, the largest differences in survival rates between the density treatments were found in the younger adults. The rates of mortality were very similar for all of those flies older than 55 days regardless of initial starting density (35–200 flies per 1-oz. bottle).

Pearl *et al.* (1927) showed that adult mortality can depend on the past history of a fly. In one experiment two cohorts were established: one at an initial density of 35 and a second at a density of 200. After 16 days survivors from each experiment were each placed at densities of 200 and their survivorship followed. The average age at death of flies kept for the first 16 days at a density of 35 was 22.8 days, while those started at a density of 200 lived to be only 19.7 days on average. Thus, prior exposure to low densities can increase an individual's probability of survival at high density relative to an individual raised at that high density. Although past population density has some effect on one's current probability of survival, current density is clearly the most important factor. Pearl *et al.* conducted a control in which flies raised at an initial density of 35 were reconstituted to a density of 35 at day 16. The average life span for these flies was 34.8 days. These results imply that a complete description of density-dependent growth in an age-structured population would require knowing not only the current age class sizes, but those for some time in the past. Although it is possible to develop such models in principle (Charlesworth, 1980), they are exceedingly difficult to analyze.

Chiang and Hodson (1950) have shown that female fecundity declines as the age and density of larvae in the culture increase. However, it is not clear from their experimental technique whether the females are actually laying fewer eggs or whether the larvae are burying eggs, which then remain uncounted. Even if females do not change the number of eggs they lay in the presence of larvae, they do change the location of eggs laid. Females lay a larger portion of their eggs on the walls of the culture as the density and age of larvae increase (Chiang and Hodson, 1950). Given the potentially high mortality of eggs buried by larvae, this behavioral flexibility in females is a useful adaptation. Chiang and Hodson have also examined female preference for laying eggs in medium differing in moisture and texture. In general females seem to prefer moist, rough surfaces as opposed to smooth, dry ones.

A number of studies have investigated the influence of crowding on female fecundity (Pearl, 1932; Bodenheimer, 1938; Robertson and Sang, 1944; Chiang and Hodson, 1950). All studies reveal that at very low densities (0.5–4 flies/cm^2) female fecundity is very sensitive to changes in

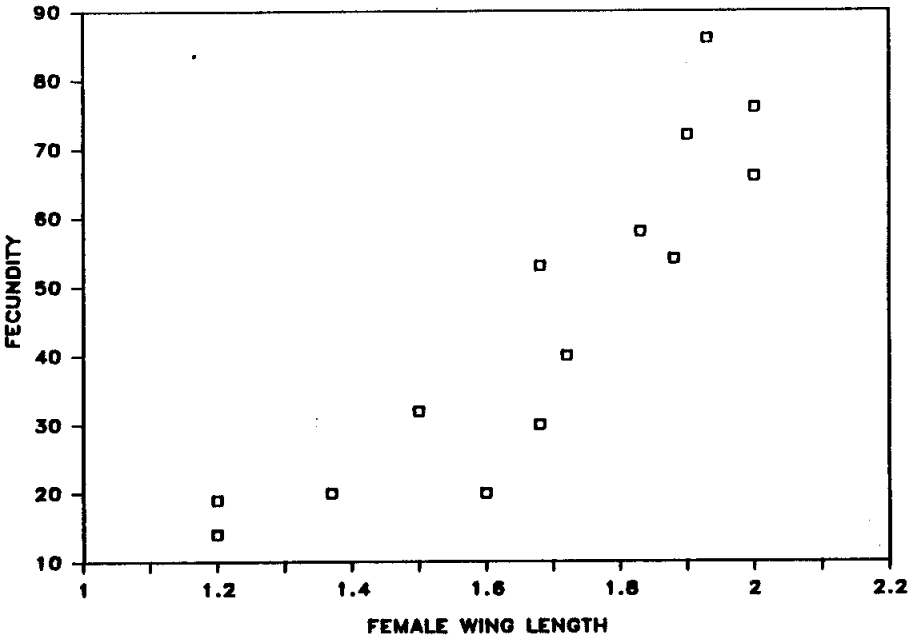


FIG. 7. Fecundity versus female adult size, as measured by wing length. [From Chiang and Hodson (1950).]

adult densities, while at densities greater than 10 flies/cm^2 female fecundity is nearly constant. Thus, studies of female fecundity carried out in 8-dram vials would yield quite different results as density changed from one mating pair to five, although all these densities are typically considered low.

It is apparent from the work considered earlier that in the absence of sufficient food the final size of adults can vary significantly. This size variation in females will inevitably lead to variation in fecundity. The results of Chiang and Hodson are reproduced in Fig. 7. Similar results have been reported by Robertson (1957) and Prout (1985). It should be noted that the females used in these studies are raised on suboptimal amounts of food or in crowded cultures.

In a quantitative genetic study of body size and egg production Robertson (1957) has found little correlation in the additive genetic components of these traits. However, these studies were conducted in uncrowded environments. The same studies conducted with limited food may show high additive genetic correlation between size and egg pro-

duction, although it should be emphasized that the strong phenotypic correlation demonstrated in Fig. 7 does not imply a positive genetic correlation (Rose and Charlesworth, 1981*a*).

Female fecundity also depends on adult nutrition. Sang (1949*d*) has shown that partially starved adult females show a decline in fecundity. In addition, Sang has shown that female fecundity may depend on the type of yeast consumed. Studies have already been described which show a decline in female fecundity with increasing density. Although this effect could be due in part to limited food, the very large decrease in fecundity observed at very low adult densities would imply that factors other than food were important. Pearl (1932) has concluded that interference from other flies and a general level of increased activity might account for decreasing female fecundity at these low densities.

A number of studies show that female fecundity may depend on the male parent (Alvarez and Fontdevila, 1981; Clark and Feldman, 1981*a*,*b*). This effect may persist over the lifetime of the female. For instance, Alvarez and Fontdevila (1981) show that singed females crossed with wild-type males show an increase in early fecundity (days 1–3) relative to singed females crossed with singed males. However, this advantage is lost at later ages. In contrast, wild-type females crossed with wild males have higher fecundity at nearly all ages relative to wild females mated with singed males.

POPULATION DYNAMICS

Some of the earliest ecological work with *Drosophila* examined the dynamics of laboratory populations. Such studies have continued intermittently to the present. The development of research in this field provides a useful example of the interaction between theory and experiment. It also illustrates the problems that are encountered when inappropriate experimental regimes are used to test theory.

This section will begin with a discussion of the different methods of maintaining *Drosophila* populations. The discussion will be followed by a more detailed description of the serial transfer system (STS) and results from various studies. Finally, the ecological and evolutionary significance of population stability will be considered.

Population Maintenance

Some of the earliest and most cited work on the population dynamics of *Drosophila melanogaster* was carried out by Raymond Pearl and his

co-workers (Pearl, 1927). Pearl's work is often used as the textbook example of logistic population growth. Pearl's method of maintaining cultures seems straightforward, but has a number of inherent problems. Into standard *Drosophila* cultures Pearl placed a small number of adults. At regular intervals the adult population were censused and returned to the original culture. Although such populations will initially show a rapid increase in adult numbers, unless the food supply is supplemented, the population will eventually go extinct. Rather than move the adult population to a fresh food source at regular intervals, Pearl added fresh food to the old culture as needed. Pearl (1927) notes that the "experiment is one in which an attempt is made to add food as the supply is used up. The technical difficulties of doing this satisfactorily with a *Drosophila* population are considerable, but with sufficient care they can be overcome in large degree." Clearly such a subjective protocol would weaken any theoretical results based on these observations. Sang (1949*d*) has noted these problems and concluded, "On the face of it, it is therefore difficult to understand how the results of such an experiment . . . fit a logistic for any reason other than the choice of the right time at which to add food and the right amount of it."

Due to these problems subsequent workers have attempted to replace food at regular intervals. This can be achieved in two ways: (1) the adult population is moved to a fresh food source or (2) the adult population is kept in the same culture with fresh food introduced at regular intervals. L'Heritier and Teissier (1933) describe an early population cage which exemplifies the second alternative. In this study new food cups were added every day. When a food cup was 20 days old it was removed. Thus at any time the population cage would have 20 food cups aged 1–20 days. The total amount of food available to the population and the rate of replenishment could thus be carefully controlled. Most population cages used today operate on the same principle (Ayala, 1968*b*).

The first method of renewing resources is exemplified by the serial transfer system (STS). Pearl (1927) actually describes a form of the STS, while refinements are described by Buzzati-Traverso (1955) and Ayala (1965*b*). In the STS there is a single adult population, which is allowed to lay eggs on fresh medium for a specified number of days, after which all surviving adults are transferred to a fresh culture and another round of egg laying commences. As adults start to emerge from the older cultures, they are collected and added to the egg-laying population of adults. Thus at any time interval the adult population consists of survivors from the previous time interval plus newly emerged adults from the old cultures. In Fig. 8 the STS is shown in which cultures are discarded when they are 4 time units old. The actual length of the time interval varies

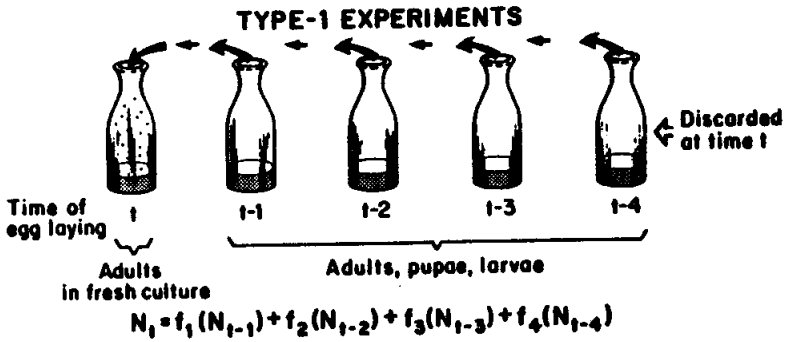


FIG. 8. The serial transfer system of maintaining *Drosophila* populations. [From Mueller and Ayala (1981*b*).] See text for additional details.

from 3 days (Buzzati-Traverso, 1955) to 1 week (Ayala *et al.*, 1973; Gilpin and Ayala, 1973; Thomas *et al.*, 1980; Pomerantz *et al.*, 1980; Hastings *et al.*, 1981; Mueller and Ayala, 1981*b*). The STS has the advantage of providing a regular supply of food and oviposition sites in addition to maintaining an adult population with overlapping generations. The disadvantage of the STS is that it is rather complicated to model (to be discussed further).

Since ecologists are most interested in examining models of population dynamics that are first-order difference equations, the following laboratory regime would seem to be the most appropriate. Adult flies are allowed 1–2 days for egg laying, after which time they are discarded. Twelve to 15 days later the newly emerged adults are collected and put in fresh cultures to start the next generation. This method of population maintenance is used commonly by population geneticists, since most population genetic models assume a fully discrete life cycle. Despite its widespread use by population geneticists, it is seldomly used by *Drosophila* population ecologists [for an exception see Prout (1985)]. The reason for this is not clear, although there may be an unconscious desire by ecologists to avoid the artificial termination of the adult life cycle. Undoubtedly, methods of population maintenance that preserve an adult population with overlapping generations would more closely resemble the "natural" ecology of *Drosophila*.

Modeling Population Dynamics of *Drosophila*

Ayala *et al.* (1973) were the first to describe a simple experimental technique which would allow density-dependent rates of population

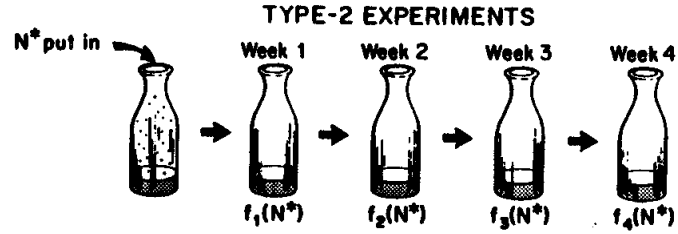


FIG. 9. The experimental protocol for estimating density-dependent rates of population growth in the STS [From Mueller and Ayala (1981*b*).]

growth to be determined in the serial transfer system. The procedure involves placing a specified number of adults N^* in a single culture. The survivors in this culture are counted 1 week (or any other time interval) later. The newly emerged progeny from this same culture are removed and counted at weekly intervals for the next 3 weeks. This experimental procedure is outlined in Fig. 9. It seems reasonable to expect rates of population growth in the STS to depend on the number of egg-laying adults that survive to the next generation, the total number of progeny produced from each week's egg laying, and the time at which these progeny emerge. This last point is especially important. Since progeny from 1 week of egg laying are being collected over a 3-week period and placed with the egg-laying adult population as soon as they emerge (see Fig. 8), it is reasonable to assume that a population in which most of the progeny emerge very early will grow at a faster rate than a population that has slowly developing progeny.

Referring to Fig. 8, one can see that the total number of egg-laying adults at time t, N_t, is simply the sum of the number surviving from the previous week, $f_1(N_{t-1})$, plus the number emerging from the 2-week old culture, $f_2(N_{t-2})$, plus the same numbers from the 3- and 4-week old cultures, $f_3(N_{t-3})$ and $f_4(N_{t-4})$. Each $f_i(N_{t-i})$ is some unspecified function describing the number of survivors or emerging progeny that come out of an i-weeks-old culture that initially had N_{t-i} adults laying eggs [see Mueller and Ayala (1981*b*) for more details]. Thus it is clear that in an STS, as in Fig. 8, N_t depends on the population size in four previous time intervals.

In the type 2 experiments shown in Fig. 9 it is obvious that each experiment provides an estimate of $f_1(N^*)$, $f_2(N^*)$, $f_3(N^*)$, and $f_4(N^*)$. These experiments can of course be replicated at each density N^* and carried out at a variety of densities to get a complete description of the population dynamics in the serial transfer system. Once the $f_i(N^*)$ have

been estimated it is possible to obtain an asymptotic rate of population growth λ_{N^*} without having to specify the functions $f(\cdot)$ (Mueller and Ayala, 1981*b*). This asymptotic rate of growth λ_{N^*} is the rate at which the population would grow if the density were maintained in the vicinity of N^* for some time. The derivation of λ_{N^*} is in many ways similar to the derivation of rates of exponential increase from a Leslie matrix (Charlesworth, 1980), where the STS has an age structure for cultures rather than individuals. With the λ_{N^*} in hand, the total change in population size at a density N^* can be estimated as

$$N_t - N_{t-1} = \lambda_{N^*}N^* - N^* = N^*(\lambda_{N^*} - 1)$$

A basic assumption of logistic population growth is that per-capita rates of population growth decline linearly with increasing densities. It is precisely this assumption that can be tested with the λ_{N^*} values derived from the type 2 experiments just described (Mueller and Ayala, 1981b, 1982). It should be emphasized that when investigating first-order difference equations that relate λ_{N^*} and N^* one cannot imply that these same equations can be used as a general description of population dynamics in the STS. This is due to the fact that, in general, rates of population growth in the STS will depend on four previous time intervals rather than one. However, for purposes of studying some general relationships between density and rates of population growth it is more convenient to use the asymptotic rates of population growth.

This methodology is not without precedent. In Smith's (1963) study of the population dynamics of *Daphnia magna* he obtained density-dependent rates of population growth only after his experimental populations had reached a stable age distribution. Thus Smith was deriving asymptotic rates of population growth empirically by allowing his populations to remove the effects of the initial arbitrary age distribution. Mueller and Ayala (1981*b*) have achieved a similar result mathematically.

Several other studies (Ayala *et al.*, 1973; Pomerantz *et al.*, 1980; Thomas *et al.*, 1980; Hastings *et al.*, 1981) have used "net productivity" estimates from type 2 experiments to test models of population growth. The net productivity is simply the sum of the survivors and all emerging progeny minus the initial density N^* from a type 2 experiment. The main difference between the net productivity value and λ_{N^*} is that net productivity does not account for the time at which survivors or progeny are added to the egg-laying population of the STS. Thus, as an estimate of the rate of population growth in the STS net productivity is biased. At densities near carrying capacity this bias is small. In particular, at carrying capacity, since each individual only replaces itself, the time at which this

occurs is immaterial and hence the bias should be zero. However, the bias will be greater at densities furthermost from carrying capacity. This bias is evident in the graphs of $N_{t+1} - N_t$ versus N_t seen in Pomerantz *et al.* (1980) and Hastings *et al.* (1981), which show a rapid rise in $N_{t+1} - N_t$ and an almost linear decline after reaching a peak. These curves should be compared to those in Mueller and Ayala (1981*b*). Hastings *et al.* (1981) argue that net productivity may be considered as useful a measurement of population dynamics as λ_{N^*}. Unfortunately, there is no direct theoretical connection between net productivity and rates of population growth in the STS as there is for λ_{N^*}. Consequently, net productivity should be regarded as a rough approximation to rates of population growth which will be biased upward at very low densities.

In Fig. 10 density-dependent rates of population growth for several populations of *D. melanogaster* are shown (Mueller and Ayala, 1981*a*). The discrete form of the theta model is

$$N_{t+1} - N_t = rN_t[1 - (K/N_t)^\theta]$$

When $\theta = 1$, the model is identical to the logistic model, and when $\theta < 1$, per-capita rates of population growth decline more rapidly than linear. From Fig. 10 it is clear that the per-capita rates of population growth for *D. melanogaster* are not linear functions of density as predicted by the logistic equation. This result appears to be quite general for *Drosophila*. It is of some interest to be able to understand the mechanism of intraspecific competition that produces these deviations from the logistic (Mueller and Ayala, 1981*b*; Haddon, 1982), although such an understanding is not essential to the development of a descriptive theory (Mueller and Ayala, 1982).

A preliminary attack on this problem would begin with an examination of density-dependent birth and death rates. In Fig. 11 are shown the probabilities of survival of males and females aged 7–14 days held at various densities for 1 week (Mueller, 1979). These rates change very slowly at low densities and would not seem of sufficient magnitude to explain the large decline in per-capita rates of population growth. Pearl *et al.* (1927) also present data on the average duration of adult life as a function of density. These data actually show increasing survivorship with increasing density over a range of low densities.

One can investigate the effects of limited food on female fecundity by using Bakker's data on food versus adult size and Robertson's data on female size versus fecundity. These results are shown in Fig. 12. Clearly, over the range of food levels tested the rate of decline in female fecundity is linear or slower than linear with decreasing food levels. It is

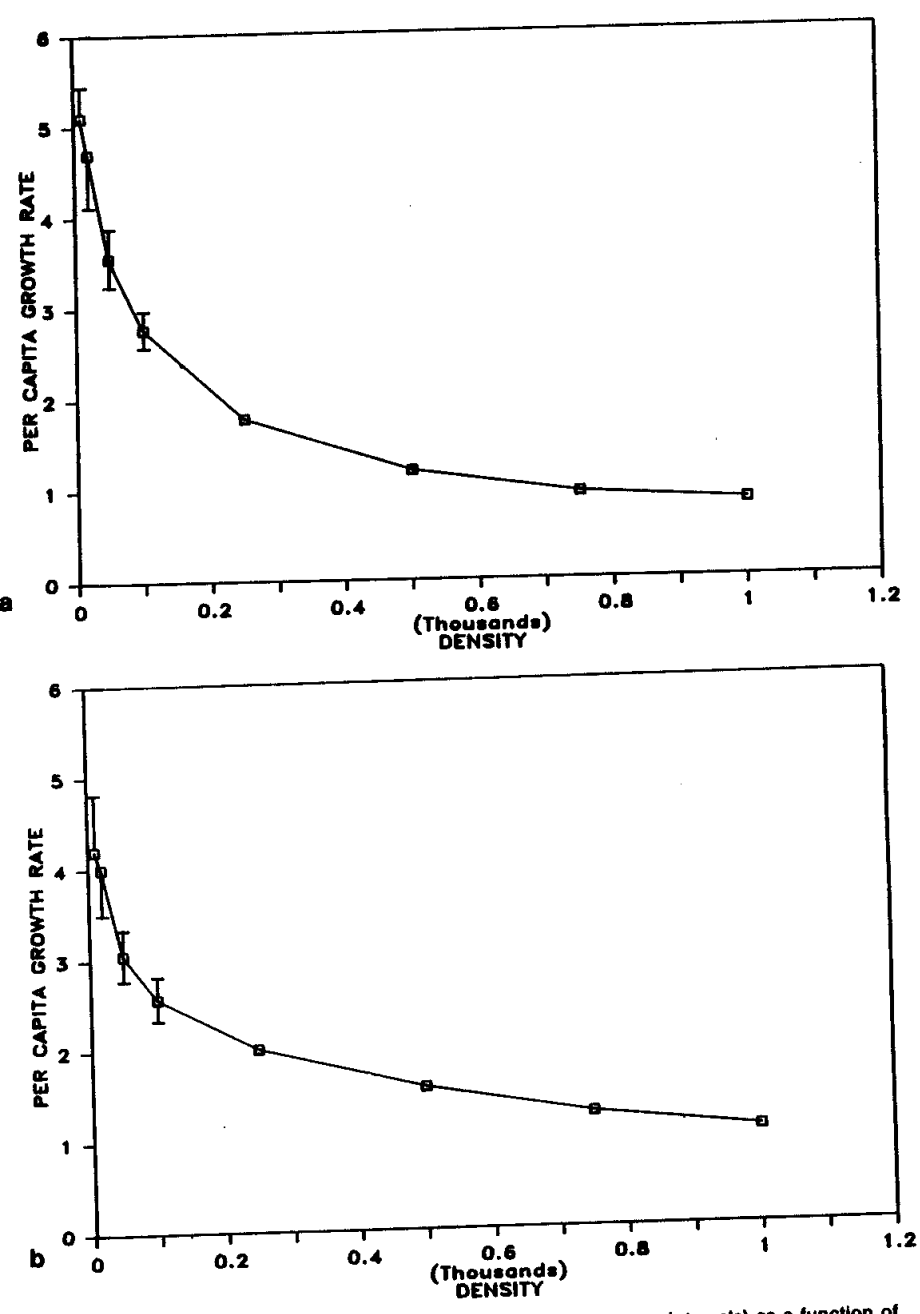
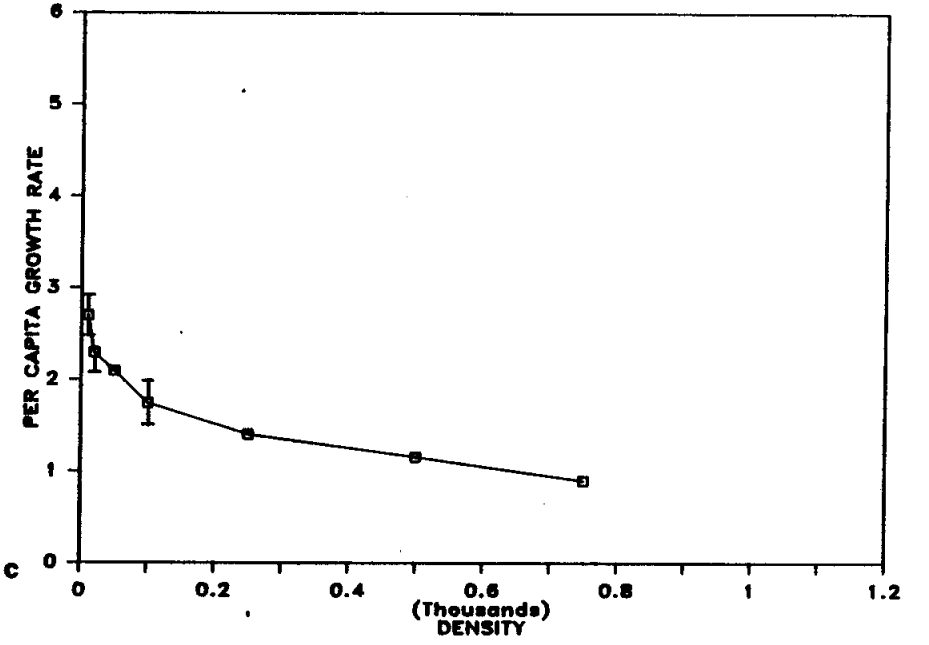


FIG. 10. Per-capita rates of population growth (with 95% confidence intervals) as a function of density for three populations of *D. melanogaster* isogenic for different second chromosomes. [From Mueller and Ayala (1981*a*).] No confidence intervals have been drawn when these were smaller than the width of the symbol. (a) Line 3, (b) line 18, (c) line 36.



c

FIG. 10. (*Continued*)

unlikely that this phenomenon alone could account for the rapid decline in per-capita rates of population growth at low densities. Chiang and Hodson (1950) described dramatic declines in fecundity at densities of 10–78 flies per ½-pint culture. These densities are at the lowest range examined in the STS. This evidence implicates rapidly declining female fecundity due to increasing adult density as the major cause of the faster than linear decline in the rates of population growth shown in Fig. 10.

Introduction of the parameter θ to the Lotka–Volterra competition model appears to result in a model that can more accurately describe the dynamics of competing populations of *D. pseudoobscura* and *D. willistoni* (Ayala *et al.*, 1973). Although the net productivity statistic was used in this paper, most density combinations were close to the two-species equilibrium. Consequently, the bias introduced by using net productivity as estimates of rates of population growth may not have been severe. For competing populations of *Drosophila*, θ is usually less than one. It would seem reasonable to suppose that interspecific competition would have the same effect on fecundity as intraspecific competition does. The size of emerging females will decline with increasing numbers of competitors,

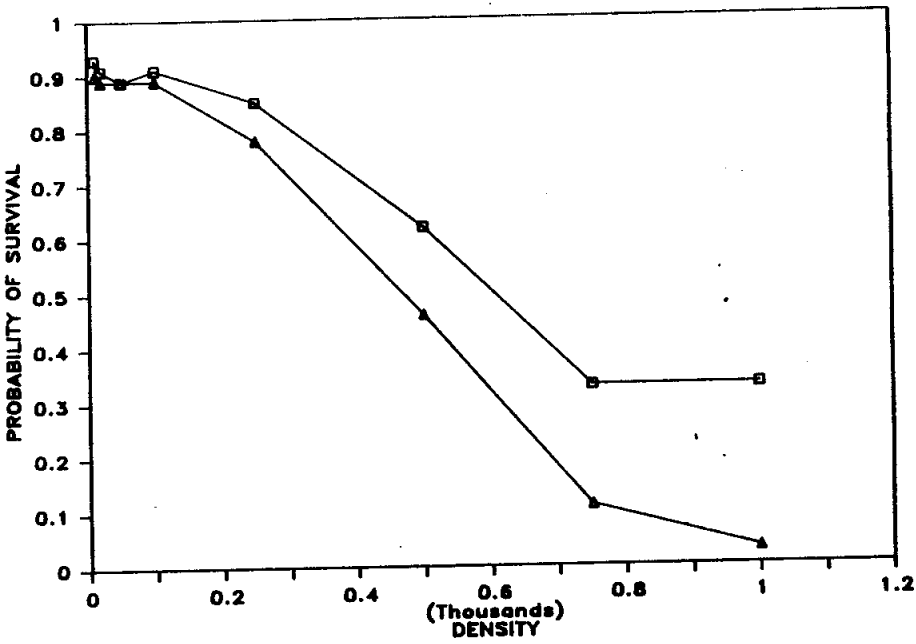


FIG. 11. The probability of surviving one week for (□) male and (△) female *D. melanogaster* as a function of the initial adult density (equal sex ratio). [From Mueller (1979).]

but the magnitude of this decline will depend not only on food availability, but also on the frequency of competing larvae and the relative competitive ability of these larvae (Bakker, 1961; Nunney, 1983).

Population Stability

For those populations in which reproduction takes place at discrete intervals, and are therefore well described by nonlinear difference equations, quantitative properties of density-dependent regulation can cause peculiar phenomena (May, 1974; May and Oster, 1976; Guckenheimer *et al.*, 1977). In particular, depending on the value of certain parameters, many difference equations can exhibit two-point, four-point, or higher order cycles or apparently chaotic population dynamics in completely deterministic environments. Most natural and laboratory populations will show some degree of fluctuation about an apparent equilibrium. However, it is often assumed that these fluctuations generally reflect some under-

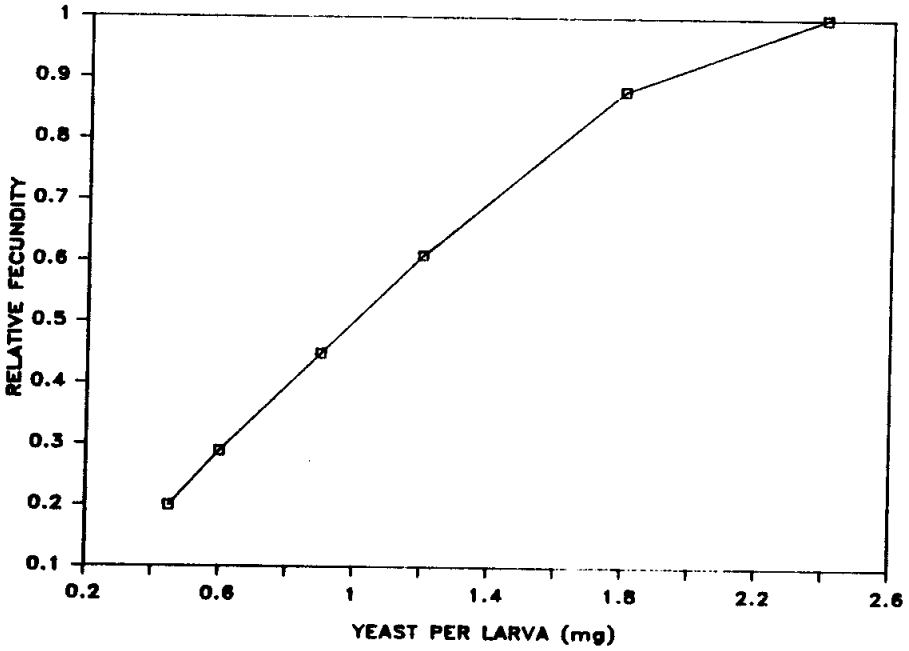


FIG. 12. Relative fecundity of wild-type *D. melanogaster* as a function of different larval food levels. The predictions are based on Bakker's (1961) data (see Fig. 3) relating adult size to food level and Robertson's (1957) data describing fecundity versus adult female size.

lying changes in the environment (e.g., temperature, moisture, or food availability). It is clearly of some importance to be able to separate variation due to environmental variability from that due to the intrinsic nature of density-dependent regulation.

Classification of a population as either possessing an asymptotically stable carrying capacity or a potentially cyclic or chaotic equilibrium requires knowledge of the linear dynamics in the vicinity of the carrying capacity [see Roughgarden (1979) for a review of the stability properties of difference equations]. In practice this has been accomplished with two different methods. The first method (Hassell *et al.*, 1976; Thomas *et al.*, 1980) has two levels of inference. At the first level a particular functional form is assumed to be an adequate description of the population dynamics. Thus, Hassell *et al.* (1976) use the first-order difference equation $N_{t+1} = \lambda N_t/(1 + aN_t)^{\beta}$ for a variety of species, while Thomas *et al.* use the theta model to analyze data from 27 species of *Drosophila*. At the second level of inference, parameters of the models must be estimated from direct observations of population growth rates (Thomas *et al.*, 1980) or by other

less direct methods (Hassell *et al.*, 1976). Once these parameters have been estimated, the linear dynamics in the vicinity of the carrying capacity are obtained by the appropriate linearization of the nonlinear equation. The second method (Mueller and Ayala, 1981*c*) utilizes observed rates of population growth in the vicinity of the carrying capacity to estimate the local linear dynamics directly. This method avoids using a specific functional description of the population's dynamics, which is bound to be an approximation, but can only be used with populations whose density-dependent rates of growth can be measured directly. For laboratory populations of *Drosophila* this last qualification is not a restriction.

Two studies have addressed the problem of dynamic stability in laboratory populations of *Drosophila*. Thomas *et al.* (1980) examined the dynamics of 27 different species of *Drosophila*, while Mueller and Ayala (1981*c*) obtained data on 25 genetically different populations of *D. melanogaster*. In both studies the dynamics in the STS were obtained. The qualitative conclusions from these two studies were the same: the overwhelming majority of populations show asymptotically stable carrying capacities. There is little indication of potentially cyclic or chaotic population dynamics. Although Thomas *et al.* (1980) and Mueller and Ayala (1981*c*) used the same experimental techniques, their methods of analysis were quite different. Some of these differences have been discussed above. In addition, Thomas *et al.* used a linearization of a first-order difference equation to obtain the local linear dynamics of the STS. As discussed previously, a complete model of the STS will be a fourth-order (or higher) difference equation. Thus, the stability analysis of Thomas *et al.* is inappropriate for the STS. Given these very different methods of analysis, it seems surprising that they demonstrate a high degree of correspondence. It may be that the net productivity measurements near the carrying capacity of Thomas *et al.* are not biased estimates of rates of population growth and thus convey the correct information regarding population stability. A reanalysis of the data is clearly the only way in which to resolve this problem.

If the results on population stability obtained for laboratory *Drosophila* are at all relevant to natural populations, it is of interest to try to uncover a mechanism of natural selection that might promote population stability. Mechanisms involving both group (Thomas *et al.*, 1980) and individual selection (Heckel and Roughgarden, 1980; Turelli and Petry, 1980; Mueller and Ayala, 1981c) have been proposed. Thomas *et al.* have argued that as a population's stability eigenvalue increases in magnitude, the smallest population size reached at equilibrium decreases. As a consequence, the probability of chance extinction should also increase with increasing instability.

If one assumes that there is genetic variation within a population that affects parameters of growth equations (e.g., r, k, and θ of the theta model) and that fitness is density dependent, then individual selection may determine population stability. The existence of genetic variation for parameters of the logistic and theta models has been demonstrated for *D. melanogaster* (Mueller and Ayala, 1981*b*). The models of Heckel and Roughgarden (1980) and Turelli and Petry (1980) examined density-dependent selection in a variable environment with populations initially possessing a stable carrying capacity. Mueller and Ayala (1981*c*) numerically studied evolution in deterministic environments with populations that initially exhibited two-point cycles. Both Turelli and Petry and Mueller and Ayala saw that the evolution of population stability could be model dependent in particular settings. However, Turelli and Petry found that under the most general conditions which they considered, natural selection always resulted in stable population dynamics and this result was robust with regard to the particular density-dependent regulating function. Mueller and Ayala argued that there may be a strong negative correlation between parameters that determine population stability and that this correlation structure may constrain a population's evolution such that it usually has a stable carrying capacity.

The experimental paradigm for determining *Drosophila* population dynamics has utilized adults as the natural census stage. The reasons for this are that adults are the most conspicuous life stage of *Drosophila* and are the most easily manipulated. However, it must be remembered that even when the adult life stage is artificially shortened to a few days, all laboratory populations will have several immature stages prior to the adult census. In an important paper, Prout (1985) has shown that estimating population dynamics from observations of changes in the adult population size over a single generation may be inherently biased. At the root of this problem is the influence of larval density on adult fecundity. If female fecundity depends on larval density to any degree, then it is impossible to represent the number of adults at time t as a function of the adult number at time $t - 1$, even in populations with fully discrete generations (see section on life-history evolution). Under these conditions eggs are the natural life stage to census. Prout demonstrates that estimates of population stability at carrying capacity can also be biased when estimated from adult-to-adult transitions. If female fecundity does not change as a function of egg (or larval) density in the vicinity of carrying capacity, then the bias produced from adult data will be zero. However, even when the dependence of female fecundity on egg density is slight, the potential bias in estimates of population stability can be large.

Prout's results naturally call into question the results of Thomas *et*

al. (1980) and Mueller and Ayala (1981*c*), since both used adult-to-adult transitions to estimate population stability. The degree to which the results of Thomas *et al.* and Mueller and Ayala may be in error will depend on the sensitivity of female fecundity to egg density in the serial transfer system. Such data have not been produced, although there is no reason to believe there will not be some dependence. The importance of Prout's theoretical results are bolstered by his own experimental data, which indicate that the eigenvalue governing stability in his experimental populations may be less than -1. This result was obtained from a first-order difference equation describing the change in the number of eggs at time t, e_t:

$$e_{t+1} = F(e_t)S(e_t)e_t$$

where $F(e_t)$ describes the effect of egg density on adult fecundity and $S(e_t)$ describes the relationship between egg-to-adult survival and egg density. Prout conducted separate experiments to estimate the functions $F(e_t)$ and $S(e_t)$; his analysis explicitly assumed that adult density has no effect on fecundity. Prout's data actually indicate a slight decline in fecundity with increasing adult density. It can be shown that even this weak dependence of adult fecundity on adult density will result in eigenvalues larger than those obtained by Prout. Consequently, the eigenvalues obtained by Prout are biased in a direction opposite to the bias present in Thomas *et al.* and Mueller and Ayala. Unfortunately, the only way to avoid the bias introduced by ignoring the effects of larval and adult density on fecundity is to observe directly the change in number of eggs from one generation to the next.

Several studies claim to have uncovered evidence of cycling in *Drosophila* populations. Shorrocks (1970) studied 14 populations of *D. melanogaster*. These populations reproduced at discrete intervals. Three populations showed strong positive autocorrelations, although the lag differed for each population. These lags occurred at two, three, and four generations. Many populations did not show any signs of a strong autocorrelation. Thus, although a few populations may have exhibited some cycling, it is certainly not a consistent phenomenon even with replicated experimental populations.

Nogueś (1977) maintained *D. subobscura* in an STS-like system. This population exhibited pronounced oscillatory behavior. These cycles were probably environmentally induced. During peaks of population growth, culture bottles tended to become overgrown with mold. Such contami-

nation may have precipitated the abrupt population decline, resulting in the cyclical behavior.

COMPETITION

Interspecific competition has assumed a major role in the theory of ecology (Roughgarden, 1979). Competition may place limits on species diversity (Abrams, 1976) and be responsible for resource partitioning (Roughgarden, 1976). When competition is especially intense, natural selection may favor genotypes that will avoid competition, resulting in a coevolution-structured community (Rummel and Roughgarden, 1983). Despite this body of work, the importance of competition in structuring natural populations has been questioned recently (Connor and Simberloff, 1979; Strong *et al.*, 1979; Connell, 1980). Although not all communities show evidence of interspecific competition, a recent review (Schoener, 1983) concludes that competition was found in 76% of the species examined in over 150 field studies.

Competition in Natural Populations

Evidence for competition in natural populations of *Drosophila* has been found by Atkinson (1979) and Grimaldi and Jaenike (1984). Atkinson collected fruits and vegetables from local markets and measured the wing length of flies emerging from these natural substrates. He also recorded the total number of adults emerging from a particular fruit and used this number as an indicator of larval densities. Atkinson found that within a particular type of fruit or vegetable there was a significant decline in the wing length of *D. melanogaster* with increasing larval densities. There was also a negative correlation between the wing length of *D. simulans*, *immigrans*, and *hydei* and the number of emerging *melanogaster*. These results provide evidence of both intra- and interspecific competition.

Grimaldi and Jaenike (1984) collected mushrooms infested with dipteran larvae and cut these in half. One half was kept in an enclosed jar and the second half was supplemented with previously frozen mushroom of the same species. *Drosophila falleni*, *putrida*, and *testacea* showed significant increases in the number of emerging adults when supplement was provided. These three species and *D. recens* also showed an increase in size (as measured by thorax length) in the supplemented jars. It is clear

that for the mycophagous *Drosophila*, resources are limiting, although it is not possible to distinguish between intra- and interspecific competition.

Competition in the Laboratory

Laboratory studies of competition with *Drosophila* have examined both intergenotypic and interspecific effects. Environmental variables such as temperature have been shown to affect interspecific (Ayala, 1966, 1971; Bierbaum and Ayala, 1985) and intraspecific (Mather and Cooke, 1962) competitive abilities. Equal numbers of *D. willistoni* and *D. pseudoobscura* were used to initiate populations kept at 18, 19, 20, 21, 22, and 25°C by Bierbaum and Ayala. At 25°C the tropical species, *D. willistoni*, competitively excluded the temperate species, *D. pseudoobscura*, while the opposite was true at 18°C. At intermediate temperatures (19–22°C) the two species coexisted for a period of 50 weeks.

Even within the homogenized environment that makes up the laboratory *Drosophila* culture it has been possible to document differences between species in habitat utilization. Merrell (1951) has shown that in competition *D. melanogaster* does better in fresh food relative to *D. funebris*, which seems to have an advantage in older food. In population cages the two species are able to coexist because the food cups naturally pass through stages that are preferred by each species.

The sibling species *D. melanogaster* and *D. simulans* also show differential utilization of experimental culture medium: *D. simulans* seems to prefer to oviposit on the center of the medium and on older surfaces relative to *D. melanogaster*, which prefers the edges of fresh medium (Moore, 1952*b*). Barker (1971) notes that *D. simulans* larvae are more often found in the lower half of the medium. The differences in habitat utilization *could* play a substantial role in competitive interactions. This point was experimentally demonstrated by Moore (1952*b*). Populations of both species were allowed to lay eggs on old and fresh food surfaces. In one treatment the next generation was started with eggs laid on the edges of the fresh food, while the second treatment utilized eggs from the center of the old food. The populations started with fresh edges showed a rapid rise in the frequency of *D. melanogaster*, with the ultimate exclusion of *D. simulans*. The populations started with old centers resulted in the fixation of *D. simulans* in one case and its near fixation in a second replicate after 13 generations.

Most laboratory studies of intra- and interspecific competition have used similar experimental techniques. Usually the effects of competition on the number of adults produced in one generation will be determined

over a range of mixtures of two competing types with the total initial density of adults or larvae held constant. This procedure can be expanded by also varying the total density. Statistical methods for analyzing these experimental data are given in Mather and Caligari (1981). In some experiments the effects of competition have been measured by determining the productivity of each competing species in the serial transfer system (Gilpin, 1974; Goodman, 1979). It is interesting that many seemingly confusing features of these experiments can be understood in light of the simplified model of larval competition presented in the preceeding section.

One consistent result from both intra- and interspecific competition studies is that the performance of a line (or species) in pure culture is not a good predictor of that line's competitive ability (Lewontin, 1955; Lewontin and Matsuo, 1963; Gale, 1964). For instance, Gale (1964) studied the competitive abilities of three lines of *D. melanogaster*. In pure culture the vestigial line had the lowest viability, but in competition it had the highest viability. A second consistent observation is that the effects of competition can be ameliorated by increasing the amount of food or decreasing the density of the population (Lewontin and Matsuo, 1963; Gale, 1964; Miller, 1964; Barker and Podger, 1970).

Consider two competing populations A and B which differ only in the parameters α and m of the larval competition model considered in the preceding section, yet have a common variance. Further assume that $\alpha_A > \alpha_B$ and $m_A > m_B$. Thus, population A is competitively superior to B, but requires more food to pupate successfully. When viabilities are determined for each population separately it is clear that population B will have a higher viability (in Fig. 1, m_B would be to the left of m_A). When these two populations compete for limited food the average individual in populations A and B will not receive the same amount of food. Instead, individuals from population A will receive more food (since they are consuming it at a faster rate) and the distribution of food consumed by A individuals will be shifted to the right of the distribution for B individuals. If this shift in the relative positions of the two distributions is sufficiently large (that is, α_A is sufficiently greater than α_B), the viability of individuals in population A will be greater than those in population B. This form of competition clearly requires no active interference or facilitation among competing types as hypothesized by Lewontin (1955). This discussion does not preclude other types of competitive interactions: it merely demonstrates that many observations of competition in complicated environments can be accounted for by a simple model of competition for limited food. Sulzbach (1980) reports no improvement in the competitive abilities of two strains of *D. melanogaster* that have competed as larvae for 23

generations relative to stocks kept in isolation. These results are not surprising if one assumes that the major component of competitive interactions in *D. melanogaster* is the ability to compete for limited food. Both the controls and experimental populations used by Sulzbach were kept at the same density and thus experienced the same levels of food availability. Thus all populations had approximately the same intensity of selection for improved ability to survive on limited food. Consequently, the evolutionary improvement of a population to intraspecific competition would also result in improved interspecific competition and *vice versa*.

The major features of more detailed studies of competition can also be understood in terms of the larval feeding model. Caligari (1980) examined the competitive abilities of two inbred lines of *D. melanogaster*: Wellington (Well) and a line selected for high chaeta number (6CL). In monocultures, 96, 72, 48, and 24 eggs of each line were placed in vials with measured amounts of yeast. The mixed cultures contained these same numbers of one line and enough eggs from the second line to make the total density 96. The 6CL monocultures had 18–29% survivorship at all densities tested. The Well monocultures had 63, 60, 42, and 23% survival at densities of 24, 48, 72, and 96 eggs, respectively. The most reasonable interpretation of these results is that the 6CL line has a genetically determined low viability which is independent of food availability. There is no difference between the number of emerging Well adults in the competition tests and the numbers emerging in the monocultures. However, the weight of the adult Well flies does decrease in the competition tests. These results can be interpreted in light of the larval competition model and by assuming that the genetic death [hard selection of Wallace (1970)] of the 6CL line occurs early in larval life. In the competition tests with 24 and 48 6CL eggs and 72 and 48 Well eggs, so few 6CL larvae survive genetic death that the survival of Well is not appreciably affected. In the tests with 72 6CL eggs and 24 Well eggs, only 16–24 6CL will survive genetic death. This leaves a total density of 40–48 larvae. In the density range of 24–48 eggs the survivorship of the Well larvae is relatively constant. This would correspond to the flat region in Fig. 2. However, as is evident from Fig. 3, the weight of adults can still be changing when adult survivorship is near its maximum.

A large number of studies have examined the evolution of competitive ability in *Drosophila* (Moore, 1952*a*; Seaton and Antonovics, 1967; Ayala, 1969; Futuyma, 1970; Barker, 1973; Sulzbach and Emlen, 1979; Pruzan-Hotchkiss, Perele *et al.*, 1980; Sulzbach, 1980; Bierbaum and Ayala, 1985). Moore (1952*a*) reports finding one line of *D. simulans* out of 20 that was not competitively excluded by *D. melanogaster* while both species were maintained in population cages. This line was superior to stocks

of *simulans* in its competitive ability with *melanogaster*. Ayala (1969) maintained *D. nebulosa* and *D. serrata* together by the serial transfer system. After 22 weeks the numbers of *D. nebulosa* increased and this was due to an increase in the competitive ability of this species (Ayala, 1969). After only three generations of selection Seaton and Antonovics (1967) recorded increases in the lines of *D. melanogaster* relative to their unselected stocks. Despite these positive findings, numerous studies have recorded no changes in competitive ability (Futuyma, 1970; Pruzan-Hotchkiss *et al.*, 1980; Sulzbach, 1980). It is worth noting that the studies reporting negative findings often contain more replicates.

Bierbaum and Ayala (1986) conducted experiments with *D. willistoni* and *pseudoobscura* to test hypotheses in the coevolution of interspecific competitors. The major evolutionary hypothesis they tested was proposed by Pimentel *et al.* (1965), which states that when two species compete, natural selection will most strongly favor an increase in the competitive ability of the less frequent species. Such a process may be responsible for the reversals of competitive dominance seen by Ayala (1966). To test the Pimentel hypothesis, Bierbaum and Ayala (1986) established three different selection regimes: in each both species were maintained in a serial transfer system and the total density of the egg-laying adult population was kept at 300 flies. The three treatments differed in their frequency of *D. willistoni*, which was either 20, 50, or 80%. The *D. willistoni* adults for each generation came from the competition cultures, while the *pseudoobscura* came from single-species stocks. Thus, only the *D. willistoni* population could adapt to the competitive environment. Eight independent populations were maintained in this fashion and allowed to respond to the competitive environment for about 30 generations.

The expectations of Pimentel *et al.* (1965) were not met. The lines kept at 50 and 20% *willistoni* had evolved a lower competitive ability than the 80% lines. Bierbaum and Ayala conclude that the primary adaptations of these populations may be to density-dependent intraspecific interactions, and that interspecific interactions play a minor role.

The conclusions of Bierbaum and Ayala are supported by quite different evidence from Wijsman (1984). In this very interesting study the effects of new mutations on the intra- and interspecific competitive abilities of two lines of *D. melanogaster* and one line of *D. simulans* were determined. Lines were treated with ethylmethanesulfonate and the inter- and intraspecific competitive abilities of all pairwise comparisons of treated and untreated lines were determined. Competitive ability was estimated by following the numbers of each competing type in population cages over many generations. Such a procedure was possible for the two lines of *melanogaster*, since one line had a compound third chromosome

which causes it to be reproductively isolated from populations with normal third chromosomes. Although inter- and intraspecific competitive ability were reduced in the newly mutated populations, these mutations had a significantly larger effect on intraspecific competitive ability than they did on interspecific competitive ability. These results may have significant implications for the evolution of intra- versus interspecific competitive ability.

Clark (1979) reports experimental evidence that interspecific competition may alter allele frequency dynamics. Clark studied a fourth-chromosome polymorphism in *D. melanogaster*. He determined the equilibrium allele frequencies in pure populations of *melanogaster* and in populations where *D. simulans* was maintained at a frequency of one-third or two-thirds. The allele frequency equilibrium reached in the two populations with *D. simulans* were similar to each other but different from that reached in the pure *melanogaster* population.

Island Biogeography

MacArthur and Wilson (1967) first suggested that the number of species on an island may represent a balance between immigration and extinction. Although the vast majority of empirical work in this field has been conducted with natural populations, laboratory populations of *Drosophila* offer a tremendous opportunity to study this process.

Wallace (1975) has conducted the only detailed study of island biogeography with *Drosophila* to my knowledge. Wallace's experimental technique was very precise and not surprisingly he was able to obtain much more detailed information than is possible in field studies. The regularity of migration episodes and the maintenance of island populations actually allows, and probably requires, a much different description of the immigration and extinction process than that given by MacArthur and Wilson (1967). I will try to outline how one might model the immigration and extinction processes on these islands, after describing the experimental techniques of Wallace.

Migration took place inside a large cage called "the island machine." On the bottom of the cage were numerous holes to which were attached shell vials with food. At regular intervals 18 species of *Drosophila* were placed in the island machine. Migration was said to occur when a fly entered a particular vial. Four preidentified vials represented the migrants for one of 30 different islands. Each group of four vials is called a unit. Rates of immigration were controlled by the duration of time that vials were attached to the machine. "Distant" islands were left on the machine

for only 4 h, while "near" islands were attached to the machine overnight. The units of each island can be thought of as different niches. At the same time that migration occurred, a specified number of females from each unit were transferred to fresh vials. On some islands the vials of each unit were maintained independently; on others there was some exchange of flies between vials of the same unit. Units were maintained until there were no flies to begin the next generation (extinction) or until 24 time units had passed (1 time unit = 3–4 weeks).

Using only species-specific extinction and immigration rates, one can describe the number of units occupied by species i on a particular island, $X^{(i)}(t)$, at any time. Such a derivation will assume that there is mixing of individuals between the vials of a single unit and the immigration and extinction probabilities apply to whole units. At any time t only immigration events that have occurred in the last 24 time units will be of interest. Let the total number of such events be $N^{(i)}(t)$. The time to extinction for each successful immigration event is Y_j, $j = 1, \ldots, N^{(i)}(t)$, and $Y_j \leq 24$. Let the time at which the jth immigration event took place be Υ_j, $t - 24 \leq \Upsilon_j < t$. Then $X^{(i)}(t)$ is given by

$$X^{(i)}(t) = \sum_{j=1}^{N^{(i)}(t)} w(t - \Upsilon_j, Y_j)$$

where $w(t - \Upsilon_j, Y_j) = 1$ if $0 < t - \Upsilon_j \leq Y_j$ or 0 otherwise. The statistical problem is then to find the distribution of $X^{(i)}(t)$ assuming $N^{(i)}(t)$ has a binomial distribution and Y_j has a truncated geometric distribution. Once this distribution is known, the probability that $X^{(i)}(t) = 0$ can be calculated and thus the total expected number of species on the island can be determined. This model provides even more detailed information. It would give the expected number of units that should be occupied by each species and the variance of this expected value. Such expectations could be compared to the observed values from Wallace's data set to determine if immigration and extinction probabilities alone can adequately predict the species composition of islands.

Wallace's (1975) data indicate that the immigration and extinction probabilities can depend substantially on the current species composition of an island. Such findings invalidate the considerations in the previous paragraphs. However, Wallace's data indicate that it is largely the presence or absence of *D. melanogaster* that affects the success of the other species. In the absence of this dominant species the extinction and immigration rates of other species may be less sensitive to the *Drosophila* community composition.

LIFE-HISTORY EVOLUTION

Life histories involve the timing of reproduction, maturation rate, and the duration of life. The theory of life-history evolution attempts to explain how natural selection might affect these various traits within certain constraints. These constraints or tradeoffs assume that limited energy will prevent the limitless improvement of life-history traits. Natural selection may fine tune a particular life-history character, such as increasing early fecundity, but only at the expense of some other life-history component (i.e., decreased late fecundity or survival). These ideas were articulated early by Pearl (1928) and have found their way into many recent formulations of life-history evolution (Gadgil and Bossert, 1970; Roughgarden, 1971; Taylor *et al.*, 1974; Stearns, 1976; Charlesworth, 1980; Iwasa and Teramoto, 1980; Mueller and Ayala, 1981*c*; Schaffer, 1983).

Empirical verification of the tradeoff hypothesis has usually involved the estimation of correlations between life-history traits from a collection of genetically or phenotypically different populations. The design of these studies is such that only estimates of phenotypic correlations are possible. The arguments presented above emphasize the changes in life-history traits during evolution. Predictions about this process require knowledge of additive genetic correlations. Unfortunately, phenotypic correlations not only may differ quantitatively, but also may be of a different sign than the additive genetic correlations (Rose and Charlesworth, 1981*a*). Phenotypic correlations of life-history traits by themselves may give totally misleading predictions concerning evolutionary dynamics. Phenotypic correlations of life-history traits also seem to depend on the degree of inbreeding in the experimental populations.

Covariation in Life Histories

The following studies were all performed with *D. melanogaster*. Using vestigial and wild-type laboratory stock, Alpatov (1932) found a consistent negative correlation between mean daily egg production and the life span of a female. However, his method of calculating these statistics may have introduced some spurious correlation (Gowen and Johnson, 1946). Gowen and Johnson (1946) examined a large number of laboratory and inbred strains. Although the average per-capita fecundity was positively correlated with life span over all lines, when egg production over a constant period was compared to longevity there was a negative correlation.

In a series of experiments Giesel and co-workers examined correlations for inbred (Giesel, 1979; Giesel and Zettler, 1980; Giesel *et al.*, 1982*a*,*b*) and some outbred populations of *D. melanogaster* (Giesel *et al.*, 1982*a*,*b*) and *D. simulans* (Murphy *et al.*, 1983). In general these studies have shown positive correlations for a host of life-history traits. For instance, the correlation among lines for reproduction at age 2 days and age of death was 0.719 and 0.578 for inbred and outbred lines, respectively (Giesel *et al.*, 1982*b*). The most complete quantitative genetic analysis of life-history traits was performed by Rose and Charlesworth (1981*a*) on flies sampled from a large outbred population. This study yielded a number of interesting observations: (1) there is substantial additive genetic variance for female fecundity at all ages and (2) there is sometimes little relationship between phenotypic and additive genetic correlations. The first observation has also been made for *D. simulans* (Murphy *et al.*, 1984). The phenotypic correlation between egg laying at days 11–15 and longevity is 0.210, while the additive genetic correlation is −0.712 (Rose and Charlesworth, 1981*a*). In contrast to many of the results from Giesel and co-workers, Rose and Charlesworth obtained negative additive genetic correlations for many traits. For instance, egg laying from days 1 to 5 is negatively correlated with longevity, last day of egg laying, egg laying days 6–10, and egg laying days 11–15 (Rose and Charlesworth, 1981*a*). The biological significance of these negative correlations was tested by conducting artificial and natural selection for early and late fitness components (Rose and Charlesworth, 1981*b*). In some cases the selection regimes produced no detectable direct or indirect results. However, natural selection for late fitness components resulted in increased late female fecundity, longevity, and duration of female reproduction, with a concomitant decrease in early female fecundity and mean egg-laying rate (Rose and Charlesworth, 1981*b*). The soundness of these results has been bolstered by their recent successful duplication (Rose, 1984*a*). The reduction in early fecundity exhibited by these populations appears to be due to a significant reduction in ovary weight in young flies (Rose *et al.*, 1984).

Work in this field has served to highlight problems that occur with the use of inbred lines as experimental material. It appears that highly inbred lines tend to exhibit correlations in fitness components that are uncharacteristic of outbred populations. Simmons *et al.* (1980) have noted a qualitative difference between newly arisen and old mutations in heterozygous condition. Viability of newly arisen mutants appeared to be uncorrelated with other fitness components in *D. melanogaster*, whereas mutations from equilibrium populations that decrease viability are compensated for by increases in other components of fitness. Perhaps of more interest is the observation of Hiraizumi (1961). He obtained rates of de-

velopment and estimates of fertility for various second-and third-chromosome homozygotes and heterozygotes. These components of fitness were negatively correlated for normal or high-fitness genotypes, but showed a positive correlation for low-fitness genotypes. A similar phenomenon was also seen by Mueller and Ayala (1981*d*). They looked at the correlation between density-dependent rates of population growth at high and low densities for a number of *D. melanogaster* populations isogenic for whole second chromosomes. These correlations were consistently positive. However, when genetically heterogeneous populations were allowed to evolve at high and low densities the resulting populations exhibited a tradeoff in density-dependent rates of population growth.

The usefulness of inbred lines for extracting evolutionary information on life-history phenomena was rigorously tested by Rose (1984*b*). Using the same populations that he had utilized in his earlier studies, Rose established 30 inbred lines by full-sib mating. Longevity and age-specific fecundities were determined for five females from each of the 30 lines. The correlations among the lines between early and late fecundity and fecundity at any age and longevity were consistently positive. As noted previously, many additive genetic correlations measured in the outbred population used to initiate this study are negative. This work shows concisely that there need be no concordance between patterns of life-history covariation derived from inbred and outbred samples of the same population.

The finding of large amounts of additive genetic variance for life-history traits by Charlesworth and Rose (1981*a*) provides useful information for predicting evolution in controlled laboratory environments. However, the usefulness of this information for gaining insights into natural populations is reduced by the existence of genotype–environment correlations. Such conditions have been observed for life-history traits of *D. simulans* at several temperatures (Murphy *et al.*, 1984) and for bristle number in *D. melanogaster* measured at several temperatures and densities (Gupta and Lewontin, 1982).

Density-Dependent Natural Selection

The theory of density-dependent selection has its origins in the works of MacArthur (1962) and MacArthur and Wilson (1967). In these works the notion that density-dependent rates of population growth could be viewed as measurements of fitness was introduced. It was also asserted that extreme environmental conditions might lead to the evolution of different population characteristics. Thus, populations kept at low densities

by density-dependent mortality (and hence having abundant resources) should evolve a high intrinsic rate of growth r, but be incapable of superior preformance at high densities. In contrast, populations usually living at high density and thus experiencing strong competition for limiting resources) should evolve high intraspecific competitive ability and enhance their carrying capacity K.

The basic ideas put forth by MacArthur and Wilson were made more explicit with the formulation of several mathematical theories (Charlesworth, 1971; King and Anderson, 1971; Roughgarden, 1971; Clarke, 1972). For instance, Roughgarden (1971) assumes that the fitness of the ijth genotype W_{ij} is a linear function of total population size N,

$$W_{ij} = 1 + r_{ij} - (r_{ij}N/K_{ij})$$

in which the values of r and K vary among genotypes. If it is assumed that an initial population is polymorphic for genotypes that show a tradeoff (i.e., genotypes with high r's have low K's and *vice versa*), the outcome of evolution in Roughgarden's model is dependent on the environment. In stable environments the genotype with the largest value of K ultimately becomes established and all other eliminated. When the population is often below its carrying capacity due to frequent episodes of density-independent mortality, the genotype with the highest r value is favored. Thus, according to this model, evolution favors the genotype that makes the highest per-capita contribution to population growth at either high or low densities, depending on environmental conditions.

Most empirical studies have dealt with the predictions of the verbal theory of r- and K-selection (Pianka, 1970, 1972; Gadgil and Solbrig, 1972). These theories have argued that phenotypes that should be correlated with high r's or increased competitive ability will also respond to density-dependent selection. Thus, r-selected phenotypes will be smaller in size, with shorter generation times, and will be more semelparous than K-selected species, which will tend to be large, long-lived, and iteroparous. It should be noted that the verbal theory represents a substantial jump from the mathematical theory. The verbal theory has used the qualitative interpretation of parameters, such as r and K of the logistic equation, to translate theoretical results of discrete-generation models to populations with overlapping generations. More detailed examination of evolution in populations with age structure and density-dependent regulation yields results at odds with the verbal predictions. For instance, natural selection will favor increased survivorship and fecundity at earlier ages in density-regulated populations (Charlesworth, 1980). If fecundity is an increasing function of size, then selection for delayed reproduction can depend on

the life stage affected by density-dependent regulation (Charlesworth, 1980). Iwasa and Teramoto (1980) have shown that the evolution of high fecundity versus high juvenile survival can depend on whether fecundity or preadult survival is subject to density-dependent regulation. Thus, not only is the presence or absence of density regulation important to life-history evolution, but the details of the manner in which it operates can be important.

Templeton and Johnston (1982) present an example of *K*-selection in a natural population which is at odds with predictions of the verbal theory. Templeton and Johnston studied the abnormal abdomen polymorphism in natural populations of *D. mercatorum*. Abnormal abdomen shows a number of pleiotropic effects, including increased early egg production and decreased longevity. During 1981 there was a severe drought, which resulted in marked declines in the size of many *mercatorum* populations and a decline in the longevity of adult flies. Since these flies breed in rotting pads of the cactus *Opuntia megacantha*, the number of available pads and the length of time they were suitable for *Drosophila* was greatly decreased as a result of the drought. During this same period there was also a marked increase in the frequency of abnormal abdomen in many populations. It appears that under these new ecological conditions the decrement in fitness caused by the reduced longevity of abnormal abdomen was more than balanced by the increase in fitness due to high early fecundity resulting in the net increase of abnormal abdomen. Thus, in an environment in which the carrying capacity was reduced, and hence overpopulated with *Drosophila*, evolution favored traits typically associated with r-selection. Templeton and Johnston correctly point out that pleiotropic genetic effects can result in life-history evolution that deviates substantially from what might be considered optimal.

The predictions of density-dependent natural selection clearly hinge on fitness being equivalent to the per-capita contribution to rates of population growth. Obviously, to test this prediction directly one must have a collection of genotypes whose density-dependent rates of population growth can be measured and compared to an independent measurement of fitness. Such an experiment is possible with populations of *D. melanogaster* isogenic for whole second chromosomes. The fitness of such genotypes relative to wild-type flies has been determined several times by direct observations of changes in genotype frequencies (Tracey and Ayala, 1974; Seager and Ayala, 1982). These experiments have been conducted in population cages at high densities. If one eliminates the data for sterile populations from Tracey and Ayala's study, the average relative fitness of second-chromosome homozygotes is 0.23. The relative fitness of these genotypes as estimated from density-dependent rates of popu-

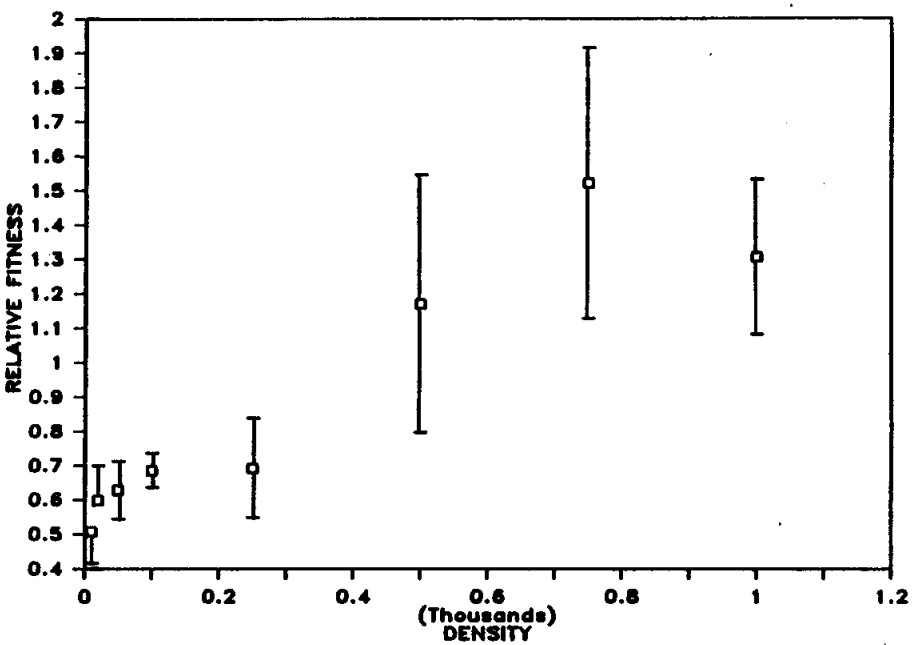


FIG. 13. Fitness (±95% confidence interval) as a function of density of 24 lines of *D. melanogaster* isogenic for different second chromosomes relative to a wild-type population. The calculations were based on density-dependent rates of population growth as explained in Mueller and Ayala (1981*a*).

lation growth are given in Mueller and Ayala (1981*a*) and reproduced in Fig. 13. These data show that at low densities there is a substantial difference between the isogenic lines and the wild-type population in rates of population growth that gradually diminish at higher densities.

Because the average isogenic line and wild-type population have similar rates of population growth at high densities, they also have similar carrying capacities. Mourão *et al.* (1972) obtained a similar result with *D. willistoni*. For 15 lines isogenic for whole second chromosomes they determined fitness relative to wild-type flies and carrying capacity in the serial transfer system. The correlation between fitness and the carrying capacity was -0.16 and not significantly different from zero.

These observations can be explained if one assumes that the isogenic lines differ most in density-independent fitness components of fecundity or larval viability and that the density-dependent functions that determine larval survival or female fecundity are quite similar for all populations (Prout, 1980; Mueller and Ayala, 1981*a*). With these assumptions it is

expected that at low densities the large differences in density-independent components will produce large differences in number of offspring and adults produced by the various lines. Such differences will be manifest in the rates of population growth. At high densities one arrives at quite different predictions. As long as most lines produce more than enough eggs and larvae than can survive to become adults, due to limited food, pupation sites, etc., then the assumption of similar density-dependent regulating functions for each line will result in similar numbers of adults appearing at these high densities. A phenomenon similar to the one outlined here may also explain the lack of correlation between competitive and noncompetitive measures of fitness observed by Haymer and Hartl (1983).

This work shows that in general some caution must be made when equating density-dependent rates of population growth with fitness. A related question is: in genetically variable populations, how will density-dependent rates of population growth respond to natural selection at extreme densities? As argued previously, inbred lines may not provide information useful for answering this question. Consequently, Mueller and Ayala (1981*d*) have carried out natural selection at high and low densities on a genetically variable population of *D. melanogaster*. After eight generations of selection, rates of population growth at one low and two high densities were measured for three low-density populations (*r*-selected) and three high-density populations (*K*-selected). At the two high densities the *K*-selected populations had significantly higher rates of population growth and net productivity, while at the low density the *r*-selected populations had the higher values, although only the difference for net productivity was statistically significant (Mueller and Ayala, 1981*d*). These results are in marked contrast to similar experiments with *E. coli* (Luckinbill, 1978). In Luckinbill's experiment the *K*-selected populations showed higher rates of population growth at all densities relative to the *r*-selected populations.

Additional work has recently been completed on the selected populations of Mueller and Ayala (Bierbaum *et al.*, 1986). Adult survival and female fecundity were examined for *r*- and *K*-selected flies raised under uncrowded conditions. There were no substantial differences between the different selected populations for these traits. Density-dependent larval survival was also examined and the weights of the emerging adults recorded. At the lowest density tested the *r*-selected larvae had a higher survival rate (0.927 versus 0.910), but the difference was not statistically significant. At two higher densities the *K*-selected larvae had significantly higher survival rates. In addition, adult male and female *K*-selected flies emerging in these high-density vials were heavier than their *r*-selected

counterparts. As discussed in the section on the laboratory ecology of *Drosophila*, there is a strong correlation between female size and fecundity for partially starved flies (Alpatov, 1932; Robertson, 1957). Using Robertson's data, it can be estimated that the *r*-selected females raised at the highest larval density should suffer an 11% reduction in lifetime fecundity relative to *K*-selected females raised under the same conditions. Thus, the higher rates of population growth exhibited by the *K*-selected populations (Mueller and Ayala, 1981*d*) may be due to both increased larval survival and female fecundity.

One aspect of the Mueller and Ayala (1981*d*) and Bierbaum *et al.* (1986) results is that the differences between the selected populations were quite small and difficult to detect at low densities, but at high densities the differences were easily detected. It may be that the selective pressure on the *r*-selected lines is not as strong as on the *K*-selected lines and thus the magnitude of response of the *r*-selected lines is diminished. It is also possible that there are inherent asymmetries in the response that populations can demonstrate. For instance, larval survival at low densities is greater than 0.90 in both populations and clearly cannot be greater than 1.0. Thus, to increase survivorship 1 or 2% may require substantial genetic and physiological changes. Such asymmetries have been seen previously with other characters (Falconer, 1981). Lastly, it is possible that as a species *Drosophila melanogaster* has experienced conditions similar to those experienced by the *r*-selected populations. Consequently, there could be less additive genetic variation for the traits under selection in these environments.

Several other studies have documented an increase in the carrying capacity of laboratory populations of *D. melanogaster* (Buzzati-Traverso, 1955; Ayala, 1965*a*, 1968*a*). Thus, it is likely that the process of adaptation observed by Mueller and Ayala (1981*d*) and Bierbaum *et al.* (1986) is a repeatable and consistent phenomenon in *D. melanogaster*.

Three other studies with *Drosophila* have attempted to observe directly the consequences of density-dependent natural selection (Taylor and Condra, 1980; Barclay and Gregory, 1981, 1982). Taylor and Condra conducted *r*- and *K*-selection with *D. pseudoobscura*. Consistent with theory, a decline in the development time of the *r*-selected population and increased adult survival of *K*-selected flies were observed. They saw no differences in intrinsic rate of increase, carrying capacity, body size, fecundity, and timing of reproduction. The *r*-selected populations were maintained by using the first 100 adults to start the next generation; thus, development time was under strong selection. Both adult survival and fecundity were measured under uncrowded conditions. The fecundity results are consistent with Bierbaum *et al.* (1986). Taylor and Condra did

not examine density-dependent rates of population growth directly, although they attempted to estimate the intrinsic rate of increase from Euler's equation and the observed birth and death reates. Thus, it is possible that if they had measured fecundity, larval survival, or rates of population growth at high densities, different results might have been obtained.

Taylor and Condra (1980) conclude that their selected populations have similar carrying capacities, since there are similar numbers of progeny produced from 2 weeks of egg laying by specific numbers of females (2–15). Their test is not a reliable indicator of the carrying capacity for two reasons. First, the equilibrium population size will depend not only on the number of progeny produced, but also on the mortality of adults. Taylor and Condra's own data indicate potential differences in adult mortality, yet their method of estimating carrying capacity does not take adult mortality into account. Second, the density conditions under which the experimental females were raised were not varied. As the work of Bierbaum *et al.* (1986) indicates, there may be substantial differences in fecundity of females raised at high and low densities.

Two other studies have examined life-history evolution in *Drosophila melanogaster* (Barclay and Gregory, 1981, 1982). Barclay and Gregory (1981) examined life-history evolution in populations that were subject to different combinations of larval and adult mortality. Although their description of the experimental techniques is not entirely clear, it seems that populations were given fresh food at 5-week intervals. The suitability of *Drosophila* medium for oviposition and the number of larvae it can sustain change drastically in 5 weeks. Barclay and Gregory would, at regular intervals of 1 or 2 weeks, remove adults and/or larvae from these cultures. Thus, in addition to the different regimes of adult and juvenile mortality, flies had to contend with a rapidly deteriorating environment. It is not at all obvious whether the most important evolutionary force in these experiments was the mortality imposed by the experimenters or the ability of larvae and adults to tolerate and survive the putrid conditions of the 5-week-old cultures. The second set of experiments by Barclay and Gregory (1982) also contain methodological problems which leave one somewhat skeptical of their results. In this study they again maintained cultures for a very long time. Due to the aging of the food there was probably little difference between their fast (changed every 20 days) and slow (changed every 40 days) food rotations. They also attempted to impose different levels of adult mortality. Unfortunately, this was not done in a controlled fashion; instead, a frog (*Hyla regilla*), with no apparent ecological relationship to *D. melanogaster*, was put in the population cage.

Most models of density-dependent natural selection have relied on

very general descriptions of the effects of density on rate of population growth. This generality is often achieved with a model that is less realistic for many specific populations (Levins, 1966). Such problems led Stearns (1977) to point out that the parameter K of the logistic equation is unrelated in any simple or obvious way to life-history traits that can be measured in many populations. Current efforts to understand density-dependent natural selection in *Drosophila* are limited largely by the absence of models that incorporate important ecological aspects of *Drosophila* biology. Although such models would be of limited applicability, they could be extremely useful for interpreting the results of studies such as that of Bierbaum *et al.* (1986). Such a model would make possible the study of the interaction between density and larval competitive ability (Bakker, 1961, 1969; Nunney, 1983). Although competitive ability should change according to the verbal theory of r- and K-selection, it is seldom explicitly included in theories of density-dependent natural selection [for exceptions see Christiansen and Loeschcke (1980), Anderson and Arnold (1983), and Asmussen (1983)]. Results of Bierbaum *et al.* have also suggested that adult size, and therefore female fecundity, may change as a result of density-dependent natural selection. A complete model of density-dependent natural selection would also incorporate this aspect of *Drosophila* biology. Thus the most desirable theory would incorporate these relevant aspects of *Drosophila* ecology as functions of parameters that could be empirically estimated.

Progress toward this goal has been made recently by L. D. Mueller (in preparation). In this model the number of eggs at time $t + 1$, e_{t+1}, is related to the number in the previous generation by

$$e_{t+1} = F(ve_t)W(ve_t)ve_t$$

The model assumes that density-independent mortality v leaves ve_t larvae in the population. Due to limited resources (e.g., food), there is additional mortality $W(ve_t)$, which results in $W(ve_t)ve_t$ adults to produce the next generation of eggs. The density-dependent mortality function $W(ve_t)$ is precisely the normal truncation function described by Nunney (1983) and outlined here in the section on the laboratory ecology of *Drosophila*. The value of this function depends on the competitive abilities α_i of the various types in the population and the minimum amount of food required for successful pupation m_i. The recursion is completed by specifying the adult per-capita fecundity $F(ve_t)$, which is also density-dependent. This function assumes that adult size, and therefore female fecundity, increases with the amount of food consumed in excess of the minimum m_i. Such an assumption is warranted given the data in Fig. 7 and Robertson's (1957)

results. This model can be used to investigate the consequences of natural selection on the evolution of intraspecific competitive ability α_i and the efficiency of food utilization m_i. This model predicts that natural selection favors increasing α and decreasing m. The intensity of selection for these parameters increases with increasing population size. Thus, they can be thought of as components of K-selection. However, changing α does not affect the equilibrium population size, while decreasing m increases the carrying capacity. Lastly, decreasing m not only will result in increased larval survival at a given density, but also will increase the fecundity (and size) of females emerging at a given density. Such results are in accord with the empirical results of Bierbaum *et al.* (1986). Finally, this model has as an additional asset parameters that can all be empirically estimated.

OVIPOSITION AND HABITAT CHOICE

Importance of Oviposition and Habitat Choice

Maintenance of Genetic Polymorphisms

Concomitant with the revelation of the large amounts of genetic variation in natural populations during the mid and late 1960s was an interest in developing theoretical explanations for the maintenance of this genetic variation. Population genetic models that incorporated different selection regimes in a variety of niches or habitats with some specified pattern of dispersal could maintain genetic variation even in the face of directional selection within each habitat. Karlin (1981) has recently provided a comprehensive review of the theory in this field. Three important characteristics of these models are: (1) the selection regime in each deme, (2) the specification of random mating either within each deme, in a common area, or in some mixture of both, and (3) a description of migration from one deme to every other. For instance, the island model (Wright, 1943) assumes that each deme receives the same fraction of migrants, while the Levene (1953) model permits a different, but constant, fraction of the adult population to disperse to each deme. Mating can occur entirely within a common area (Levine, 1953) or a fraction may stay in their deme to mate (Deakin, 1966). It is interesting that despite the variety of migration and mating structures considered in the review by Karlin (1981), observations obtained from *Drosophila* research suggest a new model. Jaenike's (1982) data on larval and adult conditioning effects on female oviposition behavior suggest the following life cycle. Viability selection

acts on egg to adult survival. Although the larval environment does not appear to affect oviposition behavior, adult conditioning does. Thus, newly emerged adults may linger in their larval habitat and become conditioned to either prefer, avoid, or be indifferent to the larval substrate. Mating then occurs in a common area and migration back to the available demes depends on the larval habitat. Although it was not motivated by specific observations, the assumption was made by Jaenike that the number of adults emerging from a niche was a function of the fitnesses of various genotypes, that is, that hard selection was operating. Jaenike's model demonstrated how environmentally induced habituation to a normally repellant substrate (niche) or an induced preference can weaken the conditions necessary for new alleles to increase when rare. Since individuals with new alleles demonstrate increased viability in the repellent substrate, the population can be thought of as adapting to a secondary host.

As discussed by Jaenike, environmentally induced dispersal and hard selection will result in the change over time of the proportion of eggs laid in (or individuals dispersing to) each environment, even in the absence of genetic variation. The dynamics of this change is described by a linear fractional equation which depends on the viability of individuals in niches a and b (W_a, W_b) and the probabilities of females dispersing to niche b, given that they were raised in niche a (c) or b (c'). It is possible that if enough time lapses, the proportion of eggs laid in each niche will approach an equilibrium. However, if

$$[c'W_b - W_a(1 + c)]^2 + 4cW_a(W_b - W_a) < 0$$

or

$$[c'W_b - W_a(1 + c)]^2 = 0$$

the number of eggs laid in each niche will not reach an equilibrium, but rather will oscillate in a regular fashion. Clearly, Jaenike's analysis of evolution in this system is predicated on the resident population having reached a stable equilibrium with respect to the number of eggs laid in each niche. The genetic model of Jaenike has recently been extended to include soft selection and an arbitrary number of niches (M. Moody and L. D. Mueller, in preparation).

The efficacy of a heterogeneous environment and habitat selection in maintaining genetic variation has been demonstrated by Jones and Probert (1980). They studied the dynamics of the white-eye allele w in *D. simulans* in constant and heterogeneous environments. White-eye flies

(*w*/*w*) avoid bright white light and move toward dim red light. Wild-type flies seem to mate less well in dim red light. Control population cages with either bright white light or dim red light were established. In each case the *w* allele was eliminated after 30 weeks, although the rate of elimination was slower in the dim red cage. An experimental cage was established that gave flies access to areas of bright white light and dim red light. The frequency of the *w* allele was quite higher in the dim red area after just a few generations. After 20 weeks the frequency of the *w* allele was still 0.32. It is quite possible that the *w* allele would have been eliminated had this experiment been continued; however, it is clear that the rate of decline of the *w* allele was much slower in the experimental cage than in either control.

Promotion of Sympatric Speciation

The idea that insects may become locally adapted to specific hosts and preferentially seek out this host is a long-standing one. Indeed, Hopkin's (1917) host selection principle stated that "an insect species which breeds in two or more hosts will prefer to continue to breed in the host to which is has become adapted." Just as geographic isolation has been invoked as a first step in the genetic differentiation of species (Mayr, 1963), it has been suggested that ecological isolation due to host preferences may serve a similar function (Thorpe, 1945). Maynard Smith (1966) showed that even in the face of random mating in each generation, the presence of niches that favored alternative genotypes and the appropriate migration schemes could maintain a genetic polymorphism. The model of Maynard Smith is actually a special case of the model developed by Moody and Mueller. Maynard Smith went on to argue that once such a polymorphism was established, the evolution of isolating mechanisms, by a number of different means, should be favored.

There are a variety of examples of potential host races that have led or are leading to speciation (White, 1978). Some of the most convincing evidence comes from Bush's work (1974) on *Rhagoletis pomonella*. However, Jaenike (1981) and Futuyma and Mayer (1980) point out that it is important to distinguish between host-associated sibling species and host races. In the later case gene flow is restricted solely or primarily because of differential host preference. Jaenike (1981) provides a list of criteria which he believes are necessary for demonstrating the existence of host races.

Oviposition Site Preference

Although oviposition site preference is a very labile behavior in *Drosophila*, progress has been made in studying environmental factors that affect this behavior. Chiang and Hodson (1950) showed that *D. melanogaster* females prefer to lay eggs on a scored surface rather than a smooth surface. Once egg laying has begun on a fresh surface, the deposition of eggs may not be random. Females of *D. pseudoobscura* and *D. melanogaster* tend to lay eggs in close proximity to other eggs (Del Solar and Palomino, 1966; Del Solar, 1968). Del Solar (1968) has also shown that there is genetic variation for this gregarious egg-laying behavior and has been successful in selecting lines of *D. pseudoobscura* that show very strong and weak propensities to aggregate their eggs.

The behavior of the neotropical species *D. flavopilosa* is opposite to the gregarious egg-laying behavior of *D. pseudoobscura* and *D. melanogaster* (Brncic, 1966). The larvae of this species develop in the flowers of the solanaceous plant *Cestrum pargui* and females lay only one egg per flower.

In addition to a preference for laying eggs near previously laid eggs, females of *D. melanogaster* seem to prefer to lay eggs in medium already colonized by larvae even if these are of a different species (Del Solar and Palomino, 1966). The effects of larval preconditioning on viability have also been studied, but the results have been equivocal.

An important component of many natural habitats of *Drosophila* is the concentration of ethanol. Indeed, the tolerance of both adults and larvae to ethanol can vary greatly between species (McKenzie and Parsons, 1972). Ethanol can also affect oviposition preference. McKenzie and Parsons (1972) report that female *D. simulans* rejected alcohol-impregnated sites, while *D. melanogaster* showed a slight preference for these same sites. Richmond and Gerking (1979) have carried out a detailed analysis of oviposition site preference in 14 species of *Drosophila* as a function of ethanol concentration. Richmond and Gerking offered females two different substrates for oviposition: agar–cornmeal–molasses medium with 9% ethanol by volume and the same medium with distilled water as the additive. For each species the percent of all eggs laid on the ethanol medium was tabulated. There was significant heterogeneity among species. The preference for the ethanol medium ranged from 7.9% for *D. paulistorum* to 97.4% for one strain of *D. melanogaster*. Unlike the study of McKenzie and Parsons, Richmond and Gerking found no significant differences between *D. simulans* and four strains of *D. melanogaster*.

The results of Richmond and Gerking depart substantially from those reported by Jaenike (1982). Jaenike utilized females of *D. melanogaster* raised on standard cornmeal–agar–molasses in oviposition preference tests. When these females were provided with a choice of standard medium and standard medium plus 7% ethanol, only 24% of all eggs were laid on the ethanol medium. It is quite difficult to explain these discrepancies in results other than to assume that some subtle difference in experimental technique is responsible. It is possible that the temperature of the medium may have differed at the time the ethanol was added. The final concentration of ethanol in the medium could thus be much less than reported. There may have also been genetic differences between the lines used in each study. Regardless of the cause, these results demonstrate that caution should be exercised when results from different labs are being compared.

Given the evolutionary significance of habitat or oviposition site preference, it is not surprising that a number of studies with *Drosophila* have been initiated to uncover environmental and genetic variation for these traits. Takamura (1980) studied the oviposition preferences of *D. melanogaster* when offered a soft (standard medium) versus a hard surface (paper). Forty isofemale lines from two natural populations showed significant variation for preference of hard versus soft medium. Takamura conducted a similar experiment on two populations of flies collected in wineries. One population was derived from eggs collected from grape seeds; the other was derived from eggs laid on grape sacs. In preference tests those flies derived from seeds laid a significantly larger proportion of their eggs on the paper surface. Thus, the hard grape seeds and soft sacs may represent different ecological niches for *D. melanogaster* and genetically based oviposition site preferences may be resulting in genetic differentiation of these subpopulations.

A substantial contribution to the empirical foundation of oviposition site preference in *Drosophila* has been made by Jaenike. In his first major work (Jaenike, 1982) the oviposition site preference of *Drosophila melanogaster, pseudoobscura, immigrans*, and *recens* was tested. Females used in this study were characterized by having developed in either standard or experimental medium as either larvae, adults, or both. The experimental medium had one of the following substances added to standard medium: NaCl, ethanol, ethyl acetate, lactic acid, piperidine, or peppermint oil. Females were placed in vials with a single slide containing the standard medium and one with the experimental medium. The percent of all eggs laid on the experimental medium was recorded. The effect of each experimental substance on a given life stage can be characterized by comparing the proportion of eggs laid on the experimental medium when the

particular life stage was raised on standard medium (c) versus this same proportion when the life stage was raised on experimental medium (c'). One very consistent result was that exposure of larvae to the experimental substances had no effect on the oviposition preference of adults; however, exposure of adults did have an effect in a number of cases. Females that show an active preference ($c > 0.5$) or aversion ($c < 0.5$) to a particular substance are said to be habituated if $c > c' > 0.5$ or $c < c' < 0.5$. Females may show an induced preference or an induced aversion if $c' > 0.5$ and $c' > c$ or $c' < 0.5$ and $c' < c$, respectively. *Drosophila melanogaster, pseudoobscura,* and *immigrans* raised on standard medium all show an aversion to peppermint oil, but when these flies have experienced peppermint oil as adults, *D. pseudoobscura* and *immigrans* show a significant habituation effect and *melanogaster* shows an induced preference. It is also clear from Jaenike's results that oviposition site choice is not always adaptive. For instance, *D. recens* is indifferent to 0.025% peppermint oil, whether or not there has been prior conditioning, even though a 0.05% concentration is lethal to adults.

The larval environment consistently has no effect on the oviposition preference of females. However, the larval environment may have a subsequent effect on adult oviposition choice if these adults linger in the larval environment for some time after emergence. Under these conditions models that assume that adult migration is dependent on the larval environment may still be justified.

Jaenike (1983) has performed similar experiments on *D. melanogaster* using several "natural" larval habitats: apples, tomatoes, bananas, and squash. The choice by females followed the same patterns previously seen: the larval environment had no appreciable effect on oviposition preference, while adult exposure to either apples or tomatoes enhanced the preference for these fruits as oviposition sites. Jaenike (1983) conducted a second set of experiments in which larval *D. melanogaster* were raised on apples, oranges, grapes, tomatoes, or onions. Females were then given a choice of all five foods for oviposition. One interesting result from this study was that adult exposure to one food (e.g., apple) resulted in an increase in the preference for another food (e.g., grape). Jaenike has called this phenomenon cross-induction.

It is logical to study the degree to which genetic differences might affect oviposition preference. Jaenike and Grimaldi (1983) studied the oviposition preference of 13 strains of *D. tripunctata* and four strains of *D. putrida* raised under identical conditions. Females were given a choice of lettuce, tomato, and three species of mushroom. The oviposition preference of *D. tripunctata* shows a significant food by strain interaction, while *D. putrida* shows no such interaction. These results indicate that

D. tripunctata has the appropriate genetic variation for host plant differentiation.

Although it appears that adult conditioning can affect female oviposition choice in an artificial situation, it would be of interest to know if such conditioning can be detected in the field. Jaenike (1986) has conducted a series of experiments with *D. melanogaster* to collect such information. His study only addresses the lability of food preference, so some caution must be exercised in extrapolating these results to oviposition preference. Adult flies were conditioned on tomatoes, grapes, and standard medium. These flies were then marked and released at field sites and the frequency of capture on either tomato or grape baits was recorded. Twenty-four hours after conditioning and release, attraction to grape or tomato in the field still depended on the prior conditioning. Those flies that were raised on grapes showed an increased preference for this bait. These results are in qualitative accord with Jaenike (1983), in which the frequency of eggs laid on grape nearly tripled in those females raised on grape rather than other foods. When the flies were again tested 4 days after conditioning there was no detectable difference in their preference for grape or tomato baits in the field. Thus, environmental conditioning of food preference is a labile behavior, with the effect vanishing between 1 and 4 days. It is interesting that laboratory studies of conditioned behavior show that *D. melanogaster* will exhibit these effects for up to 24h (Tempiel *et al.*, 1983). One should not conclude that any correlation between the larval environment and adult food preference will be completely lost in a single day, since those adults returning to their larval environment due to conditioning will have this preference reinforced and thus continue to prefer (or avoid) their larval environment for a few more days. These results do imply that one would expect a gradual decay in the correlation between food preference and larval habitat.

Habitat Choice in the Field

Certainly the relevance of genetically or environmentally induced habitat choice is greatest if these effects can be demonstrated in the field. Consequently, a large number of studies have been aimed at determining the degree of habitat choice in natural populations. The various studies sometimes differ substantially, which makes comparisons difficult. Some factors which seem to be important in habitat choice are sex, genotype, previous experience, food used in baits, and species of yeast. This review of habitat choice will proceed by considering each of these factors.

Previous Experience

Several studies have already been considered which convincingly demonstrate that adult conditioning can have a substantial effect on subsequent oviposition and habitat choice. In addition, this conditioning effect appears to be lost in 1–4 days if not reinforced, at least for *D. melanogaster*. Several studies have indicated the lack of detectable habitat preferences in the field (Jaenike, 1978; Atkinson and Miller, 1980; Turelli, Coyne and Prout, 1984). Jaenike (1986) argues that this may largely be a consequence of conditioning that results in less than perfect fidelity. Suppose that there are two habitats *A* and *B* in which *Drosophila* breed and feed. Assume also that the choice exhibited for either *A* or *B* is determined in part by prior conditioning. The standard field experiment consists in collecting flies in habitat *A* or *B*, and marking and releasing them, and then recapturing flies in the same two areas. Clearly, if flies that were originally caught in area *A* are almost always recaught in area *A*, then some degree of habitat preference can be inferred. However, in the sample of flies originally caught in area *A* there will be some that actually prefer area *B* due to less than perfect conditioning or genetic effects. This same error of misclassification occurs among the recaptured flies. If one knew the genotype and prior conditioning of released flies, then the sort of errors just described would only occur among the recaptured population. In the Jaenike (1986) field study prior conditioning and genotypes were known for released flies and thus the ability to detect differences in habitat choice is much greater than in previous studies. Jaenike (1986) shows how this prior information can allow one to detect statistically significant differences with sample sizes an order of magnitude less than those required by standard methods.

Food Used in Baits

From a number of studies considered previously it is clear that the attractiveness of certain foods varies with species, sex, and genotype and also depends on the prior experience of an individual. These facts imply that it will be difficult to make inferences concerning the absolute or relative abundance of species of *Drosophila* by just enumerating the species caught in a particular trap.

The choice of food used in traps also has important consequences for habitat choice experiments. Most studies can be divided into two categories: those that use food unlikely to be encountered by *Drosophila* out of doors (Taylor and Powell, 1978; Atkinson and Miller, 1980) and those that use foods that represent natural oviposition and larval habitats

(Turelli *et al.*, 1984). When "unnatural" foods are used, the habitats under consideration are really different geographic localities chosen by the experimenter for reasons that may or may not be important in habitat selection by *Drosophila*. Those studies may fail to detect "habitat" choice for the geographic areas chosen even when there may be highly specific preferences for the unknown and unobserved oviposition sites. Similarly, these experiments may uncover a preference for the habitat in which a fly is initially captured even though utilization of oviposition sites and foods may be identical across habitats.

Such problems as those just discussed are clearly reduced when natural oviposition sites can be identified and utilized in baits. Turelli *et al.* (1984) studied habitat choice of *D. melanogaster/simulans* and *pseudoobscura* in fruit orchards. Two experiments studied attraction to known breeding sites: oranges and grapefruits in one, figs and peaches in the other. Turelli *et al.* quantify their results with an index of choice $\Delta = P_{x|x} - P_{x|y}$, where $P_{x|y}$ is the probability of recapture in habitat x given that the fly was initially caught in y, and $P_{x|x}$ is similarly defined. Thus, $-1 \leq \Delta \leq 1$, with $\Delta = 1$ implying absolute habitat fidelity and $\Delta = -1$ implying absolute avoidance. Their results indicate a small but significant fidelity for the pooled *D. melanogaster/simulans* sample ($\Delta = 0.087$) on figs and peaches, but *pseudoobscura* shows no preference or negative Δ. This last result is in sharp contrast to the habitat preference ($\Delta = 0.185$–0.306) Taylor and Powell (1978) found for *D. pseudoobscura*. Given the differences in techniques utilized by Taylor and Powell and by Turelli *et al.*, one can only conjecture about the reasons for the different results. As mentioned previously, it might happen that despite the preference for geographic localities observed by Taylor and Powell (1978), there may be no difference in underlying preference for oviposition sites. If one assumes that the results of Taylor and Powell imply differences in oviposition preference, then one might conjecture that their study sites represent different but relatively stable oviposition sites. This situation can be contrasted with the orchards studied by Turelli *et al.*, which have an abundance of different oviposition sites over short distances. If adult habitat preference is largely governed by prior experience, then a difference in oviposition site availability could explain the different results from these field studies.

Sex

Differences between sexes in habitat choice have been seen by Richardson and Johnston (1975), Shorrocks and Nigro (1981), and Jaenike (1985, 1986). For instance, Jaenike (1986) saw that prior adult conditioning

could affect subsequent attraction to baits in the field. *Drosophila melanogaster* males and females were both affected, although there were quantitative differences in the response. In contrast, *D. tripunctata* males were unaffected by prior experience, while females showed a marked effect: that is, those females raised on tomatoes showed a preference for tomato relative to controls.

Genotype

Several lines of evidence indicate that there are genetic differences between flies found in different habitats (Stalker, 1976; Taylor and Powell, 1977) and that genotypes differ in their habitat preference (Kekić *et al.*, 1980; Jaenike and Grimaldi, 1983; Jaenike, 1986). Kekić *et al.* (1980) report habitat preference for individuals of *D. subobscura* caught in light and dark areas. Flies from each area were brought into the laboratory and the phototactic behavior of the F_1's was observed in a light maze. Offspring from flies caught in light areas were more positively phototactic than those caught in dark areas. As discussed previously, Jaenike and Grimaldi (1983) reported that oviposition preference varied significantly among strains of *D. tripunctata*, but not in strains of *D. putrida*. Similarly, for *D. tripunctata* that had been preconditioned and released in the field, strain genotype had a significant effect on habitat preference.

Yeasts

Differential attraction to yeasts has been demonstrated in *D. buzzatii* and *aldrichi* (Barker *et al.*, 1981*a*,*b*), *pseudoobscura* and *persimilis* (Dobzhansky *et al.*, 1956; Klaczko *et al.*, 1985), *azteca, occidentalis, pinicola, miranda, melanogaster, californica, immigrans*, and *victoria* (Carson *et al.*, 1956), and a variety of tropical species (DaCunha *et al.*, 1957). Although these results indicate that preference tests should standardize the type of yeast used, it is not clear how important this phenomenon may be in nature. In many hosts a large number of yeast species have been isolated (Carson *et al.*, 1956; de Cunha *et al.*, 1957; Heed *et al.*, 1976; Starmer *et al.*, 1976, 1981). This lack of correspondence between yeasts and habitats means that preferences for different yeasts need not translate into habitat preference. Heed *et al.* (1976) conclude that yeasts alone do not limit certain desert *Drosophila* to particular cacti. *Drosophila pachea*, for instance, is found almost exclusively in senita cactus rots (Fellows and Heed, 1972). This is apparently due to *D. pachea*'s nutritional requirement for a sterol found in the senita cactus. However, the profile of yeast species found in the gut of adult *D. pachea* is similar to the species'

composition of the senita cactus (Starmer *et al.*, 1976, 1981). It should be noted that several species of yeast were misclassified or lumped together in Starmer *et al.* (1976); however, a more precise classification of these species was carried out by Starmer *et al.* (1981). Thus, although *D. pachea* is a specialist on senita cactus, it seems to be a generalist with regard to available yeast species.

SUMMARY

In addition to the many empirical findings of interest on their own, this review has attempted to outline the importance of research on a model organism. The depth of knowledge of the ecology and genetics of *Drosophila* permit a more detailed analysis of evolutionary phenomena. A few examples that illustrate this point follow.

A large number of seemingly unrelated observations from intra- and interspecific competition experiments can be understood after considering the details of *Drosophila* larval competition. Repeated observations show faster than linear declines in per-capita rates of population growth in laboratory populations of *Drosophila*. This can be explained, at least partly, by the great sensitivity of female fecundity to changes in adult density. Even determining population dynamics in simplified laboratory environments can require a detailed knowledge of *Drosophila* ecology. As shown by Prout (1985), the life stages affected by changes in density can have significant effects on estimates of rates of population growth. Density-dependent natural selection may result in increased larval viability and female fecundity in *Drosophila*. These predictions follow only after considering the details of *Drosophila* ecology.

Many of the recent results in life-history evolution, density-dependent natural selection, the evolution of competitive ability, and oviposition preference suggest and will be followed by more detailed studies. It is hoped that future studies will attempt to integrate findings from past research and gather more information on the genetic basis of these traits. *Drosophila* should continue to be a unique research tool for some of the more interesting questions in evolutionary ecology.

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REFERENCES

Abrams, P., 1976, Limiting similarity and the form of the competition coefficient, *Theor. Popul. Biol.* **8**:355–375.

Alpatov, W. W., 1932, Egg production in *Drosophila melanogaster* and some factors which influence it, *J. Exp. Zool.* **63**:85–111.

Alvarez, G., and Fontdevila, A., 1981, Effect of the singed locus on the egg production curve of *Drosophila melanogaster*, *Can. J. Genet. Cytol.* **23**:327–336.

Anderson, W. W., and Arnold, J., 1983, Density-regulated selection with genotypic interactions, *Am. Nat.* **121**:649–655.

Asmussen, M. A., 1983, Density-dependent selection incorporating intraspecific competition. II. A diploid model, *Genetics* **103**:335–350.

Atkinson, W. D., 1979, A field investigation of larval competition in domestic *Drosophila*, *J. Anim. Ecol.* **48**:91–102.

Atkinson, W. D., and Miller, J. A., 1980, Lack of habitat choice in a natural population of *Drosophila subobscura*, *Heredity* **44**:193–199.

Ayala, F. J., 1965*a*, Evolution of fitness in experimental populations of *Drosophila serrata*, *Science* **150**:903–905.

Ayala, F. J., 1965*b*, Relative fitness of populations of *Drosophila serrata* and *Drosophila birchii*, *Genetics* **51**:527–544.

Ayala, F. J., 1966, Reversals of dominance in competing species of *Drosophila*, *Am. Nat.* **100**:81–83.

Ayala, F. J., 1968*a*, Genotype, environment, and population numbers, *Science* **162**:1453–1459.

Ayala, F. J., 1968*b*, An inexpensive and versatile population cage, *Drosophila Information Service* **43**:185.

Ayala, F. J., 1969, Evolution of fitness. IV. Genetic evolution of interspecific competitive ability in *Drosophila*, *Genetics* **61**:737–747.

Ayala, F. J., 1971, Competition between strains of *Drosophila willistoni* and *D. pseudoobscura*, *Experientia* **27**:343.

Ayala, F. J., Gilpin, M. E., and Ehrenfeld, J. G., 1973, Competition between species: Theoretical models and experimental tests, *Theor. Popul. Biol.* **4**:331–356.

Bakker, K., 1961, An analysis of factors which determine success in competition for food among larvae of *Drosophila melanogaster*, *Arch. Neerl. Zool.* **14**:200–281.

Bakker, K., 1969, Selection for rate of growth and its influence on competitive ability of larvae of *Drosophila melanogaster*, *Neth. J. Zool.* **19**:541–595.

Barclay, H. J., and Gregory, P. T., 1981, An experimental test of models predicting life-history characteristics, *Am. Nat.* **117**:944–961.

Barclay, H. J., and Gregory, P. T., 1982, An experimental test of life history evolution using *Drosophila melanogaster* and *Hyla regilla*, *Am. Nat.* **120**:26–40.

Barker, J. S. F., 1971, Ecological differences and competitive interaction between *Drosophila melanogaster* and *Drosophila simulans* in small laboratory populations, *Oecologia* **8**:134–156.

Barker, J. S. F., and Podger, R. N., 1970, Interspecific competition between *Drosophila melanogaster* and *Drosophila simulans*: Effects of larval density on viability, development period and adult body weight, *Ecology* **51**:170–189.

Barker, J. S. F., and Starmer, W. T., eds., 1982, *Ecological Genetics and Evolution: The Cactus–Yeast–Drosophila Model System*. Academic Press, New York.

Barker, J. S. F., Parker, G. J., Toll, G. L., and Widders, P. R., 1981*a*, Attraction of *Drosophila buzzatii* and *D. aldrichi* to species of yeasts isolated from their natural environment. I. Laboratory experiments, *Aust. J. Biol. Sci.* **34**:593–612.

Barker, J. S. F., Toll, G. L., East, P. D., and Widders, P. R., 1981*b*, Attraction of *Drosophila buzzatii* and *D. aldrichi* to species of yeasts isolated from their natural environment. II. Field experiments, *Aust. J. Biol. Sci.* **34**:613–624.

Bierbaum, T. J., and Ayala, F. J., 1986, The coevolution of interspecific competitors: An experimental test in *Drosophila*, manuscript.

Bierbaum, T. J., Mueller, L. D., and Ayala, F. J., 1986, Density-dependent evolution of life history characteristics in *Drosophila melanogaster*, manuscript.

Bodenheimer, F. S., 1938, *Problems of Animal Ecology*, London.

Brncic, D., 1966, Ecological and cytogenetic studies of *Drosophila flavopilosa*, a neotropical species living in *Cestrum* flowers, *Evolution* **20**:16–29.

Bush, G. L., 1974, The mechanism of sympatric host race formation in the true fruit flies (*Tephritidae*), in: *Genetic Mechanisms of Speciation in Insects* (M. J. D. White, ed.), pp. 3–23, Australian and New Zealand Book Co., Sydney.

Buzzati-Traverso, A. A., 1955, Evolutionary changes in components of fitness and other polygenic traits in *Drosophila melanogaster* populations, *Heredity* **9**:153–186.

Caligari, P. D. S., 1980, Competitive interactions in *Drosophila melanogaster*, *Heredity* **45**:219–231.

Carson, H. L., Knapp, E. P., and Phaff, H. J., 1956, Studies on the ecology of *Drosophila* in the Yosemite region of California. III. The yeast flora of the natural breeding sites of some species of *Drosophila*, *Ecology* **37**:538–544.

Charlesworth, B., 1971, Selection in density-regulated populations, *Ecology* **52**:469–474.

Charlesworth, B., 1980, *Evolution in Age-Structured Populations*, Cambridge University Press, Cambridge.

Chiang, H. C., and Hodson, A. C., 1950, An analytical study of population growth in *Drosophila melanogaster*, *Ecol. Monogr.* **20**:173–206.

Christiansen, F. B., and Loeschcke, V., 1980, Evolution and intraspecific exploitative competition. I. One-locus theory for small additive gene effects, *Theor. Popul. Biol.* **18**:297–313.

Clark, A., 1979, The effects of interspecific competition on the dynamics of a polymorphism in an experimental population of *Drosophila melanogaster* *Genetics* **92**:1315–1328.

Clark, A. G., and Feldman, M. W., 1981*a*, Density-dependent fertility selection in experimental populations of *Drosophila melanogaster*, *Genetics* **98**:849–869.

Clark, A. G., and Feldman, M. W., 1981*b*, The estimation of epistasis in components of fitness in experimental populations of *Drosophila melanogaster* II. Assessment of meiotic drive, viability, fecundity and sexual selection, *Heredity* **46**:347–377.

Clarke, B., 1972, Density-dependent selection, *Am. Nat.* **106**:1–13.
Connell, J. H., 1980, Diversity and the coevolution of competitors, or the ghost of competition past, *Oikos* **35**:131–138.
Connor, E. F., and Simberloff, D., 1979, The assembly of species communities: Chance or competition, *Ecology* **60**:1132–1140.
Da Cunha, A. B., Shehata, A. M. E., and de Oliveira, W., 1957, A study of the diets and nutritional preferences of tropical species of *Drosophila*, *Ecology* **38**:98–106.
Deakin, M. A. B., 1966, Sufficient conditions for genetic polymorphism, *Am. Nat.* **100**:690–692.
De Jong, G., 1976, A model of competition for food. I. Frequency-dependent viabilities, *Am. Nat.* **121**:67–93.
Del Solar, E., 1968, Selection for and against gregariousness in the choice of oviposition sites by *Drosophila pseudoobscura*, *Genetics* **58**:275–282.
Del Solar, E., and Palomino, H., 1966, Choice of oviposition in *Drosophila melanogaster*, *Am. Nat.* **100**:127–133.
Dobzhansky, T., Cooper, D. M., Phaff, H. J., Knapp, E. P., and Carson, H. L., 1956, Studies on the ecology of *Drosophila* in the Yosemite region of California. IV. Differential attraction of species of *Drosophila* to different species of yeasts, *Ecology* **37**:544–550.
Falconer, D. S., 1981, *Introduction to Quantitative Genetics*, 2nd ed., Longman, London.
Fellows, D. P., and Heed, W. B., 1972, Factors affecting host plant selection in desert-adapted cactiphilic *Drosophila*, *Ecology* **53**:850–858.
Futuyma, D. J., 1970, Variation in genetic response in laboratory populations of *Drosophila*, *Am. Nat.* **104**:239–252.
Futuyma, D. J., and Mayer, G. C., 1980, Nonallopatric speciation in animals, *Syst. Zool.* **29**:254–271.
Gadgil, M., and Bossert, W., 1970, Life historical consequences of natural selection, *Am. Nat.* **104**:1–24.
Gadgil, M., and Solbrig, O. T., 1972, The concept of *r*- and *K*-selection: Evidence from wild flowers and some theoretical considerations, *Am. Nat.* **106**:14–31.
Gale, J. S., 1964, Competition between three lines of *Drosophila melanogaster*, *Heredity* **19**:681–699.
Giesel, J. T., 1979, Genetic co-variation of survivorship and other fitness indices in *Drosophila melanogaster*, *Exp. Gerontol.* **14**:323–328.
Giesel, J. T., and Zettler, E. E., 1980, Genetic correlations of life historical parameters and certain fitness indicies in *Drosophila melanogaster*: r_m, r_s, diet breadth, *Oecologia* **47**:299–302.
Giesel, J. T., Murphy, P. A., and Manlove, M. N., 1982*a*, The influence of temperature on genetic interrelationships of life history traits in a population of *Drosophila melanogaster*: What tangled data sets we weave, *Am. Nat.* **119**:464–479.
Giesel, J. T., Murphy, P. A., and Manlove, M. N., 1982*b*, An investigation of the effects of temperature on the genetic organization of life history indices in three populations of *Drosophila melanogaster*, in: *Evolution and Genetics of Life Histories* (H. Dingle and J. P. Hegmann, eds.), pp. 189–207, Springer, New York.
Gilpin, M. E., 1974, Intraspecific competition between *Drosophila* larvae in serial transfer systems, *Ecology* **55**:1154–1159.
Gilpin, M. E., and Ayala, F. J., 1973, Global models of growth and competition, *Proc. Natl. Acad. Sci. USA* **70**:3590–3593.
Goodman, D., 1979, Competitive hierarchies in laboratory *Drosophila*, *Evolution* **33**:207–219.

Gowen, J. W., and Johnsen, L. E., 1946, Section on genetics and evolution on the mechanism of heterosis. I. Metabolic capacity of different races of *Drosophila melanogaster* for egg production, *Am. Nat.* **80**:149–179.

Grimaldi, D., and Jaenike, J., 1984, Competition in natural populations of mycophagous *Drosophila*, *Ecology* **65**:1113–1120.

Guckenheimer, J., Oster, G., and Ipaktchi, 1977, The dynamics of density dependent population models, *J. Math. Biol.* **4**:101–147.

Gupta, A. P., and Lewontin, R. C., 1982, A study of reaction norms in natural populations of *Drosophila pseudoobscura*, *Evolution* **36**:934–948.

Haddon, M., 1982, Frequency dependent competitive success in an age-structured model, *Am. Nat.* **120**:405–410.

Hassell, M., Lawton, J., and May, R. M., 1976, Pattern of dynamical behavior in single-species populations, *J. Anim. Ecol.* **45**:471–486.

Hastings, A., Serradilla, J. M., and Ayala, F. J., 1981, Boundary-layer model for the population dynamics of single species, *Proc. Natl. Acad. Sci. USA* **78**:1972–1975.

Haymer, D. S., and Hartl, D. L., 1983, The experimental assessment of fitness in *Drosophila*. II. A comparison of competitive and noncompetitive measures, *Genetics* **104**:343–352.

Heckel, D., and Roughgarden, J., 1980, A species near its equilibrium size in a fluctuating environment can evolve a lower intrinsic rate of increase, *Proc. Natl. Acad. Sci. USA* **77**:7497–7500.

Heed, W. B., Starmer, W. T., Miranda, M., Miller, M. W., and Phaff, H. J., 1976, An analysis of the yeast flora associated with cactophilic *Drosophila* and their host plants in the Sonoran Desert and its relation to temperate and tropical associations, *Ecology* **57**:151–160.

Hiraizumi, Y., 1961, Negative correlation between rate of development and female fertility in *Drosophila melanogaster*, *Genetics* **46**:615–624.

Hopkins, A. D., 1917, A discussion of C. G. Hewitt's paper on "Insect Behavior," *J. Econ. Entomol.* **10**:92–93.

Iwasa, Y., and Teramoto, E., 1980, A criterion of life history evolution based on density dependent selection, *J. Theor. Biol.* **84**:545–566.

Jaenike, J., 1978, Host selection by mycophagous *Drosophila*, *Ecology* **59**:1286–1288.

Jaenike, J., 1981, Criteria for ascertaining the existence of host races, *Am. Nat.* **117**:830–834.

Jaenike, J., 1982, Environment modification of oviposition behavior in *Drosophila*, *Am. Nat.* **119**:784–802.

Jaenike, J., 1983, Induction of host preference in *Drosophila melanogaster*, *Oecologia* **58**:320–325.

Jaenike, J., 1985, Genetic and environmental determinants of food preference in *Drosophila tripunctata*, *Evolution* **39**:362–369.

Jaenike, J., 1986, Intraspecific variation in food preference of *Drosophila*, *Biol. J. Linn. Soc.*, in press.

Jaenike, J., and Grimaldi, D., 1983, Genetic variation for host preference within and among populations of *Drosophila tripunctata*, *Evolution* **37**:1023–1033.

Jones, J. S., and Probert, R. F., 1980, Habitat selection maintains a deleterious allele in a heterogeneous environment, *Nature* **287**:632–633.

Karlin, S., 1981, Classifications of selection–migration structures and conditions for a protected polymorphism, in: *Evolutionary Biology*, Vol. 14 (M. K. Hecht, B. Wallace, and G. T. Prance, eds.), pp. 61–204, Plenum Press, New York.

Kekić, V., Taylor, C. E., and Andjelković, M., 1980, Habitat choice and resource specialization by *Drosophila subobscura*, *Genetika* **12**:219–225.

King, C. E., and Anderson, W. W., 1971, Age-specific selection. II. The interaction between *r* and *K* during population growth, *Am. Nat.* **105**:137–156.

King, C. E., and Dawson, P. S., eds., 1983, *Population Biology: Retrospect* and *Prospect*, Columbia University Press, New York.

Klaczko, L. B., Powell, J. R., and Taylor, C. E., 1983, *Drosophila* baits: Yeasts and species attracted, *Oecologia* **59**:411–413.

Levene, H., 1953, Genetic equilibrium when more than one ecological niche is available, *Am. Nat.* **87**:331–333.

Levins, R., 1966, The strategy of model building in population biology, *Am. Sci.* **54**:421–431.

Lewontin, R. C., 1955, The effects of population density and composition on viability in *Drosophila melanogaster*, *Evolution* **9**:27–41.

Lewontin, R. C., and Matsuo, Y., 1963, Interaction of genotypes determining viability in *Drosophila busckii*, *Proc. Natl. Acad. Sci. USA* **49**:270–278.

L'Heritier, P., and Teissier, G., 1933, Etude d'une population de Drosophiles en equilibre, *C. R. Acad. Sci. Fr.* **197**:1765–1767.

Luckinbill, L. S., 1978, *r*- and *K*-selection in experimental populations of *Escherichia coli*, *Science* **202**:1201–1203.

MacArthur, R. H., 1962, Some generalized theorems of natural selection, *Proc. Natl. Acad. Sci. USA* **48**:1893–1897.

MacArthur, R. H., and Wilson, E. O., 1967, *The Theory of Island Biogeography*, Princeton University Press, Princeton.

Mather, K., and Caligari, P. D. S., 1981, Competitive interactions in *Drosophila melanogaster*. II. Measurement of competition, *Heredity* **46**:239–254.

Mather, K., and Cooke, P., 1962, Differences in competitive ability between genotypes of *Drosophila*, *Heredity* **17**:381–407.

May, R. M., 1974, Biological populations with non-overlapping generations: Stable points, stable cycles and chaos, *Science* **186**:645–647.

May, R. M., and Oster, G., 1976, Bifurcations and dynamic complexity in simple ecological models, *Am. Nat.* **110**:573–599.

Maynard-Smith, J., 1966, Sympatric speciation, *Am. Nat.* **100**:637–650.

Mayr, E., 1963, *Animal Species and Evolution*, Harvard University Press, Cambridge.

McKenzie, J. A., and Parsons, P. A., 1972, Alcohol tolerance: An ecological parameter in the relative success of *Drosophila melanogaster* and *Drosophila simulans*, *Oecologia* **10**:373–388.

Merrell, D. J., 1951, Interspecific competition between *Drosophila funebris* and *Drosophila melanogaster*, *Am. Nat.* **85**:159–169.

Miller, R. S., 1964, Larval competition in *Drosophila melanogaster* and *D. simulans*, *Ecology* **45**:132–148.

Moore, J. A., 1952*a*, Competition between *Drosophila melanogaster* and *Drosophila simulans*. II. The improvement of competitive ability through selection, *Proc. Natl. Acad. Sci. USA* **38**:813–817.

Moore, J. A., 1952*b*, Competition between *Drosophila melanogaster* and *Drosophila simulans*. I. Population cage experiments, *Evolution* **6**:407–420.

Mourão, C. A., Ayala, F. J., and Anderson, W. W., 1972, Darwinian fitness and adaptedness in experimental populations of *Drosophila willistoni*, *Genetica* **43**:552–574.

Mueller, L. D., 1979, Fitness and density dependence in *Drosophila melanogaster*, Ph. D. Thesis, University of California, Davis.

Mueller, L. D., and Ayala, F. J., 1981*a*, Fitness and density dependent population growth in *Drosophila melanogaster*, *Genetics* **97**:667–677.

Mueller, L. D., and Ayala, F. J., 1981*b*, Dynamics of single-species population growth: Experimental and statistical analysis, *Theor. Popul. Biol.* **20**:101–117.

Mueller, L. D., and Ayala, F. J., 1981*c*, Dynamics of single-species population growth: Stability or chaos? *Ecology* **62**:1148–1154.

Mueller, L. D., and Ayala, F. J., 1981*d*, Trade-off between *r*-selection and *K*-selection in *Drosophila* populations, *Proc. Natl. Acad. Sci. USA* **78**:1303–1305.

Mueller, L. D., and Ayala, F. J., 1982, Population dynamics in the serial transfer system: Comments on Haddon's model, *Am. Nat.* **120**:548–550.

Murphy, P. A., Giesel, J. T., and Manlove, M. N., 1983. Temperature effects on life history variation in *Drosophila simulans*, *Evolution* **37**:1181–1192.

Nogueś, R. M. 1977, Population size fluctuations in the evolution of experimental cultures of *Drosophila subobscura*, *Evolution* **31**:200–213.

Nunney, L., 1983, Sex differences in larval competition in *Drosophila melanogaster*: The testing of a competition model and its relevance to frequency dependent selection, *Am. Nat.* **121**:67–93.

Parsons, P. A., 1980, Isofemale strains and evolutionary strategies in natural populations, in: *Evolutionary Biology*, Vol. 13 (M. K. Hecht, W. C. Steere, and B. Wallace, eds.), pp. 175–217, Plenum Press, New York.

Parsons, P. A., 1981, Evolutionary ecology of Australian *Drosophila*, a species analysis in: *Evolutionary Biology*, Vol. 14 (M. K. Hecht and G. T. Prance, eds.), pp. 297–349, Plenum Press, New York.

Pearl, R., 1927, The growth of populations, *Q. Rev. Biol.* **2**:532–548.

Pearl, R., 1928, *The Rate of Living*, Knopf, New York.

Pearl, R., 1932, The influence of density of population upon egg production in *Drosophila melanogaster*, *J. Exp. Zool.* **63**:57–83.

Pearl, R., Miner, J. R., and Parker, S. L., 1927, Experimental studies on the duration of life. XI. Density of population and life duration in *Drosophila*, *Am. Nat.* **61**:289–317.

Pianka, E. R., 1970, On *r*- and *K*-selection, *Am. Nat.* **104**:592–596.

Pianka, E. R., 1972, *r* and *K* selection or *b* and *d* selection? *Am. Nat.* **106**:581–588.

Pimentel, D., Feinberg, E. H., Wood, P. W., and Hayes, J. T., 1965, Selection, spatial distribution and the co-existence of competing fly species, *Am. Nat.* **99**:97–109.

Pomerantz, M. J., Thomas, W. R., and Gilpin, M. E., 1980, Asymmetries in population growth regulated by intraspecific competition: Empirical studies and model tests, *Oecologia* **47**:311–322.

Prout, T., 1980, Some relationships between density-independent and density-dependent population growth, in: *Evolutionary Biology*, Vol. 13 (M. K. Hecht, W. C. Steere, and B. Wallace, eds.), pp. 1–68, Plenum Press, New York.

Prout, T., 1985, The delayed effect on adult fertility of immature crowding: Population dynamics, *Am. Nat.*, in press.

Pruzan-Hotchkiss, A., Perelle, I. B., Hotchkiss, F. H. C. and Ehrman, L., 1980, Altered competition between two reproductively isolated strains of *Drosophila melanogaster*, *Evolution* **34**:445–452.

Richardson, R. H., and Johnston, J. S., 1975, Ecological specialization of Hawaiian *Drosophila*, *Oecologia* **21**:193–204.

Richmond, R. C., and Gerking, J. L., 1979, Oviposition site preference in *Drosophila*, *Behav. Genet.* **9**:233–241.

Robertson, F. W., 1957, Studies in quantitative inheritance. XI. Genetic and environemtnal correlation between body size and egg production in *Drosophila melanogaster*, *J. Genet.* **55**:428–443.

Robertson, R. W., and Sang, F. H., 1944, The ecological determinants of population growth in a *Drosophila* culture, *Proc. Roy. Soc. Lond. B* **132**:258–291.

Rose, M. R., 1984*a*, Laboratory evolution of postponed senescence in *Drosophila melanogaster*, *Evolution* **38**:516–526.

Rose, M. R., 1984*b*, Genetic covariation in *Drosophila* life history: Untangling the data, *Am. Nat.* **123**:565–569.

Rose, M. R., and Charlesworth, B., 1981*a*, Genetics of life history in *Drosophila melanogaster*. I. Sib. analysis of adult females, *Genetics* **97**:173–186.

Rose, M. R., and Charlesworth, B., 1981*b*, Genetics of life history in *Drosophila melanogaster*. II. Exploratory selection experiments, *Genetics* **97**:187–196.

Rose, M. R., Dorey, M. L., Coyle, A. M., and Service, P. M., 1984, The morphology of postponed senescence in *Drosophila melanogaster*, *Can. J. Zool.* **62**:1576–1580.

Roughgarden, J., 1971, Density dependent natural selection, *Ecology* **52**:453–468.

Roughgarden, J., 1976, Resource partitioning among competing species—A coevolutionary approach, *Theor. Popul. Biol.* **9**:388–424.

Roughgarden, J., 1979, *Theory of Population Genetics and Evolutionary Ecology: An Introduction*, MacMillan, New York.

Rummel, J. D., and Roughgarden, J., 1983, Some differences between invasion-structured and coevolutionary-structured competitive communities: A preliminary theoretical analysis, *Oikos* **41**:477–486.

Sang, J. H., 1949*a*, The ecological determinants of population growth in a *Drosophila* culture. III. Larval and pupal survival, *Physiol. Zool.* **22**:183–202.

Sang, J. H., 1949*b*, The ecological determinants of population growth in a *Drosophila* culture. IV. The significance of successive batches of larvae, *Physiol. Zool.* **22**:202–210.

Sang, J. H., 1949*c*, The ecological determinants of population growth in a *Drosophila* culture. V. The adult population count, *Physiol. Zool.* **22**:210–223.

Sang, J. H., 1949*d*, Population growth in *Drosophila* cultures, *Biol. Rev.* **25**:188–219.

Sang, J. H., McDonald, J. M., and Gordon, C., 1949, The ecological determinants of population growth in a *Drosophila* culture. VI. The total population count, *Physiol. Zool.* **22**:223–235.

Schaffer, W. M., 1983, The application of optimal control theory to the general life history problem, *Am. Nat.* **121**:418–431.

Schoener, T. W., 1983, Field experiments on interspecific competition, *Am. Nat.* **122**:240–285.

Seager, R. D., and Ayala, F. J., 1982, Chromosome interactions in *Drosophila melanogaster*. I. Viability studies, *Genetics* **102**:467–483.

Seaton, A. P. C., and Antonovics, J., 1967, Population inter-relationships. I. Evolution in mixtures of *Drosophila* mutants, *Heredity* **22**:19–33.

Shorrocks, B., 1970, Population fluctuations in the fruit fly (*Drosophila melanogaster*) maintained in the laboratory, *J. Anim. Ecol.* **39**:229–253.

Shorrocks, B., and Nigro, L., 1981, Microdistribution and habitat selection in *Drosophila subobscura* Collin, *Biol. J. Linn. Soc.* **16**:293–301.

Simmons, M. J., Preston, C. R., and Engels, W. R., 1980, Pleiotropic effects on fitness of mutations affecting viability in *Drosophila melanogaster*, *Genetics* **94**:467–475.

Smith, F. E., 1963, Population dynamics in *Daphnia magna* and a new model for population growth, *Ecology* **44**:651–663.

Stalker, H. D., 1976, Chromosome studies in wild populations of *D. melanogaster*, *Genetics* **82**:323–347.

Starmer, W. T., Heed, W. B., Miranda, M., Miller, M. W., and Phaff, H. J., 1976, The ecology of yeast flora associated with cactophilic *Drosophila* and their host plants in the Sonoran Desert, *Microbiol. Ecol.* **3**:11–30.

Starmer, W. T., Phaff, H. J., Miranda, M., Miller, M. W., and Heed, W. B., 1981, The

yeast flora associated with the decaying stems of columnar cacti and *Drosophila* in North America, in: *Evolutionary Biology*, Vol. 14 (M. K. Hecht, B. Wallace, G. T. Prance, eds.), pp. 269–295, Plenum Press, New York.

Stearns, S. C., 1976, Life history tactics: A review of the ideas, *Q. Rev. Biol.* 51:3–47.

Stearns, S. C., 1977, The evolution of life history traits: A critique of the theory and a review of the data, *Annu. Rev. Ecol. Syst.* 8:145–171.

Strong, D., Szyska, L., and Simberloff, D., 1979, Tests of community-wide character displacement against null hypothesis, *Evolution* 33:897–913.

Sulzbach, D. S., 1980, Selection for competitive ability: Negative results in *Drosophila*, *Evolution* 34:431–436.

Sulzbach, D. S., and Emlen, J. M., 1979, Evolution of competitive ability in mixtures of *Drosophila melanogaster*: Populations with an initial asymmetry, *Evolution* 33:1138–1149.

Takamura, T., 1980, Behavior genetics of choice of oviposition site in *Drosophila melanogaster*. II. Analysis of natural population, *Jpn. J. Genet.* 55:91–97.

Taylor, C. E., and Condra, C., 1980, *r*- and *K*-selection in *Drosophila pseudoobscura*, *Evolution* 34:1183–1193.

Taylor, C. E., and Powell, J. R., 1977, Microgeographic differentiation of chromosomal and enzyme polymorphisms in *Drosophila persimilis*, *Genetics* 85:681–695.

Taylor, C. E., and Powell, J. R., 1978, Habitat choice in natural populations of *Drosophila*, *Oecologia* 37:69–75.

Taylor, H. M., Gourley, R. S., Lawrence, C. E., and Kaplan, R. S., 1974, Natural selection of life history attributes: An analytical approach, *Theor. Popul. Biol.* 5:104–122.

Tempiel, B. L., Bonini, N., Dawson, D. R., and Quinn, W. G., 1983, Reward learning in normal and mutant *Drosophila*, *Proc. Natl. Acad. Sci. USA* 80:1482–1486.

Templeton, A. R., and Johnston, J. S., 1982, Life history evolution under pleiotropy and *K*-selection in a natural population of *Drosophila mercatorum*, in: *Ecological Genetics and Evolution: The Cactus–Yeast–Drosophila Model System* (J. S. F. Barker and W. T. Starmer, eds.), pp. 225–239, Academic Press, New York.

Thomas, W. R., Pomerantz, M. J. and Gilpin, M. E., 1980, Chaos, asymmetric growth and group selection for dynamical stability, *Ecology* 61:1312–1320.

Thorpe, W. H., 1945, The evolutionary significance of habitat selection, *J. Anim. Ecol.* 14:67–70.

Tracey, M. L., and Ayala, F. J., 1974, Genetic load in natural populations: Is it compatible with the hypothesis that many polymorphisms are maintained by natural selection? *Genetics* 77:569–589.

Turelli, M., and Petry, D., 1980, Density-dependent selection in a random environment: An evolutionary process that can maintain stable population dynamics, *Proc. Natl. Acad. Sci. USA* 77:7501–7505.

Turelli, M., Coyne, J. A., and Prout, T., 1984, Habitat and food choice in orchard populations of *Drosophila*, *Biol. J. Linn. Soc.* 22:95–106.

Wallace, B., 1970, *Genetic Load*, Prentice-Hall, Englewood Cliffs, New Jersey.

Wallace, B., 1975, The biogeography of laboratory islands, *Evolution* 29:622–635.

White, M. J. D., 1978, *Modes of Speciation*, Freeman, San Francisco.

Wijsman, E. M., 1984, The effect of mutagenesis on competitive ability in *Drosophila*, *Evolution* 38:571–581.

Wright, S., 1943, Isolation by distance, *Genetics* 28:114–138.