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Genotype, Environment, and Population Numbers

Animal numbers are regulated by the genetic composition of the population and by environmental factors.

Francisco J. Ayala

In his work *On the Origin of Species,* Darwin wrote that "the causes which check the natural tendency of each species to increase in numbers are most obscure. . . . We know not exactly what the checks are even in a single instance." The regulation of population numbers is of major importance for the understanding of natural selection and biological evolution. It has implications of economic interest, particularly for the control of animal pests. Finally, it is a major problem for modern man who has become aware that the quality of human life is seriously threatened by the so-called "population explosion."

Population biology is concerned with the distribution and abundance of organisms. The factors considered when studying a particular population are the relationship of the animals to their food, to the places where they live, to the weather, and to other animals that share the same food or place to live, that prey on them, or that are related to them in any way. Unfortunately the genetic constitution of the population is usually not given sufficient attention. Populations of a species are treated as if they were genetically homogeneous in space and in time. Yet, to understand the causes which regulate animal numbers, both genetic and environmental factors must be considered.

Students of natural populations of animals encounter many difficulties, particularly in the estimation of adult numbers and the causes of mortality (*1*). Some problems can more easily be approached in laboratory studies, which permit control of the more important factors, while one or a few variables are manipulated at a time. Models can be produced; the validity of which must, of course, be ultimately tested in the field.

Drosophila flies are particularly favorable organisms for laboratory studies of some population problems. They multiply rapidly in cultures which are easy to maintain at moderate expense. Moreover, much is known about their biology, since they have been intensively studied for the last 60 years. I now describe some experimental approaches using drosophila that have provided information on the factors which regulate population numbers.

Innate Capacity for Increase

All components of the life cycle of drosophila are influenced by the genetic constitution of the flies. Genetic variation has been found to affect fertility of females and hatchability of eggs (*2*), fertility and mating activity of males (*3*), rate of development (*4*, *5*), longevity (*6*), and others. The ability of a population to increase in numbers or to maintain a certain size is related to these properties of the flies. However, it is not clear how they interact with each other to determine reproductive capacity. A statistic variously named the Malthusian parameter, intrinsic rate of natural increase, or innate capacity for increase has been proposed which

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incorporates the significant components of the life cycle into a single value (*7–9*).

The innate capacity for increase in numbers, r_m, may be defined as the maximum rate of increase attained by a population at any particular combination of quality of food, temperature, humidity, and so forth, when the quantity of food, space, and other animals of the same species are kept at an optimum, and other organisms of other species are excluded. The population is assumed to have a constant age schedule of births and deaths. Essentially, the ability of a population to increase in numbers depends upon the birth rate and the survival rate of the animals. The number of animals will increase, remain constant, or decrease depending on whether the birth rate is greater than, equal to, or smaller than the death rate. The rate of change depends on the magnitude of the difference between birth rate and death rate. To estimate the innate capacity for increase of a population the distribution of ages must be considered since the expectation of births and the probability of death vary with age. For a population with a stable age distribution, that is, with a constant age schedule of births and deaths, the innate capacity for increase is connected with the schedules of fecundity and mortality by the expression:

$$\int_0^\infty e^{-r_m x} l_x m_x \delta x = 1$$

where e is the base of natural logarithms, l_x the probability at birth of being alive at age x, m_x the number of female offspring produced per unit time by a female aged x, and 0 to ∞ the life-span. To estimate r_m the integration is replaced with a summation over discrete time intervals:

$$\sum_0^t e^{-r_m x} l_x m_x = 1$$

The detailed procedure for estimating r_m from this equation is given by Andrewartha and Birch (*8*). The accurate solution of the equation requires data not easily obtained, as well as some laborious calculations, although various approximations which simplify the operations are usually acceptable. Sometimes it is preferable to use a related statistic, the finite rate of increase ($\lambda = \text{antilog}_e\ r_m$). While r_m measures the infinitesimal rate of increase, λ can express the rate of increase per day, per week, or for any time interval.

Table 1. Mean productivity and population size after equilibrium of various geographic strains of two related drosophila species. Measurements are 44 for productivity and 17 for population size.

Population	Temperature (°C)	Productivity (No./food unit)	Population size
	Drosophila serrata		
Sydney	25	550 ± 17	1782 ± 76
Cooktown	25	568 ± 20	2221 ± 80
Popondetta	25	477 ± 13	1828 ± 90
Sydney	19	483 ± 13	1803 ± 87
Cooktown	19	486 ± 12	2017 ± 84
Popondetta	19	357 ± 8	1580 ± 52
	Drosophila birchii		
Cairns	25	351 ± 16	1262 ± 83
Popondetta	25	152 ± 9	469 ± 49
Cairns	19	324 ± 11	1091 ± 66
Popondetta	19	121 ± 5	428 ± 33

Genetically different populations of *D. pseudoobscura* have different innate capacities for increase in numbers (*10*). Populations polymorphic for certain chromosomal arrangements, and therefore carrying more genetic variability, had greater capacity for increase than monomorphic populations. *Drosophila pseudoobscura* flies with irradiated genetic material have a lower capacity for increase than nonirradiated controls (*11*). Geographic races of the same species also have different innate capacities for increase (*12*). Given any genetic constitution, the statistic r_m is very sensitive to differences in temperature (*10–12*) and in quality of food (*13*).

The statistic r_m has been criticized as being an abstraction far removed from nature. Indeed, while it provides some information about certain physiological characteristics of a population, its relevance to natural conditions is limited. Natural populations do not have stable age-distributions. Estimates of r_m obtained for any particular population are applicable only for the conditions of temperature, humidity, quality of food, and so forth, under which the experiments are carried out. In Tantawy's experiments (*11*) the population with the highest capacity for increase at 15°C had the lowest at 25°C. Finally, r_m measures the capacity for increase when the quantity of food and space are kept at an optimum and there are no competitors. In nature, food and a place to live may be limited or inaccessible; the chances of an animal to survive and multiply depend on its ability to compete with other animals.

Role of the Genotype

The regulation of population numbers may be studied in the laboratory under conditions more nearly approximating those existing in the field. One approach consists of introducing a genetically defined population into a restricted environment with a limited supply of food provided at regular intervals. Environmental factors like moisture and temperature are also controlled. After a few generations population numbers usually reach an equilibrium and thereafter oscillate about a mean equilibrium level. At equilibrium the rate of births equals the rate of deaths. The effect of genetic constitution on population numbers may be studied by comparison of the performance of genetically different populations which are treated identically. Conversely, treatment of genetically identical populations may be modified to ascertain the effect of selected environmental components on population size.

A variant of this method is the "serial transfer" technique, which has proven to be useful in the experimental study of population regulation in drosophila. Adult flies are introduced into an experimental "cage," usually a glass jar, with a measured amount of food and allowed to lay eggs for a specified period of time, usually 2 or 3 days. At regular intervals the flies are transferred to new cages with fresh food. When adult flies begin to emerge in the cages where the eggs were laid, they are collected, counted and weighed under anesthesia, and then added to the cage containing the adult population. The ovipositing adult flies are thus always in a single cage with fresh food, while a number of cages contain eggs, larvae, pupae, and newly emerged adults. The adult population is anesthetized and censused at regular intervals. The technique also provides information about the number of births, that is the number of flies emerging, per unit food or per unit time. From the rate of birth and the population size, estimates may be obtained of the average longevity of adult flies.

The serial transfer technique was employed to study the performance of several geographic strains of *D. serrata* and *D. birchii*, two sibling species common in eastern Australia and New Guinea (*14*). Strains of *D. serrata*, collected at Popondetta, New Guinea; Cooktown, Queensland; and about 200 kilometers north of Sydney, New South Wales, were used, while *D. birchii* was collected at Cairns, Queensland, and at Popondetta, New Guinea. These strains represent populations adapted to very different climates, and may therefore be rather different genetically. The Popondetta and Sydney strains were collected at about 9° and 33° south latitude, respectively, separated by 2700 kilometers.

Experimental populations (300 flies each) were established in the laboratory with descendants of the flies collected in the field. Two populations were started with each strain, one kept at 25°C and the other at 19°C. They were observed for a year, which corresponds to about 17 and 10 generations at 25°C and 19°C, respectively. The populations increased rapidly, reaching by the third generation an equilibrium size around which they oscillated thereafter (*15*). The mean number of flies produced per food unit and the mean population size from the fourth generation on are given in Table 1. Standard erorrs for the means indicate the amplitude of the oscillations around the levels of equilibrium.

There are striking differences among the genetically different strains in their ability to exploit the experimental environment. The Cooktown strain of *D. serrata* has the largest population size at either temperature. At 25°C, the Popondetta and Sydney strains have approximately equal size, but the Sydney population is larger at 19°C, which suggests that Sydney flies may be adapted to live in a climate considerably colder than that of Popondetta.

There is no strict correspondence between rate of birth and average population numbers. The number of flies emerging per unit time is approximately the same in the Sydney and Cooktown populations at either temperature, but the Cooktown population is larger in average size. This means that under the experimental conditions the average longevity of the Sydney flies is smaller.

In *D. birchii,* the Cairns populations have greater productivity and size than those from Popondetta. The considerable difference in adaptation to the experimental environment of these two strains reflects the large genetic differences existing between them (*14*).

Table 2. Mean productivity and population size after equilibrium of various hybrid populations of drosophila. Measurements are 41 for productivity and 15 for population size.

Population	Temperature (°C)	Productivity (No./food unit)	Population size
	Drosophila serrata		
Sydney × Cooktown	25	593 ± 16	2360 ± 74
Sydney × Popondetta	25	622 ± 18	2541 ± 117
Cooktown × Popondetta	25	540 ± 18	2419 ± 76
Sydney × Cooktown	19	554 ± 19	2418 ± 171
Sydney × Popondetta	19	572 ± 14	2448 ± 86
Cooktown × Popondetta	19	479 ± 12	2227 ± 172
	Drosophila birchii		
Cairns × Popondetta	25	342 ± 26	1331 ± 123
Cairns × Popondetta	19	303 ± 10	1203 ± 55

Genetic Variability

Carson (*16*) detected differences in the productivity and size of experimental populations of *D. robusta* derived from different geographic localities. The performance of a strain collected at the center of the geographic distribution of the species (central population) was superior to that of another strain collected at the margin of its distribution. This seems to be the case also for *D. serrata.* Central populations of drosophila have been observed to possess greater genetic variability than marginal populations. The superior performance of central populations in the laboratory has been explained by arguing that populations with greater genetic variability are more efficient in adapting to a new environment.

The role of genetic variability in the adaptation of a population to a new environment can be directly approached in the laboratory. "Hybrid" populations can be produced by mass-crossing two strains. Females of, say, strain A are mated with males of strain B, and females of strain B with males of strain A. If a large number of parents are used the progenies of the two reciprocal crosses will contain most of the genetic variability present in both parental strains. Mass-crosses between each two strains were made among the three strains of *D. serrata* and the two of *D. birchii.* Experimental populations established with progenies of the mass-crosses were studied for about a year at 25°C and 19°C. Table 2 shows the mean productivity and size of these hybrid populations. Hybrid populations have larger size, and, generally, also greater productivity, than the corresponding parental populations (Tables 1 and 2). Comparison of the mean of the hybrid populations with the means of the two parental populations with the Student's *t*-test showed that the productivity and size of the hybrid populations are always significantly greater (*15*).

In serial transfer experiments with *D. pseudoobscura,* the average size and average productivity of a population polymorphic for two chromosomal arrangements were greater than those of either one of two monomorphic populations (*17*). The fitness of certain chromosomal arrangements of *D. pseudoobscura* was positively correlated with the initial amount of genetic variability (*18*). In experiments where *D. pseudoobscura* and *D. serrata* were competing for food and living space, the average numbers of *D. pseudoobscura* were greater in the populations with more genetic variability. In *D. melanogaster* the average population size of a strain carrying several mutant genes was about one-third the size of a wild-type population. A hybrid population, having both wild-type and the mutant genes, was superior to both parental populations (*19*).

Evolutionary changes occur in the adaptation of a population to an experimental environment by natural selection. The observed superior performance of populations with greater initial genetic variability is likely to result from natural selection being more efficient in those populations where more genotypes are available for selection. In the experiments, selection is intensive since food and space are quite restricted. The amount of food available is sufficient for the development of probably less than 1 percent of the eggs laid. The adult flies also compete intensively for food and space in the extremely crowded cages. The average longevity of *D. serrata* in the experiments is about 9 and 13 days at 25°C and 19°C, respectively (*15*). Under optimum conditions their average longevity is about 25 and 45 days at 25°C and 20°C, respectively (*12*).

If the populations are adaptating gradually to the experimental environment as a result of evolutionary changes, it might be possible to observe this process and measure it in some way. The adaptation of the populations to the environment may be measured by their numbers. Larger population size implies greater efficiency in transforming the limited resources of food and space into biomass, or living matter. The progressive adaptation of a population to an experimental environment could be measured by a gradual increase in population numbers while the environmental conditions remain constant.

The performance of two populations, one established with the Popondetta strain and the other with the progenies of Sydney × Popondetta mass-crosses, was studied for 18 months at 25°C and at 19°C (*20*) (Fig. 1). A statistic, the coefficient of regression of population numbers on time, was used to evaluate the apparent increase in population size. The coefficients of regression are positive, and statistically different from zero, in the four populations (Fig. 1). The populations have gradually shown greater adaptation to the experimental environment.

The Popondetta populations increased at an average rate of 10.5 flies per week at 25°C and 8.4 flies per week at 19°C. The corresponding rates of increase per week are 19.5 and 20.4 for the hybrid populations. The rate of increase in the hybrid populations is approximately double that in the Popondetta populations. The experiment shows measurable evolution over a short time span in *D. serrata*. Moreover, it provides one of the few available biological illustrations of Fisher's (*9*) fundamental theorem of natural selection: "The rate of increase in fitness of any organism at any time is equal to its genetic variance in fitness at that time." The rate of evolution is considerably larger in the hybrid populations, which have greater genetic variance, than in the Popondetta populations.

The gradual increase in population size may conceivably be due to environmental, rather than to genetic, changes. Although temperature, amount and quality of food, space, and all other components of the physical environment were kept constant within measurable limits, it is possible that undetected modifications of the environment may have occurred. This possibility was tested by comparison of the performances of control populations directly established from the laboratory stocks with populations derived from the experimental populations described above (*21*). The experimental populations had greater productivity and larger average size than the controls demonstrating their superior genetic adaptation to the experimental environment.

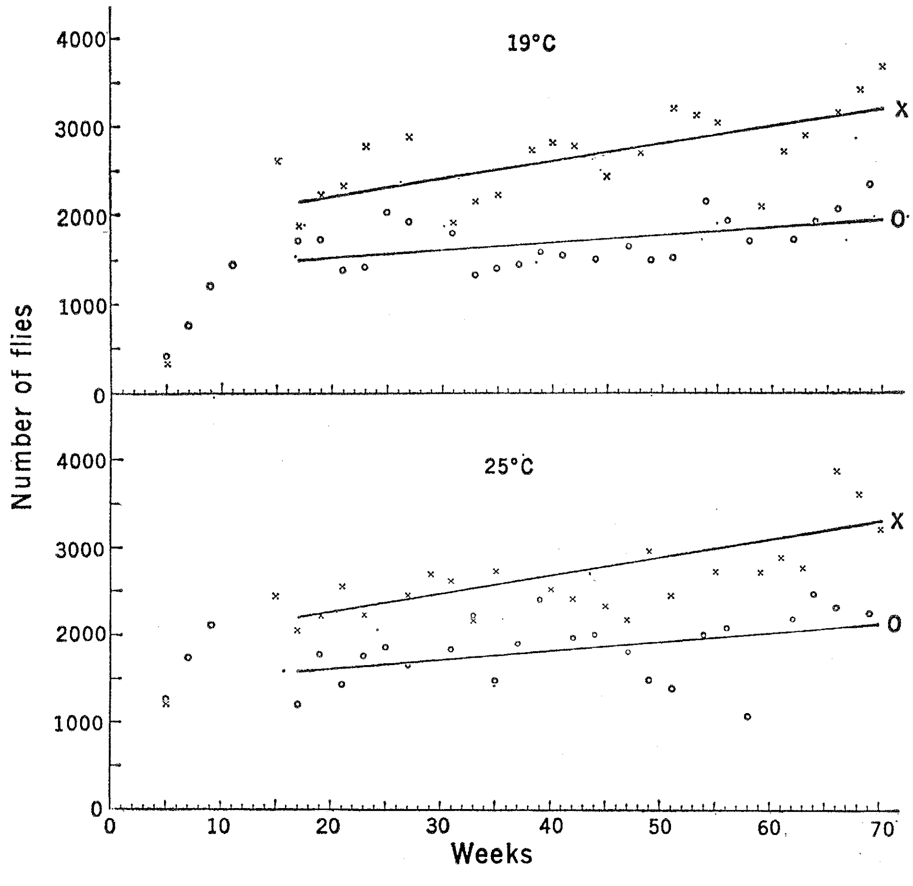

Fig. 1. Population size of four experimental populations of *Drosophila serrata* at two temperatures. *X*, Hybrid population; *O*, Popondetta population.

Radiation and Selection

The process of mutation ultimately furnishes the materials for adaptation to changing environments. Genetic variations which increase the reproductive fitness of a population to its environment are preserved and multiplied by natural selection. Deleterious mutations are eliminated more or less rapidly depending on the magnitude of their harmful effects. High-energy radiations, such as x-rays, increase the rate of mutation (*22*). Mutations induced by radiation are random in the sense that they arise independently of their effects on the fitness of the individuals which carry them. Randomly induced mutations are usually deleterious. In a precisely organized and complex system like the genome of an organism, a random change will most frequently decrease, rather than increase, the orderliness or useful information of the system. A potentially beneficial mutation induced by radiation is likely to have occurred in the past history of a population. If the population has lived for a long time in the same environment mutations beneficial in that environment may already be incorporated in the gene pool of the population. Mutational changes are more likely to be beneficial to the population when the environment changes.

Experiments can be made to test whether an increase in genetic variance induced by x-radiation might result in an increase in the reproductive fitness of the population. Certain conditions must be fulfilled for such experiments to succeed. Large numbers of individuals must be irradiated to make more probable the induction of some favorable mutations. The dosage should not be too large lest the potential selection of favorable induced mutations be more than counteracted by deleterious mutations. Finally, the population should be exposed to a new environment, as different as possible from that to which they are adapted, to increase the chance of a measurable rate of evolutionary change during the experimental period.

Experiments designed to meet these requirements were carried out with *D. serrata* flies at 25°C and at 19°C (*23*). At each temperature two populations were irradiated and a third one was the control. The males of the experimental populations were given 1000 roentgen of x-rays in each of three consecutive generations and mated to the nonirradiated females. The populations were maintained by the serial transfer technique.

Figure 2 shows the changes in population numbers at 25°C. The two irradiated populations decreased in size during the first 6 weeks, owing presumably to the elimination of carriers of deleterious mutations. Thereafter there was a rapid increase in the size of the two experimental populations which became considerably larger than the control from week 10 until the experiment was terminated. Comparable results were observed at 19°C. Table 3 contains the mean productivity and size of the six populations from weeks 16 to 41.

Natural selection resulted in better adapted genotypes in the irradiated than in the control populations, as measured by either their size or their productivity. The increase in the rate of evolution of the irradiated populations can be measured as follows. The differences in size between each irradiated population and the control are obtained for each measurement throughout the experimental period and the coefficient of regression of the differences on time is calculated. The two irradiated populations at 25°C increased in size at a rate of 26 and 41 flies per week faster than the controls. At 19°C the increase in the rate of evolution of the irradiated populations over the control was 36 and 46 flies per week.

Comparable results were obtained with *D. birchii* (*23*), and with two irradiated populations of *D. serrata* studied for nearly 3 years (*24*). Carson did not observe any sustained increase in the size of irradiated populations of *D. melanogaster* (*25*). His experiments, however, were conducted under conditions different in several important respects (*23*). Radiation-induced mutations in *D. pseudoobscura* increased the fitness of certain chromosomes when natural selection was operative, but not otherwise (*26*). The conclusion is that the genetic variability induced by high frequency radiation may result, after several generations of strong natural selection, in more efficient adaptation of a population to a new environment. Needless to say, this conclusion has no application to man with his long generation time and limited reproductive capacity. Moreover, human values would hardly allow for the enormous price in lives and physical misery that the species would have to pay for such hypothetical improvement of its adaptation to the environment.

Table 3. Mean productivity and population size of four irradiated populations of *Drosophila serrata* and their controls.

Population	Temperature (°C)	Productivity (No./food unit)	Population size
Control	25	198 ± 7	1294 ± 50
Exp. 1	25	317 ± 10	1955 ± 65
Exp. 2	25	378 ± 9	2558 ± 98
Control	19	118 ± 14	498 ± 110
Exp. 1	19	250 ± 10	1358 ± 102
Exp. 2	19	259 ± 9	1515 ± 75

Temperature, Food, Space

The size of a population living in a certain environment depends upon its genetic constitution. I have expounded at some length the genetic aspect of the regulation of population numbers because in discussions of this topic genetic considerations are often ignored altogether. Animal populations, however, do not live in a vacuum. The effect of the genotype depends on the environment of the organism. I shall now consider several experiments with drosophila flies which indicate the effect of various components of the environment on the size of animal populations.

Animals can survive and multiply only within certain temperature ranges. Within the survival range, temperature affects various properties of the organisms. In drosophila temperature influences fertility (*2, 27*), speed of development and longevity (*10, 12*). Humidity also affects reproductive efficiency (*28*). The innate capacity for increase in numbers of various geographic strains of *D. serrata* and *D. birchii* is nearly double at 25°C that at 20°C (*12*). *Drosophila pseudoobscura* of various genetic compositions had an average capacity for increase more than double at 25°C that at 16°C (*10*).

"The amount of food for each species of course gives the extreme limit to which it can increase." There is little argument about this statement from Darwin's *On the Origin of Species*. There is, however, considerable debate about whether food is a major check of animal numbers. According to Lack (*1*) the numbers of many species of birds, and also of many other animals, are limited by food. Andrewartha and Birch (*8*) think instead that shortage of material resources, such as food, is probably the least important among the possible ways in which the numbers of a population may be limited. Crowding and food limitation, however, affect longevity, as well as fecundity and speed of development of drosophila (*29*). Quality as well as quantity of food is important (*13, 30*).

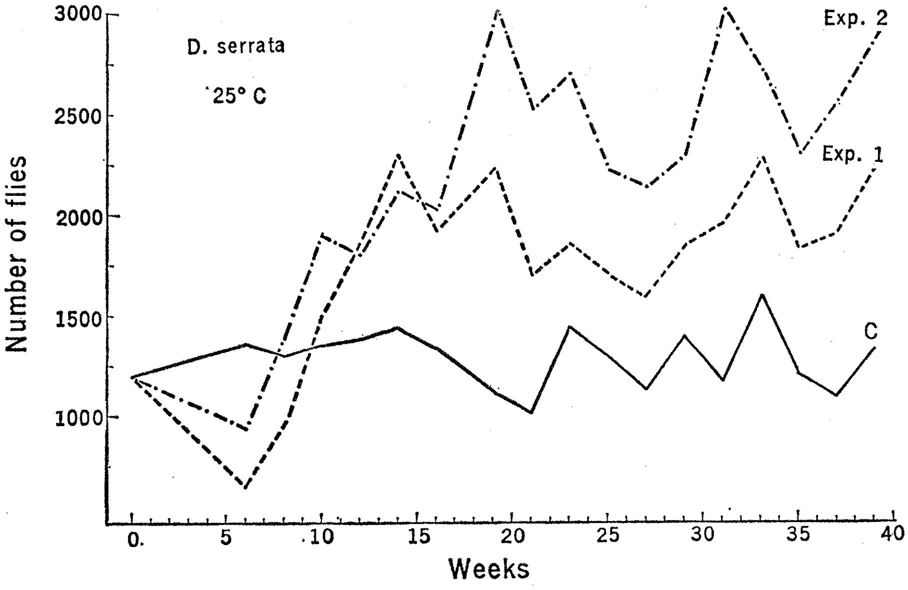

Fig. 2. Size of three populations of *Drosophila serrata* at 25°C; *C*, control population; *Exp-1* and *Exp-2*, irradiated populations.

Table 4. Effects of temperature (25°C versus 10°C), transfers per week (2 versus 3), and genetic composition (hybrid versus Popondetta strain) in eight populations of *Drosophila serrata*. The standard errors for the mean and the treatments are the same within each column. The effects are indicated as average deviations from the mean.

	Productivity per food unit			Population size	
	No.	Biomass (mg)	Indiv. weight (mg)	No.	Indiv. weight (mg)
Mean	535.3	296.0	0.560	2670	0.627
Temp.	+ 24.8*	+ 2.4	− 0.016*	− 370*	− 0.025*
Transfers per week	+ 20.9*	+ 14.8*	− 0.005	− 208*	+ 0.009*
Genetic composition	+ 66.8*	+ 39.6*	− 0.004	+ 394*	− 0.021*
Standard error	5.8	5.7	0.003	45	0.003

* The effect is statistically significant, $P < .05$.

When a population is growing with a limited amount of food and space, the number of animals per unit of food and space rises. Eventually, an equilibrium must be reached when the number of births per unit time equals the number of deaths. The average size of a population, however, need not be proportional to the rate of births. Of two populations with the same number of births per unit time, one will be twice as large as the other if the average longevity of the animals in the first population is also double. The large increase in human numbers during recent times has been due more to increase in average longevity than to increase in rate of births.

An experiment with *D. serrata* illustrates this point. Temperature and amount of food were each studied at two levels. The temperature was either 25°C or 19°C, the amount of food was either two or three food units per week. Genetic composition was also a variable, the populations being either the Popondetta strain or the hybrid, Sydney × Popondetta. All possible combinations among the variables were made (factorial design). Thus, there was a Popondetta population at 25°C with three food units per week; a second at 25°C with two food units; a third at 19°C with three food units; and a fourth at 19°C with two food units. Four parallel Sydney × Popondetta populations were also established. The populations were maintained by the serial transfer technique, and therefore the living space for the adult flies was equal in the eight populations (*31*).

The hybrid populations have considerably greater productivity and size than the Popondetta populations (Table 4). This confirms again that a greater initial genetic variance results, with natural selection, in better adapted genotypes.

The effects of temperature are clear. The number of flies produced is slightly larger at 25°C than at 19°C. The flies developed at the higher temperature are, however, smaller; in fact, the biomass produced per food unit is the same at either temperature. The average population number at 19°C is about 30 percent larger than at 25°C. Since somewhat fewer flies are added per unit time to the populations at 19°C, the average longevity of these flies must be considerably greater, about 40 percent, than in the 25°C populations (*31*) (Table 4).

The effects of food amount (Table 4) are most interesting. Populations receiving three food units per week are only about 17 percent larger than populations transferred twice a week. The number of flies born per food unit is nearly equal for both populations. Nearly 50 percent more flies are added per week to the populations with three food units, but their average numbers are only 17 percent greater. The increase in amount of food, and therefore in numbers of births, results in a decrease in average longevity with but a small increase in population size. The limiting factor is presumably living space. The available space in the cages is about 400 cubic centimeters, a very restricted space indeed for the average 2670 flies living in it.

Table 5. Performance of three genetically different populations of *Drosophila pseudoobscura* in competition with *Drosophila serrata*. The numbers are means of six replicates calculated from weeks 6 to 47. CH and AR are two chromosomal arrangements.

	Flies emerging (No./per week)	Old flies (No.)
Population 1		
D. pseudoobscura (CH)	60.4	64.5
D. serrata	264.1	299.6
Population 2		
D. pseudoobscura (AR)	107.0	144.6
D. serrata	138.8	150.7
Population 3		
D. pseudoobscura (CH and AR)	123.8	152.6
D. serrata	144.4	151.1

It is unlikely that living space is ever so limited for natural populations of drosophila. The lesson is that rate of births may not be strictly correlated with average population size; and that factors other than food may exercise the primary control of population numbers even when the number of individuals developing to maturity depends on the amount of food. The numbers in the experimental populations are simultaneously limited by both food and space. Food is a limiting factor, for an increase in amount of food produces an increase in number. Since the increase in number is not proportional to the increase in food, space is postulated as the additional limiting factor. In nature, predators or other components of the environment may take the limiting role played by living space in the experiments.

Population density may be simultaneously limited by more than one factor. This question was further pursued in an experiment with *D. serrata* in which the amount of space as well as the amount of food was varied (*32*). A factorial design was used with a total of 18 populations. The mean number of flies for all populations was 1145. An increase or decrease in the amount of food of 33 percent produced an increase or decrease of 26 percent in population size, respectively. A change of 33 percent in the amount of space resulted in a 10 percent change in population size. Again both food and space are limiting factors of population numbers, although within the range studied food plays a greater role than space. Comparable results have been obtained with several geographic strains of *D. serrata*, and with *D. birchii* (*33*), *D. melanogaster* and *D. pseudoobscura* (*34*).

Cooperation and Competition

Other animals of the same species are not always competitors for the available resources of food and space. Laboratory studies have shown that there exist various forms of cooperation among individuals of the same species. The most obvious form of cooperation is, of course, the need for sexually reproducing organisms of finding a mate. But undercrowding as well as overcrowding is frequently harmful. In drosophila, the viability of the larvae (*4*), longevity, and other properties of the flies (*29*) generally have an optimum at intermediate densities. The presence of larvae, or their metabolic products, of different genetic constitution enhances the larval viability of some strains but not of others (*4, 35, 36*). Particularly interesting is the discovery that female flies prefer to overposit near the places where eggs have already been laid by other females (*37*). Del Solar has demonstrated that this "gregarious" tendency is genetically controlled.

Interactions among animals of related species influence their numbers. Larval viability of drosophila can be enhanced or handicapped by the presence of larvae of other drosophila species in the same cultures (*36, 38*). In laboratory populations, if two species share limited resources of food and space, one species will generally eliminate the other within a few generations (*39*). However, I have demonstrated that with the serial transfer technique two species of drosophila can coexist if the environment is properly adjusted (*40*). For instance, at 25°C *D. nebulosa* eliminated *D. serrata* in four or five generations; at 19°C both species coexisted until the experiment was terminated after some 60 generations.

Coexistence of two species in a relatively uniform and constant environment seems to contradict the so-called "competitive exclusion principle." If two related species share at least one essential resource available in limited quantity, one species will be at advantage in the exploitation of the limited resource. According to the competitive exclusion principle, the relative advantage of one species will accumulate over time with the eventual elimination of the other species. The serial transfer technique, which permits the study of competition independently among the adult and among the larvae, makes possible an explanation for the coexistence of two species. It seems that one species is at an advantage in the larval stage while the other species is at advantage in the adult stage. Or, looking at it differently, one species is at an advantage in the exploitation of one limited resource—food, and the other species is at an advantage in the exploitation of a different limited resource—living space for the adults. The selection pressure is different among the larvae than among the adults. The relative advantages cancel each other at certain relative frequencies of the two species. The equilibrium frequencies are observed to be stable. It seems that an increase in the frequency of one species results in a net disadvantage for that species until the equilibrium is restored. Thus, the phenomenon of frequency-dependent selection previously observed at the intraspecific level (*41*) apparently occurs also at the interspecific level.

When two or more species share the same environmental resources, the numbers of each species depend on its genetic constitution as well as on the genetic constitution of the competing species. This can be illustrated by an experiment with *D. serrata* and *D. pseudoobscura* (*42*). There were three types of populations depending on the genotypes of *D. pseudoobscura.* The genetic constitution of *D. serrata* was the same in all populations; *D. pseudoobscura* was either polymorphic for two chromosomal arrangements (CH and AR), or monomorphic for CH or AR. There are six replicates for each type, with a total of 18 populations. The populations were started with 300 flies of each species and kept at 23.5°C for 47 weeks. *D. pseudoobscura* flies decreased in frequency from their original 50 percent during the first few weeks. By the third generation an equilibrium was reached and the relative frequency of each species remained approximately constant thereafter until the experiment was terminated (Table 5).

The numbers of *D. pseudoobscura* are greater in the monomorphic AR than in the monomorphic CH population, and larger in the polymorphic than in either monomorphic population. Although the genetic composition of *D. serrata* was the same in all populations, the average numbers of this species depend on the genetic composition of *D. pseudoobscura.*

Summary

The abundance of animals is regulated by factors both internal and external to the animals. Of major importance is the genetic constitution of the population, which has too often been ignored in ecological studies. Laboratory experiments with drosophila flies show that populations with greater genetic variability have larger population sizes. The rate of evolution of a population becoming adapted to a new environment is positively correlated with the initial amount of genetic variability in the population.

Temperature, humidity, and other climatic factors affect population numbers. Food and a place to live may jointly limit the maximum size that a population can reach. Finally, the biotic components of the environment influence the size of animal populations.

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