POPULATION EFFECTS OF NATURAL SELECTION*

ROBERT H. MACARTHUR
Division of Biology, University of Pennsylvania,
Philadelphia, Pennsylvania

This paper has two themes. The first is that the traditional approach to population ecology, via the fluctuation and interaction of species populations, is about the hardest possible. The second is that where natural selection proceeds along an unambiguous course, it controls population processes in a simple, readily understandable, way. The remarkably precise convergence of unrelated forms whose activities are similar shows how nice is the control exercised by selection over phenotype.

The central difficulty in understanding populations as an outcome of natural selection arises from the fact that the good of the species is not always equivalent to the good of the individual genotype, and conversely. There is plenty of direct evidence that more fit genotypes replace less fit, and there is plenty of circumstantial evidence (mostly from the fossil record) that more fit species replace less fit. But the relative magnitudes of these processes and the equilibrium they reach are unknown and hence controversial. Only when what is good for the species coincides with what is good for the genotype is it easy to understand the population effects of natural selection. In what follows a collection of examples is presented, in no particular order, and with no pretense of reviewing the literature. The very nature of the predictions made requires that we consider fairly orderly populations. It seems much harder to make interesting predictions about the more erratic populations which are more appropriately treated by the methods of Andrewartha and Birch (1954). See also Birch (1960).

SEX RATIO

One of the most impressive examples of an understanding reached by applying knowledge of natural selection is Fisher's (1958) theory of sex ratio, proposed in 1930 and further discussed by Kolman (1960) and Bodmer and Edwards (1960). When every individual has a parent of each sex, the group of all males must contribute (except for sex chromosomes) the same as the group of all females to the genetic ancestry of future generations. Then, other things being equal, whichever sex is present in short supply has greater value per individual and hence is favored by natural selection. This accounts for an approximately equal frequency of males and females. More

generally, males and females are not always equally easy to rear, and, to achieve the greatest fitness parents should have a biased sex ratio. Finally, an X-chromosome trait which results in excess production of females will be represented in more of the next generation than will its allele, so that the theory doesn't apply to sex-linked genes. However, any autosomal gene suppressing such a trait will, of course, be favored so that, because of the large number of autosomes, sex ratio determination may tend to become autosomal, leaving the first theory correct.

BIRTH RATE, DEATH RATE, AND GEOGRAPHIC DISTRIBUTION

Lack (1957) has suggested that birth rate is adjusted to the largest value the parents can successfully rear to reproducing age. When there is no parental care, the limits are set by the total volume of eggs the female can lay, but their size and number may be adjusted (Hutchinson, 1951). Slobodkin and Richman (1956) have listed some reasonable exceptions which don't, however, affect the validity of the argument. This leaves largely unexplained the puzzling correlation between clutch size and the magnitude of inevitable hazards to which a bird is subject. Lack (1949) suggests that birds generally lay larger clutches in high latitudes not because mortality is greater there, but because high latitude food and day length make possible larger clutches. Without rejecting this argument, a different viewpoint gives considerable extra insight. Consider, instead, the natural selection of a species' distribution. Briefly, a species will only settle where its birth rate exceeds its inevitable mortality. And if, due to severe climate and the hazards of longer migration, mortality is always greater at high latitudes, then so must clutch size be higher, or the species won't live there. More precisely, birth rate and death rate are both functions of latitude (say) and population density. The species will, by natural selection, choose that geographic distribution for which zero-density birth rate exceeds zero-density death rate and then at each such place will increase in population density until the births and deaths balance. (A zero-density birth rate is, of course, the limit of the birth rate as population density approaches zero.) This argument does not necessarily predict an ever increasing birth rate as we proceed to higher latitudes. But it does make this a likely tendency and also explains the high clutch sizes observed on mountains (Johnston, 1954). There is virtually no direct evidence bearing on this theory. A corollary for which there is supporting evidence (Mayr, 1946; MacArthur, 1959) is that migrants will settle in greatest density in places where the summer increase in food supply is greatest.

"CONVEX" ACTIVITIES

Consider an adaptation which caused a bird to feed only on one of the suitable kinds of tree in a forest. Then during the daily rounds of food gathering the bird would be passing through many trees in which it could not feed. Or, consider an adaptation which predisposed a bird to feed on only one kind of insect in a habitat in which many other kinds of insect of simi-
lar form and palatability were present. Then, during its daily rounds, the bird would encounter many potential food items which it could not exploit. In both of these examples, the bird is making inefficient use of its resources and wasting energy. Contrast with these a bird adapted for eating all palatable insects encountered in all kinds of trees, specialization occurring in the feeding height. Such a bird would move through the forest at the proper height, feeding more or less continuously, and normally would be more fit.

Such efficient activities may be called "convex" in the sense that, given any two activities for which the species is adapted, the species is also adapted for intermediate activities. (There is a mathematical theory of convex bodies, which is appropriate.) Feeding sites may fail to be convex (as in the first example) and the nature of acceptable food may be (as in the second example). It seems that natural selection would always favor convex foods and would normally favor convex feeding sites. Only when the advantage due to specialization to a patchy food source outweighs the disadvantage caused by the wasted activity will food sites fail to be convex. Fruit eating birds such as parrots are an obvious example. Notice that while specialization of a bird to a single tree species may not be convex, specialization of a small organism like an insect is much more likely to be. For, while a bird daily forages in many trees, a caterpillar may do all its feeding on one branch. No systematic evidence seems to have been gathered on this subject.

DIVERSITY OF SPECIES

When adjacent habitats support different numbers of species, the reason is presumably that one in some way will support more than the other, for otherwise natural selection would favor a redistribution. Why would one habitat offer greater opportunity than a second? This is best understood as follows: A single herbivore feeding on all the kinds of plant food or a single carnivore eating all the herbivores would have to be a "jack-of-all-trades," and, presumably, for this reason a "master of none." Thus an incoming, specialized species would find what is often called an "unoccupied niche" (although it is hard to see what was unoccupied) and would persist in that habitat. Further species would continue to enter as long as the increased efficiency due to specialization was not outweighed by loss of efficiency because of the non-convex activities resulting from many species. There is no evidence on whether this limit has ever been reached, but in any case, adjacent occupant's habitats should, on the average, show about equal degrees of specialization. Bearing this in mind, the number of species occupying a habitat should be proportional to some measure of the diversity of the habitat and, from what was said about convex activities, we might expect bird species diversity at a given latitude to be controlled not by plant species diversity but instead by some structural diversity of the habitat. This appears correct [MacArthur and MacArthur (in press), where it is shown that the vegetation profile of a habitat, and not the number of plant species, controls bird species diversity].
THE DIFFICULTY OF UNDERSTANDING SPECIES INTERACTIONS

A predator which "harvests" its prey so as to achieve the largest possible continued yield must prudently avoid overeating and thus reducing the prey population to such a low level that it can no longer produce at a large rate. A population composed of such predators would face a more certain future than one which dangerously reduces its food level. On the other hand, a genotype which enabled its bearer to exploit food supplies to a scarcer level would outcompete others and hence be more fit (at least in times of food shortage). Who can say, then, whether or not natural selection will normally lead to prudent harvesting of food? At least the concentration of prudent eaters must be always on the decrease and chance processes may be required for selection for prudence. But without knowledge about this it is difficult to make predictions bearing on predator-prey or competition interactions. And "limiting factors" are equally intractable. In fact the evidence suggests that nearly all factors are often "limiting" since they interact.

It is worth mentioning that there is no ambiguity about one aspect of predator behavior. For if a predator depends upon fluctuating food supplies it will surely be better off to switch its attentions to whichever food is the most available. If several food species alternate being most available, then specialization to feed on one or the other would often be harmful. Thus while prey often have one principal predator to specialize on escaping, the predators usually cannot specialize on hunting that prey.

DISCUSSION AND CONCLUSIONS

There are innumerable other questions on which this approach could be used with profit. But these are sufficient to suggest the following way of looking at ecological problems: There seems to be good evidence, for birds at least, that the combined density of individuals of all species is controlled by the amount of food available. For instance, Crowell (1961) has found that the few Bermuda species have as many combined individuals as the many mainland species, each Bermuda one occupying a wider variety of habitats (but not a wider variety of feeding activities) than that species does on the mainland where additional species are present. Now, as indicated in the last paragraph there is evidence on the number of species the habitat will support. The mean abundance of the species is then quite predictable—the total density divided by the number of species. And when adequate theories of relative abundance become available [a start has been provided, see MacArthur (1960), Hairston (1959)] then a fairly complete understanding of the equilibrium abundances of stable populations such as birds will be achieved.

LITERATURE CITED


Lack, D., 1949, Comments on Mr. Skutch’s paper on clutch size. Ibis 91: 455-458.


