

coolest location, especially as the cage is often cleaned with water and is damp. It did not take our pet long to locate this cool spot.

A summer trip to a new home in the mountains brought strange experiences for our bird. At first robins, jays and chickadees which scolded about his cage seemed to bother and worry him considerably. When I went to the cage to see what all the fuss was about, I found the bird nervous and trembling. However, in a day or so he adjusted himself to the new environment, and the strange birds with their new notes failed to worry him any more. He simply sat and intently watched them. Apparently tiring of looking, he would yawn and then stretch his wings out at full length; then grasping his perch tightly he would furiously flap his wings for several moments. Nevertheless he was probably again wishing that he could escape, if only for long enough to make one quick stab at his tormentors.

In taming this wildest of desert birds our experiences as a whole have been exceedingly satisfactory. We have learned much about the life habits of this comparatively rare species, that would have been almost impossible to learn in any other way. And while I watch our bird in his cage, intently gazing at the great out-of-doors, and think that perhaps I should give him his freedom, I stop to wonder if he is not better off where he is. For I remember the fate of three young falcons that we came to know and banded a few years ago. Within a few weeks all had been reported as shot. Probably my falcon is better off as he is. Either way the life of these royal birds is not just all that we wish it could be.

*Claremont, California, April 9, 1934.*

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## OVER-POPULATIONS AND PREDATION: A RESEARCH FIELD OF SINGULAR PROMISE

By PAUL L. ERRINGTON

Recent publication (Errington, *Ecology*, 15, 1934, pp. 110-127) has been made of evidence supporting a modification of the broad principle advanced by McAtee (*Smithsonian Misc. Coll.*, 85, 1932, p. 141) that "predation tends to be in proportion to population" and later restated by him to conclude "... the proportion, however, rising and falling progressively with the increase or decrease in numbers of the available food organisms" (*Proc. Roy. Ent. Soc. London*, 81, 1933, pp. 113-126). McAtee's emphasis upon availability of prey being the chief factor governing the food habits of predatory species has been particularly substantiated by our ecological studies on bob-white (*Colinus virginianus*) in the north-central United States.

McAtee, summarizing the results of a tremendous amount of research (80,000 bird stomach examinations) in a short statement, neither intended nor attempted to discuss in full detail the food habits of, or the effects of predation on, any individual species. From the standpoint of a concise generalization pertaining to predators and prey as a whole, McAtee's principle of proportional predation may be about as close to the truth as we are capable of approaching.

Fundamental as this may be, we need further amplification of predator and prey relationships to give a clearer insight into the mechanics of predation. Its exceptions, its modifications, its pertinent corollaries, within the limits of our know-

ledge and our capacities for investigation, are in need of a great deal more scientific sorting and digestion than they have thus far received. In the case of the bob-white, availability as prey to predatory species is not necessarily in proportion to population, an inevitable conclusion to be drawn from existent field data (Errington, *Trans. Wis. Acad. Sci. Arts Letters*, 28, 1933, pp. 1-35). We have, for bob-white, recorded winter survivals of strong populations with very little loss from natural enemies.

Material or heavy predation upon vigorous adult winter bob-whites appeared largely confined to that proportion of the population which was in excess of the capacity of the environment properly to accommodate. Aside from those that may have been weak, injured, or individually handicapped from some similar cause, the birds that bore the brunt of predation were the ones situated in inferior or overcrowded habitats and hence dangerously exposed to attack by reason of their insecurity of position.

Incidental or accidental predation (distinguished from "material" predation) attending well-situated populations, as measured to date, has been so low (rarely greater than 6% per 90 days) that it probably has not greatly exceeded what would have been the natural winter mortality from age alone had there been no predators.

So far as we have been able to ascertain, the apparent definiteness of maximum winter carrying capacity of a given environment for bob-white is governed by the quality and distribution of food and cover and by the intolerance of the bob-white, as a species, toward overcrowding. As populations ascend past the maximum carrying capacity of the land, they become vulnerable to predation in proportion to their *surplus*, seemingly irrespective of kinds and numbers of predators ordinarily present.

We have fragmentary evidence that this type of population vulnerability—or population security, if one wishes to think of it in that light—applies to species other than bob-white under winter conditions. Indeed, it conceivably may apply to many species showing territorial intolerance as non-breeding adults. (Territorial intolerance in the breeding season should probably not be considered in connection with the present discussion because of the variables introduced by mating behavior.)

Perhaps many species not showing any conspicuous territorial intolerance may have population levels at which they are no longer materially vulnerable to predation, or, in other words, are rendered unavailable to predators by virtue of their security of position. I would suspect that any one of numerous species may have a virtually ineradicable residuum which would not have to be a small residuum. We have records of bob-white populations as substantial as a bird per four acres—about the highest density that we have been able to census with desired accuracy—being so well situated as winter adults as to be practically untouchable by natural enemies, including those known to be of formidable types.

From this it may be justifiable to suggest that McAtee's principle might be more truly applicable to *overpopulations* rather than simply to populations as they may occur in nature. But then the question may arise if the greater part of most distinctly mobile populations (or those capable of movement into better grades of habitats) may not in actuality be more or less overpopulations for their particular environmental niches, except probably for species that have been reduced to low densities on account of exploitation or persecution by man, or on account of epizootics, storms or other drastic though possibly temporary or unusual emergencies.

Apart from populations consisting mainly of immature animals which exhibit varying degrees of helplessness, I think that conspicuous invertebrate populations especially, and populations of the more prolific vertebrates, may often be essentially over-populations. In the latter event it may not make a great deal of difference

whether one may say that predation is in proportion to population or to overpopulation.

It may make vastly more difference which is the case, however, in the true evaluation of the role of predation in the life history of a given prey species. If the prey species is of exceptional esthetic, scientific or economic consequence, the problem of either management or control could very well be simplified by a better understanding of the extent to which the pressure of its natural enemies may be significant or only incidental or immaterial.

Here is a research field barely scratched and a field of almost endless potentialities. It is a field to demand the utmost in investigational background, ecological technique, ingenuity, and interpretation. Its difficulties constitute a challenge, as does its basic importance to a balanced human society.

What do we know about what *actual* effect predation may have upon animal populations? What is the *actual* effect of increase or reduction in numbers of given predatory species, from the standpoint of animal populations? The obvious trend of modern ecological data is toward the conclusion that predation does not play nearly the part in determining population levels of wild species as was thought a comparatively few years ago.

The productivity of the Scottish grouse moors under intensive management is well known; and well known also is the stringent suppression of predators practiced in connection with management there. To predator control is attributed much of the productivity, but logical questions may be asked as to how much may be due to the constant persecution of predators and how much to the raising or maintaining of the general habitability of the environment so far as concerns food and cover, or how much may be due to something else, perhaps to something totally unrelated to conscious management.

It is safe to say that we know next to nothing about the effects of predation upon population in the overwhelming majority of instances to which has been paid any critical attention at all. Scientifically acceptable facts on this subject are rare, and rarer still are those from which have been extracted more than their most superficial meaning. It is not necessarily true that A would be abundant if B were scarce, simply because B preys upon A.

The all inclusive "anti-vermin" complex of some sportsmen, with its extravagances and its dogmas, is but one manifestation of our lack of knowledge, whatever else it may be in analysis. The perennial controversies among scientists themselves point to a continued need of studying predation both from the standpoints of predator and of prey; if possible, simultaneously and in the same areas and under conditions favoring the acquisition of salient ecological data.

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