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INDIVIDUAL DIFFERENCES BETWEEN ANIMALS AND THE NATURAL REGULATION OF THEIR NUMBERS

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SUMMARY

(1) A model of population regulation by emigration is developed based on (i) spatial and temporal heterogeneity of natural environments; (ii) unequal resource partitioning among individuals of single species populations. This latter phenomenon has not previously been taken into account by theoretical ecologists, although it is of basic importance for regulation of population density.

(2) Unequal resource partitioning increases the stability of a confined population and allows emigration of some population members into suboptimal and hostile areas to evolve by individual selection.

(3) In a local habitat supplied by a constant inflow of food, animal density is lower and food density is higher when emigration occurs, than without emigration.

(4) Regulation of population density by emigration allows for the adjustment of this density to the amount of food, in such a way that mortality is not directly due to food shortage but to other agents (predators, adverse weather conditions, etc.).

(5) Animals with overlapping generations and cyclic changes in population density can emigrate at lower density level, than that determined by food supply at any given point in time. At high densities such populations can also exhibit reduced reproduction, which under certain circumstances can be considered as an adaptation.

(6) Population outbreaks are thought of as a failure of population regulation by emigration resulting from spatial homogeneity of the environment. Homogeneity diminishes both differences among individuals in local populations and differences between local habitats and their surroundings, these in turn can make regulation by emigration impossible

INTRODUCTION

According to the present state of ecological theory, emigration of animals into hostile or suboptimal areas is not considered as an important mechanism of natural regulation of animal numbers because such emigration, as pointed out by MacArthur (1972), cannot evolve by individual selection being of selective disadvantage for migrants. The evolution of emigration and other behavioural mechanisms of population regulation have been explained by group selection (Wynne-Edwards 1962; Van Valen 1970; Gilpin 1975). It seems that all the difficulties in accepting emigration as a mechanism of population regulation which has evolved by individual selection result from an assumption, widely accepted by theoretical ecologists, that animals within a single species population are like identical molecules which differ only in sex and age. This paper is an attempt to demonstrate, without invoking group selection, that animal density can be regulated by

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emigration if differences among animals, other than sex and age, and not necessarily genetical, are taken into account.

Unfortunately, the long-held theoretical assumption that animals are identical has had a profound effect on ecology, so that very little is known about resource division amongst individuals or about differences in their reproduction and survival. It seems that because of this assumption, field ecologists report much less about individual differences among animals in their learned journals and textbooks, than they actually know. The assumption mentioned above appears to be confirmed to a certain degree by ecological laboratory investigations. Laboratory populations are kept under standard conditions, which usually means that they are maintained in very homogeneous artificial habitats and the methods by which the animals are fed and counted homogenize these populations even more. In such habitats large differences between individuals can hardly arise, and if they do they are often lost. For these reasons the results obtained in laboratories can be highly biased, showing smaller individual differences than those existing in the field, and conforming better to present ecological theory than field data.

The differences between individuals will be considered here in terms of food partitioning among population members. If all individuals take about the same share of food, then a decrease in the amount of food per individual below its maintenance cost brings about the death of the entire population. Populations behaving in this way were defined by Nicholson (1954) as showing 'scramble' competition, they are subject to violent fluctuations and they can easily become extinct through shortage of food. Such a situation can be easily found in the laboratory due to small differences among individuals.

Although no good data concerning resource partitioning within a single population can be found in the ecological literature, it seems that the scramble type of competition is a rare phenomenon, and that both plants and animals exhibit rather a 'contest' (Nicholson 1954) type; some individuals take as much or almost as much as they require, while others get nothing or almost nothing. The resources seem unequally partitioned and this inequality increases when resources become scarce. A mechanism of unequal resource partitioning can be clearly seen in competition for light among plants; an individual plant which by a random accident happens to become a little taller, subsequently takes more light and overgrows its competitors. There are no good reasons to reject the idea that very similar mechanisms of positive feed-back operate among animals; those which are slightly better fed or are in a somewhat better place can, therefore more easily obtain a higher proportion of food and a much better place to live than their competitors.

A formal description of food partitioning among animals can be given by assuming that the probability of an individual encountering a food particle is an increasing function of food density and of the amount of food taken previously by this individual. This assumption leads to food partitioning which approaches a lognormal distribution. If there is a constant maximum number of food particles which can be taken by each individual and if food is abundant, then all individuals take approximately the same number of food particles irrespective of how many they encounter. Therefore if food is abundant, individual differences in food intake are small and they increase if food is scarce.

As mentioned, although resource partitioning within a single species population is a much neglected area of ecological research, some evidence confirming unequal partitioning does exist. Among many vertebrates unequal resource division is brought about by dominance hierarchies which are especially well pronounced when resources are scarce. Inequality of resource partitioning is well expressed in differential growth of population

members. For example salamander *Ambystoma maculatum* larvae exhibit a skewed distribution of body size, more skewed when the median of body size for the whole population decreases (Wilbur & Collins 1973). An increase in coefficient of variation with decreasing body size during bad years was found in a field population of wood pigeons (Murton, Isaacson & Westwood 1966). Differences in breeding success of *Drosophila* males (Bateman 1948) suggest that there are large individual differences among insects, which can also influence the competition for food.

The model of the regulation of animal population density presented here is based on two phenomena: (i) unequal resource partitioning described above and (ii) spatial and temporal heterogeneity of the natural environments. While the study of the former phenomenon is neglected, the importance of the latter is now becoming recognized (Wiens 1976; Levin 1976). A recent study by Taylor & Taylor (1977) has elucidated mechanisms by which population regulation due to movement in relation to spatial and temporal heterogeneity can be brought about.

THE BASIC MODEL

Consider an animal population of a single species with non-overlapping generations, in a unit of space where the intrinsic rate of natural increase r is positive. Changes in number of animals N and amount of food V within this space unit are given in discrete units of time t , equal to the generation time. There is a constant inflow C of food per unit of time, per unit of space.

A rank $x = 1, 2, \dots, N$ is assigned to each individual and this rank determines the amount, y of food it takes, as described by

$$y(x) = a \left(1 - \frac{a}{V} \right)^x \quad (1)$$

where a is a parameter determining the maximum amount of food an individual can take and it is assumed that the total food available $V > a$. The function $y(x)$ as defined by eqn (1) and shown in Fig. 1 is a simplified description of food partitioning and it is applied to the model presented here for its two properties: (i) it describes both unequal food partitioning and increase of this inequality when food is scarce, and (ii) its application to the model makes analytical solution possible, which is not the case when food partitioning is based on a lognormal or another more realistic distribution. In order to make the presentation of the model more general it is assumed that the number of animals N is large enough so that, when calculating food intake of N individuals, integration from $x = 0$ to $x = N$ instead of summation from rank $x = 1$ to rank $x = N$ can be applied.

Let R denote the amount of food required by one individual to attain reproductive age and to produce one offspring. From eqn (1) the number L of animals (Fig. 1) which receive enough food to produce at least one offspring is given by

$$L = \frac{\ln(R/a)}{\ln(1 - a/V)}. \quad (2)$$

Note that L denotes both the number of successful animals per unit of space considered, and a rank such that if $x > L$, an individual of rank x dies without leaving progeny, due to the shortage of food.

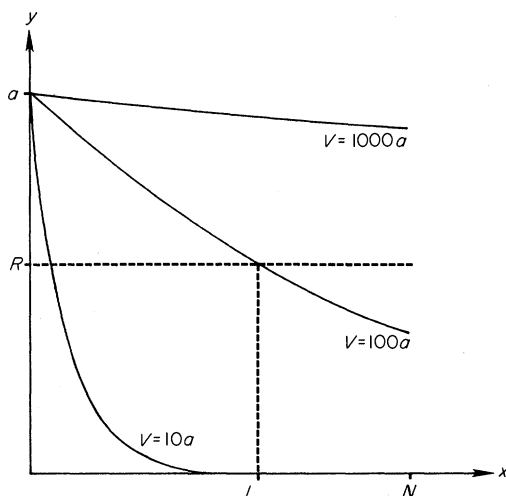


FIG. 1. Amount of food y taken by an individual as a function of its rank x , as defined by eqn (1), for three different food densities. For the density $V=100a$, the graph shows also the potential number of animals L which could take at least R units of food. Note that L can be either smaller or larger than the number of animals present $N(N=100)$, depending on food density V .

The amount of food V in the next unit of time $t+1$ is given by

$$V_{t+1} = V_t + C - \int_0^{N_t} y dx$$

which, after substituting (1) and integrating, yields

$$V_{t+1} = V_t + C - \frac{a(q_t^{N_t} - 1)}{\ln q_t} \quad (3)$$

where $q_t = 1 - a/V_t$.

Reproduction of animals is assumed to be linearly related to the amount of food taken and since an amount R is used to maintain the individual and to produce one offspring, each animal of rank $x \leq L$ produces $1 + (y - R)h$ offspring, where h is the efficiency of turning food eaten into progeny. L_t does not depend on the density of animals N_t , but it is a function of V_t , defined by eqn (2).

When $L_t \leq N_t$, the number of animals in the next generation is given by

$$N_{t+1} = L_t + h \int_0^{L_t} (y - R) dx$$

while $(N_t - L_t)$ animals die without leaving any progeny. After substituting eqn (1) and integrating, the above equation yields

$$N_{t+1} = \frac{1}{\ln q_t} [(1 - hR) \ln(R/a) - h(a - R)]. \quad (4)$$

Note that if $L_t \leq N_t$, then N_{t+1} does not depend on N_t , but is determined by V_t .

When $L_t > N_t$, the number of animals in the next generation is given by

$$N_{t+1} = N_t + h \int_0^{N_t} (y - R) dx$$

while there is room for $(L_t - N_t)$ animals to immigrate and to reproduce.

After substituting eqn (1) and integrating, this equation yields

$$N_{t+1} = N_t(1 - hR) + \frac{ah}{\ln q_t}(q_t^{N_t} - 1). \quad (5)$$

Note that if $L_t > N_t$ population increases $N_{t+1} > N_t$.

An example of changes in animal number N and the amount of food V , as determined by eqns (3)–(5) is shown in Fig. 2. From eqn (3) the isocline of the equation $\Delta V = 0$ ($\Delta V = V_{t+1} - V_t$) is given by

$$\hat{N}_{\Delta V=0} = \frac{1}{\ln q} \ln \left(1 + \frac{C}{a} \ln q \right).$$

When $L_t \leq N_t$ the isocline $\hat{N}_{\Delta N=0}$ of the equation $\Delta N = 0$ ($\Delta N = N_{t+1} - N_t$) is given by the right hand side of the eqn (4). When $L_t > N_t$, no isocline for the positive value of V and N exists, because $N_{t+1} > N_t$. The isoclines (Fig. 2), as well as numerical calculations, suggest that the system is stable and this was confirmed by local stability analysis. The stability is due not only to a constant inflow of food, which makes the isocline $\hat{N}_{\Delta V=0}$ a decreasing function of V , but also to the isocline $\hat{N}_{\Delta N=0}$ being an increasing function of V .

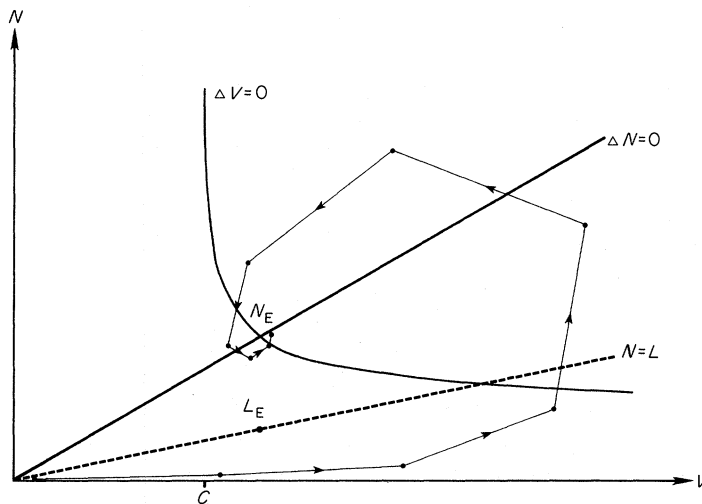


FIG. 2. An example of changes in animal N and food V densities as determined by difference equations (thin lines with arrows), presented on a phase plane with coordinates V and N . Above and on the right of the isocline $\Delta V = 0$ food density V decreases, while above and on the left of the isocline $\Delta N = 0$ animal density N decreases. The isocline $N = L$ (broken line) determines the density L of animals which reproduce at a given food density V . N_E shows the animal equilibrium density after reproduction, while L_E denotes the equilibrium density of the reproducing part of the population. The following values of parameters were used in this graph: $a = 10$, $R = 6$, $C = 1000$, $h = 1$. The initial values are $V_0 = 100$, $N_0 = 1$.

Consider a set of local habitats, i.e. parts of space where the intrinsic rate of natural increase r is positive, surrounded by a hostile environment such that the survival s of migrants moving from one local habitat to another is relatively low. With the constant inflow of food C per unit of space, each local habitat supports a stable local population, which after reproduction has an equilibrium density N_E (Fig. 2). Random causes acting with probability p per local habitat per unit of time reduce the population density from N_E

to density M , where $0 \leq M < L$. This implies that there is room for $(L - M)$ immigrants per unit of space, to enter and reproduce. Competition among immigrants can be neglected if migrant survival s is low. If a migrant which left a local habitat can, during its lifetime encounter only one other local habitat, then the probability Q_E that a migrant will succeed in leaving at least one offspring is

$$Q_E = sp. \quad (6)$$

The probability Q_s that an individual which does not emigrate will produce at least one offspring is determined by its rank: $Q_s = 1$ for ranks $x \leq L$ and $Q_s = 0$ for ranks $x > L$. Emigratory behaviour, as determined by an individual rank x in relation to the rank L is assumed to be hereditary, and therefore, in the global population containing individuals from all local populations, one can expect selection for emigratory behaviour such that animals would emigrate if their rank $x > L$ and would refrain from emigration if $x \leq L$, providing that $Q_E > 0$.

If individuals of rank $x > L$ emigrate outside the local habitats and do not take their share of food, eqn (3) has to be modified, so that

$$V'_{t+1} = V'_t + C - \int_0^{L_t} y dx.$$

After substituting eqns (1) and (2) and integrating, the above equation yields

$$V'_{t+1} = V'_t + C - \frac{R-a}{\ln q}. \quad (7)$$

If $L_t > N_t$ no emigration takes place and therefore the amount of food V in the next unit of time is given by eqn (3). It does not matter, for the dynamics of a single local population whether animals die or emigrate, therefore the dynamics of animal density are given by eqns (4) and (5).

An example of changes in animal N and food V densities, when emigration occurs, is given in Fig. 3. The isocline of equation $\Delta V' = 0$ is from eqn (7) given by

$$\hat{V}_{\Delta V' = 0} = \frac{a}{1 - e^{(R-a)/C}}$$

and is perpendicular to the V -axis, making the system even more stable than this system without emigration (Fig. 2). Note that emigration considerably increases the food density V at equilibrium. It also increases the equilibrium animal density after reproduction N_E and the equilibrium density L_E of the reproducing part of the population (Fig. 3), because the reproducing population can use food which in the absence of emigration would have been used by individuals with rank $x > L$. On the other hand N_E without emigration is higher than L_E with emigration; therefore, if no emigration occurs, the local population density will be higher, with mortality due to food shortage.

APPLICATION AND EXTENSIONS OF THE MODEL

The unit of space within which the model is considered should be large enough to represent the entire population (including all ranks) and small enough so that there is competition among animals within the unit, more precisely so that all individuals of higher rank influence the food intake of lower ranks.

The concept of rank was introduced here to make the model manageable but it does not necessarily imply social ranks or a social hierarchy. Animals can be ranked according to their weights, the sizes of their territories or other indices of their individual performance,

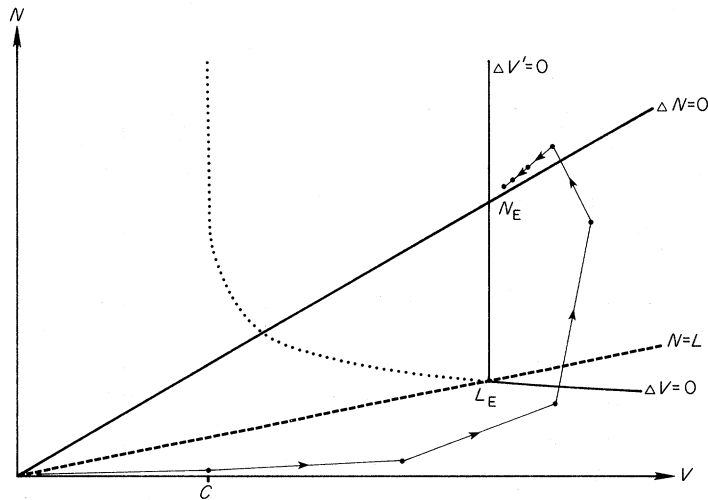


FIG. 3. The same as Fig. 2 but with emigration of all individuals of rank $x > L$. Note that the emigration changes isocline $\Delta V = 0$ into the isocline $\Delta V' = 0$, within the part of the phase plane where $N > L$.

which determine their individual food intake and the number of offspring they produce. For the evolution of emigration, well defined ranks are of importance for ranks close to L only.

It is assumed that the ranks are assigned at random in relation to the genetic basis of the emigratory behaviour. This does not exclude a possibility of a correlation between the rank of parents and the rank of their progeny. Such a correlation may be or may not be hereditary in character. If a strong selection against a genetic trait occurs in the population, one can expect the individuals with this trait to have lower ranks. In such a situation the migrating individuals can differ genetically from nonmigrating ones.

Equation (1) relating individual food intake y to rank x should not be considered as the best description of food partitioning, but as a first approximation which makes investigation into the consequences of inequality among members of a single population, possible. A more realistic description of food partitioning when an analytical solution is not required, can be based on the lognormal distribution. The particular form of the function $y(x)$ given by eqn (1) does not seem to be of great importance. An attempt was made to develop the model presented here using the function $y(x)$ given by equation $y(x) = aV/x^w$, where a and w are constants between zero and unity. This form of the function $y(x)$ assumes that: (i) there is no constant maximum food intake by an individual, (ii) individual food intake is linearly related to food density V and (iii) when food is scarce inequality among individuals does not increase. In spite of these differences, the model based on this equation exhibits the same essential properties which make the evolution of emigration possible, as the model developed from eqn (1). Equation (1) seems to conform better with empirical data and for this reason the model based on it is put forward here.

The model presented here can also be applied to populations with overlapping generations by redefining R as the maintenance cost per individual per unit of time. In such populations, ranking of individuals can be age-dependent, with young individuals having the lowest ranks and migrating as the first ones if there is no room for them. Other consequences of overlapping generations will be discussed later.

Local habitats can be of any size, as long as the size does affect the possibility of emigration outside, and the local habitats do not cover so large a proportion of the whole area, that the reduction of migrants outside the local habitats cannot occur. This is an important difference between this model and all models of group selection in which the size of the local habitats and their genetic isolation is important (Levins 1970; Gilpin 1975). No genetic isolation was assumed here and the evolution of emigration is due to individual selection only.

When studying a natural population it is often difficult to determine the boundaries between the local habitats and the hostile environment outside. In such a case the model explains the evolution of an interesting phenomenon, namely that animal population density is adjusted to its food supply but death due to hunger is rarely an agent which brings about this adjustment. If there is a reduction of food density V , this decreases L and increases the number of migrants ($N - L$). These migrants die from adverse weather conditions, predator pressure or other nonspecific agents.

The reduction of the population density from equilibrium N_E to the density M ($0 \leq M < L$) can be the result of (i) an appearance of new unpopulated local habitat, (ii) an increase in the amount of food supply or a fast return to the normal level after a temporary decrease, or (iii) a reduction of animal density due to predators, diseases or adverse weather conditions. The cases mentioned above are very common in nature and they can also occur in very stable ecosystems.

The probabilities of survival and leaving at least one offspring for nonmigrating Q_s and migrating Q_E individuals, as used in the model, are very crude measures of individual fitness. If a habitat colonized by a migrant is empty, the migrant can leave many more than one offspring, therefore its fitness should be much higher than the probability Q_E as defined by eqn (6). A much more complicated model is required to estimate this fitness, but as long as it is higher than zero the evolution of emigration is possible.

Q_s is a function of individual rank x decreasing with ranks close to rank L . To decide whether to migrate or to stay and attempt to reproduce, an individual has to perceive its own rank x in relation to the rank L . This involves estimation of (i) its own physiological and ecological status, (ii) the density of other individuals, especially those which are better fed and have a better chance of survival, (iii) the density of available food, and (iv) the possibility of exchanging rank with another individual. The inaccuracy of these estimations can be considered in terms of the variation of the real values of L around its estimated value \bar{L} . Variation of L changes the Q_s of individuals with rank close to \bar{L} ; therefore Q_s can be presented as a cumulative probability distribution of L along the x -axis. This is shown in Fig. 4, using the normal probability distribution, which demonstrate that inaccuracy of the estimation of L increases the rank number above which animals emigrate from \bar{L} to L' . Using similar arguments it is possible to determine Q_s as a function of varying maintenance cost R or food density V , since L is determined by R and V by means of eqn (2).

The mechanism of the evolution towards emigration above rank L' can be visualized as follows. Assume that the amount of food y taken by an individual during its lifetime is positively correlated with the number of food particles v it encounters per hour at an early stage of its life. According to this correlation a group of animals from all local populations which encountered v_0 particles per hour would get on the average \bar{y}_0 units of food in their lifetimes ($\bar{y}_0 < R$). If every individual in the group gets the same amount of food equal to the average \bar{y}_0 then all of them should emigrate from their local populations, because no one has a chance to leave a single offspring. If on the other hand the mean \bar{y}_0 is based on

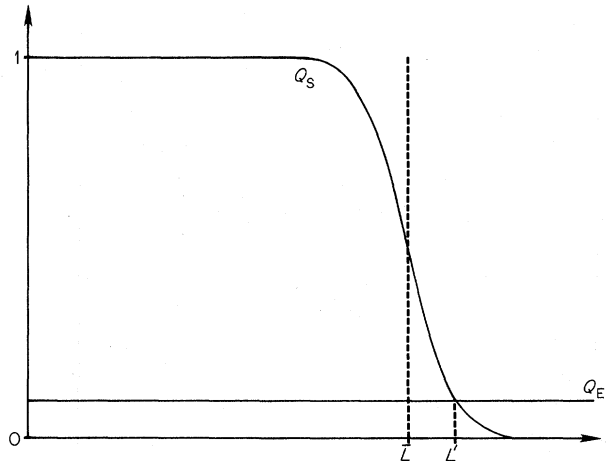


FIG. 4. Probabilities of producing at least one offspring for individuals which do not migrate Q_S and those which migrate Q_E as functions of individual rank x . If L is normally distributed random variable (standard deviation equal to 0.1 was applied in this graph), Q_S is given by cumulative distribution with mean \bar{L} . The graph shows that it is of selective advantage to emigrate above rank L' instead of L .

different values of y , such that 10% of individuals from this group get $y > R$ units of food, and if $Q_E < 0.10$, then the probability of survival of nonmigrants from this group is higher than that of migrants. This implies that, under the circumstances described above, it is of selective advantage for the individual which encounters v_0 food particles per hour to refrain from emigration. Note that the error of the prediction of y from v can be due either to the environment or to the behavioural features of the animals.

If animals emigrate above rank L' , instead of above \bar{L} , it moves the isocline $\Delta V' = 0$ (Fig. 3) to the left. In an unpredictable habitat this isocline can move leftward to the point of intersection of the isoclines $\Delta V = 0$ and $\Delta N = 0$ (Fig. 2), and then the density of animals is regulated by mortality due to a shortage of food instead of by emigration.

Emigration usually occurs at the early stages of an animal life; therefore the model assumes that migrants leave their local habitats before taking any food. If animals do take a certain amount of food before emigration, then either this food can be included in the reproductive cost of their parents or eqn (7) should be modified.

An important feature of the model is that at the equilibrium N_E there is high food density V when emigration occurs (Fig. 3) but low food density without the emigration (Fig. 2). This can help to answer an important ecological question discussed by Hairston, Smith & Slobodkin (1960), Wynne-Edwards (1962) and others, namely why do animals not deplete their food supply? When answering this question one has to take into account not only emigration but also other differences between field and laboratory populations. Animal populations in the laboratory are usually supplied with homogeneous food in high concentration, their density per space unit is high and directly regulated by food shortage, and there are many undernourished individuals which would eat any food particles left by other members of the population. Since no emigration is allowed, the best strategy for an individual is immediate survival, without taking into account whether future survival and reproduction are really possible. In the field, however, food of high quality is often dispersed and the animals are often time-limited. If an individual has a lower rank and it occupies a home range of inferior quality, if it were vacated, no

individual of higher rank would occupy it. In addition, adverse weather conditions or predator pressure do not allow the survival of low rank individuals, which in the laboratory or under human protection would be able to survive and reproduce. If food quality and quantity is low, it is better to emigrate, but if no emigration is possible, maximum utilization of all available food is the best strategy.

If the model presented here has a counterpart in nature, one can expect that a steady state population density, regulated by emigration, could be maintained in the laboratory, by removing individuals which exhibit migratory behaviour. If animals are not sufficiently different, either they should all emigrate or all of them should stay. The possibility of maintaining such 'free' populations was confirmed experimentally for *Hydra* (Lomnicki & Slobodkin 1966) and for *Tribolium* (Zyromska-Rudzka 1966). By removing floating individuals of *Hydra*, it was possible to maintain a stable population at a level several times lower than the level of a confined population with the same amount of food and space. Members of these free populations resembled individuals found in the field, in that they were well fed and budding, unlike those in the confined populations where they were starved. In the free populations after feeding, some food particles were left, while none remained in the confined ones. These results were obtained in spite of the homogeneous conditions in which the populations were kept, including random food distribution and the scrambling of the populations daily by changing the containers in which they were kept. To study other animal species in this way, it will probably be necessary to maintain more diverse and stable laboratory habitats and to use more sophisticated means of deciding which animals are migrants which should be removed.

SOME CONSEQUENCES OF OVERLAPPING GENERATIONS

Taking into account the unequal resource partitioning in populations with overlapping generations, two questions can be asked.

(1) How can overlapping generations influence the density level at which emigration from a local population occurs?

(2) Under what circumstances can one expect a reduction in births or complete absence of reproduction? Reduction in births is considered here as an absolute reduction in the number of progeny produced in a unit of time and surviving to reproductive age, not merely a reduction in the number of eggs laid.

I will consider these questions for a local population subjected to regular oscillations; they can either be brought about by innate cyclicity in the system of animals and their food supply or can be due simply to cyclic changes in food abundance. A simplified example of a local population with (i) unequal resource partitioning, (ii) overlapping generations, and (iii) cyclic oscillations in the amount of food, expressed as changes in L , is presented in Fig. 5. This example demonstrates that a reduction in number of progeny, as well as emigration of animals of rank $x < L$ are possible if two additional conditions are fulfilled: (iv) animals are able to recognize the stage of the cycle and (v) as far as reduction in births is concerned, such a reduction increases the possibility of longer survival and later reproduction. A more realistic model than that presented in Fig. 5 should also include a larger number of animals, mortality as a function of individual age, with the senile animals moved to lower ranks, number of progeny as a decreasing function of rank x , and increasing longevity with a decreasing natality. Such a realistic model would be difficult to present in a single figure, but it would not change the conclusions presented here.

To recognize the stage of the cycle, information about food density is not sufficient, and additional information about the density of other individuals is required (Fig. 5). This can explain why high population density brings about decreased reproduction in a situation where animals have enough food and there are no other physical reasons for reduced reproduction. Two hypotheses explaining the reduced reproduction at high densities can be given. The first hypothesis is that high density in the field is a signal for emigration, and if no emigration is allowed, emigratory behaviour degenerates into abnormal aggressive

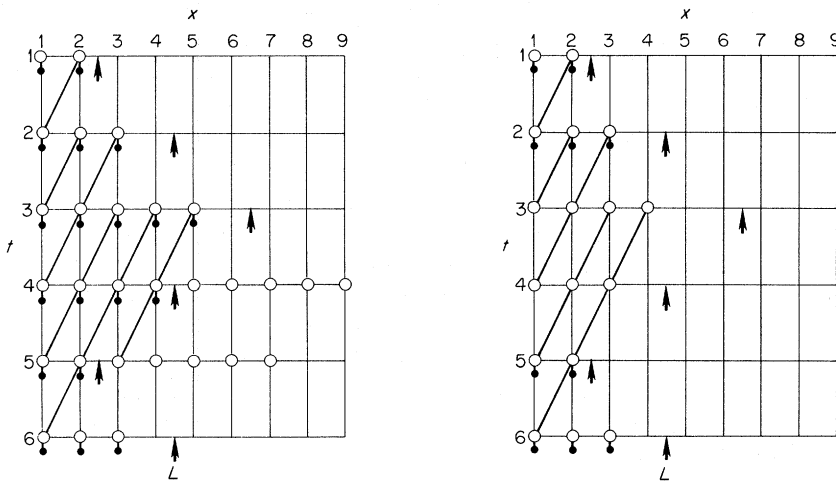


FIG. 5. Survival and reproduction of animals in a simplified local population assuming that the amount of food oscillate regularly, so that $L=2, 4, 6, 4, 2, 4, \dots$. Individuals (o) are ranked and maintain their position by changing rank $x-1$, in every unit of time. It is assumed for simplicity that in every unit of time one individual of the highest rank ($x=1$) dies and all individuals of rank $x \leq L$ reproduce giving one offspring (●) each. In the next time unit newly born individuals take the lowest rank available. Individuals of rank $x > L$ do not reproduce and do not survive the next time unit. The diagram on the left considers the case of no reduction in births and no emigration. Note that the reproduction at time $t=3$ and $t=4$ is unnecessary because progeny produced then cannot survive in the local population. An individual which at time $t=3$ has rank $x=5$ can survive until time $t=5$ only, but its progeny cannot survive. Due to low reproductive rate, rank 4 at time 2 and rank 6 at time 3 are not filled. It is of advantage for an immigrant to enter at time 2, but not at time 3.

The diagram on the right considers the same population with reduced reproduction and emigration below L level, to demonstrate that no loss of fitness within the local population occurs. For the sake of clarity possible advantages of individuals which reduce their reproduction and emigrate below the L level are not shown. Within the global population the selective advantage of an individual emigrating below the L level (the individual of rank 5 at time 3) is determined by probability Q_E of finding a better place to live and reproduce. Abstention from reproduction at time 3 and 4 depends on whether it is more advantageous to refrain from reproduction in order to reproduce later or to produce progeny which would emigrate with a possibility of finding less crowded local habitats.

behaviour which brings about decreased reproduction and increased mortality. For species without aggressive behaviour, this can be induced by abnormally high concentration of some chemical compounds, which in nature can serve to induce emigration, or by other agents which play a similar role. Here the reduced reproduction is a by-product of emigratory behaviour, resulting from an abnormal condition of the confined populations. Data on the behaviour of rodents exposed to high densities (Archer 1970) supports this first hypothesis.

The second hypothesis is that the reduced reproduction at high density is an adaptation, which can sometimes occur in the field, and which allows individuals to reproduce later when their population density is low and the conditions for leaving progeny are better. Such adaptation can evolve when migrant survival is low as compared with advantages of later reproduction which can allow the leaving of progeny in the same local habitat. Note that such reduced reproduction is of selective advantage when ranks are well defined, so that newly born individuals are in different positions than their parents (Fig. 5). If this hypothesis has a counterpart in nature one should expect increased reproduction after a population with well defined ranks has been scrambled. Petrusiewicz (1957, 1963) has studied the occurrence of population growth in confined populations of laboratory mice both spontaneous growth and that induced by altering the population social structure. The social structure was altered by changing the cages in which the populations were kept (Petrusewicz 1957) and by temporary removals and introductions of several individuals (Petrusewicz 1963); both resulted in significant increases in the occurrence of the population growth.

This raises an interesting point: an increase in population density may not always be the result of better ecological conditions (more food, fewer predators, favourable weather) but can be due to any interference which scrambles the population or obstructs the flow of information among population members concerning their density and their ranks. These can be brought about by many different agents, which may not necessarily be related to animal mortality or natality. Theoretically it is possible that any human activity such as use of chemicals, ploughing or mowing could have this effect. Reduced reproduction is of selective advantage in an environment which is more or less predictable. When an animal encounters quite new conditions, which do not ensure later improvement, it is not advantageous to refrain from reproduction, but rather to reproduce at any cost. This can be one of the reasons for population stability in natural ecosystems, as compared with man-made ecosystems.

SPATIAL HETEROGENEITY AND ANIMAL POPULATION OUTBREAKS

The explanation of population outbreaks, which seem to be more common in homogeneous and cultivated areas than in natural and diverse ones, is an old and still important task of animal ecology. Arguments developed by ecologists to explain this phenomenon are based mainly on the concept of stability of the entire ecosystem (May 1973) and relations between species diversity and stability (Pielou 1975). Using the present model the population outbreaks can be explained by properties of the single species population and its environment, without invoking the dynamics of the entire ecosystem. This makes further theoretical investigations much simpler and generates hypotheses easier to test. A similar, more detailed model, explaining population regulation in terms of the differential movements of individuals in heterogeneous environments, but without taking into account unequal resource partitioning was developed by Taylor & Taylor (1977).

In the model presented here population outbreaks are thought not to be a result of low stability of the difference equations describing changes in density of animals N and their food V , but a failure of the population's regulation by emigration, so that the equilibrium is at low food density (Fig. 2) and the population is directly regulated by starvation.

In a heterogeneous environment one can expect large differences in animal reproduction and survival at different points of the space, and these differences may allow the existence of many species, resulting in a high species diversity. From the point of view of a

single species, spatial heterogeneity can be thought of as macroheterogeneity, which divides the space into local habitats and the hostile environment outside, and microheterogeneity, which operates with a local habitat. Microheterogeneity makes the home range of an individual different from the home range of its neighbour and therefore it can promote and increase individual differences and inequality in resource partitioning. Large differences among individuals bring about well defined ranks, which in turn allow the regulation by emigration at the level L instead of higher level (Fig. 4). Macroheterogeneity makes possible the regulation of the global population by reducing the number of migrants before they reach other local habitats.

On the other hand, in a homogeneous environment ecological conditions are uniform, which is unfavourable for many species and favourable for only a few species. For these few species there is no hostile environment outside the local habitats, since the entire area forms one large local habitat. Therefore, migration does not reduce the population density, but simply moves animals to other similar places. Without the possibility of finding a less crowded place, animals try to survive and reproduce; this brings about depletion of the food supply, which eventually results in a population crash.

CONCLUSIONS

Models of population genetics are derived from the genetic properties of individuals. In a similar way, the ecological model of population exponential growth is derived from the biological properties of individuals. This seems to be a very good research strategy, since we know much more about individuals than about populations, and it should be more widely applied in ecology by deriving ecological models from physiological, behavioural and ecological properties of individuals. In contrast to this strategy, the logistic equation and models based on it are not derived from the properties of individuals but from the behaviour of the entire population; more precisely from a statistical relation between population density and per capita population growth. This relation is used in the logistic equation without taking into account its variance, so that nothing is known about the distribution of reproduction and death probabilities among population members at different densities. The assumption that all individuals are equally affected by increasing population density disagrees with empirical evidence, mentioned earlier in this paper, and leads theoretical population biology into a blind alley. Using this assumption, regulation of population density by means of emigration from optimal habitats cannot be explained by individual selection. In addition, population models with discrete regulation, which make use of the logistic assumption predict chaos for quite realistic sets of parameters (May 1976).

In order to get out from this blind alley one has to study resource partitioning among members of competing single species populations, as well as distribution of reproductive abilities and death probabilities within these populations. The present model is an attempt to show what are the consequences of unequal resource partitioning on ecological theory. Compared with the logistic equation the model is much more complicated; growth of a confined population is described by exponential increase when $N < L$, by reproduction of stronger population members and mortality of weaker ones when $N > L$, and by a possible adaptive reduction in natality as a reaction to high density. On the other hand, much field data, which describe adjustment of the population size to food supply by dispersion and other behaviourally induced phenomena (Wynne-Edwards 1962), can be explained by this model without invoking group selection. Also, data from the laboratory (Huffaker

1958) and from the field (Errington 1946) concerning predation suggest that a model of predator-prey system can be developed on the basis of the model presented here.

This model, like many other ecological models, is very general; however it generates predictions which can be easily tested in the field or in the laboratory. The model can be falsified by any of the following phenomena found in nature.

(i) Decreased variation with a decreasing mean of body size, weight, individual food intake or other indices of individual fitness, as a result of competition among population members.

(ii) Complete extinction, i.e. the death of all individuals, of a local population in the field due to depletion of resources by this population.

(iii) Higher fitness of emigrating individuals which can be determined by size, weight or other indices. This does not apply to long range seasonal migrations like those in birds but to the emigrations from the optimum habitats outside.

(iv) No increase in population density if part of an area, where animals are abundant, is enclosed for several generations, making emigration impossible.

In addition, the concept of population stability, in the sense of regulation below starvation level, and species diversity can be tested by comparing species diversity with the magnitude of spatial differences in reproduction and survival of animals of a given population.

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