Vol. 100, No. 912 The American Naturalist May–June, 1966

"COMMUNITY STRUCTURE, POPULATION CONTROL, AND COMPETITION"—A CRITIQUE

WILLIAM W. MURDOCH*

Department of Zoology, University of Michigan, Ann Arbor

In attempting to formulate general theories of population control, ecologists are faced with the problem that every population is, in some sense, unique. Nevertheless, one persists in the attempt to arrive at general statements about a given class of phenomena by distinguishing these features which are common to different populations. The bulk of the present paper is an analysis of a publication by Hairston, Smith, and Slobodkin (1960) which is an interesting attempt to produce such a set of generalizations about broad groups of organisms, and as such is a rare event in ecology. The authors' conclusions, if valid, would be of great significance, and there is evidence in the literature (Hairston, 1964; Hazen [Introduction], 1964; Kormondy, 1965; Mayr, 1963) and in the absence of published contrary opinion, of their being accepted uncritically. At this point, therefore, it seems worthwhile recording some reasons for suspecting that this attempt at generality, though ingenious, is mistaken. In addition, if my interpretation is correct, problems of methodology are raised which are not obvious at first sight, and for this reason it is important to present criticism of this aspect of the paper under discussion.

It will be assumed that the reader is familiar with the contents of Hairston et al. The structure of that paper is as follows: (1) several observations are stated and (2) by a series of logical steps (3) certain conclusions are reached about how the abundance of organisms in nature is determined, in particular that "populations in different trophic levels are expected to differ in their methods of control." The conclusions concern producer, decomposer, herbivore and carnivore (predators and parasites) trophic levels, and, though some of the following criticisms apply to all groups, for brevity mainly herbivores and carnivores will be discussed here. The authors' arguments concerning these two groups may be summarized as follows: (1) Depletion of green plants by herbivores is rare. (2) Rare instances of depletion do occur when herbivores are naturally or artificially protected from their predators (Kaibab deer, spraying of forest insects). From these two observations it is concluded that "the usual condition is for populations of herbivores not to be limited by their food supply." (3) Herbivores are not limited by the weather. This point is supported by observations and arguments which are not the concern of the present paper. (4) It follows that since herbivores are neither food limited nor weather limited, "the remaining general method of herbivore control is predation."

---

*Present address: Department of Biological Sciences, University of California, Santa Barbara, California.

(5) Finally, "predators and parasites, in controlling the populations of herbivores, must thereby limit their own resources and as a group they must be food limited."

It is important to discuss the frame of reference of the criticisms before proceeding. Hairston et al. note certain observations about natural communities and argue that, given the truth of these observations, certain conclusions follow. The basic observations are that organic matter accumulates at a negligible rate and that vegetation is not seriously depleted by herbivores or climatic catastrophies. Appropriately they point out exceptions to these conditions, such as successional stages, and it must be noted that, since the basic conditions are not fulfilled there, the arguments based on them are unlikely to hold; therefore, it cannot with reason be expected that the conclusions will hold. It is possible that some climax terrestrial systems (which is what the authors are concerned with) exist where one or other of the original observations do not hold, for example organic matter may accumulate. However, I agree with the authors that such situations probably are rare and that their observations seem to be true for most climax terrestrial systems. These then are the "usual conditions" described by the authors and these are accepted for the rest of this paper. We are interested in the authors' conclusions that under "usual conditions" organisms in different trophic levels are limited in different ways. It should be noted, therefore, that the finding of a climax terrestrial community in which one of the observations does not hold would cast no doubt on the hypotheses concerning the usual condition of limitation, though it disproves a different generalization, (which the authors did not make explicitly) namely that the original observations hold universally in climax terrestrial systems. To state the position more succinctly, one of the observations from which the authors derive their ideas is that, in general, the world is green (to use Dr. Slobodkin's apt phrase); this is *not* the hypothesis. The hypothesis seeks to explain how the world remains green, and the existence of "non-green" situations does not test this hypothesis.

Finally, this critique does not seek to disprove the conclusions of the original paper. Thus it seems likely that many populations of herbivores are limited by predation, that many populations of producers, carnivores, and decomposers may be resource limited, and there is evidence from specific studies that competition may occur commonly in nature. The critique does seek to show that the conclusions do not follow irrevocably from the observations, that such conclusions cannot be arrived at deductively in any case, and that these conclusions, viewed as hypotheses, cannot be tested in their present form. Finally, the paper tries to suggest some ways in which the ideas might be modified to a testable form.

The original paper is essentially deductive, and one can attempt to criticize in three ways any hypothesis arrived at deductively by examining: (1) the material truth of the premises, (2) the formal structure and internal consistency of the argument, and (3) by challenging the conclusions on the basis of methodology. The following critique will include these kinds of criticisms, in order, though no attempt is made to make the critique exhaustive.

Two major premises or assumptions of the paper are disputed. The first is that we can conclude that herbivores are not food limited because green plants are not eaten out, and there are two reasons for rejecting it. (a) The first reason is that all of the green plant material may not be edible to the species present in a given area. In rejection of this idea it has been suggested that no part of the vegetation will be inedible to all the herbivores present; however the work of Painter (1951) and that summarized by Beck (1965) indicates that there is continual evolution of plants to avoid being eaten, just as there is evolution of the herbivores. In addition the above suggestion involves use of an assumption (that in any area over an appropriate span of time there are herbivores capable of getting at and eating all the vegetation) to support the theoretical proposition that herbivores are not food limited. (b) It is suggested that the first-mentioned premise can be rejected also because it ignores the possibility that organisms may be food limited without depleting their food supply. This point will be elaborated below.

The second premise to be disputed is not explicitly stated in the paper. It is that there are only three ways in which the numbers of animals (particularly herbivores) can be limited: i.e., by food depletion, by weather, and by predation, the argument being that if two of these are not responsible for limitation the third must be. However, this classification of modes of limitation is not exhaustive, and other possibilities do remain. They include limitation by (1) resources other than food supply, e.g., nesting or oviposition sites, or "space"; (2) self-regulatory systems of the type postulated by Chitty (1960), Wellington (1960) and others; and (3) kinds of food limitation not considered in the paper, e.g., relative shortage of food (Andrewartha and Birch, 1954), insufficient supply of the right kind of food (Dixon, 1963; Eisenberg, 1965). Well illustrated examples of these types of limitation are difficult to find, and the works quoted here generally are interpretations of situations rather than experimental demonstrations (as Drs. Hairston and Smith have pointed out). However, adequate experimental demonstrations of *any* kind of limitation, especially in climax terrestrial systems, are exceedingly rare. In any case it should be noted that since the argument in the 1960 paper is mostly a logical structure, there is no onus on the critic to show that many or most, or even some, herbivores are in fact limited in these ways; it is sufficient to point out the existence of such possibilities.

The question of food limitation mentioned here raises the general point that we cannot determine if some kind of limitation is occurring merely by making simple observations of the kind "green plants are abundant." Any causal relation between the density of a population and its food supply may be rather complex and not discernible from superficial observation (Murdoch, 1966; Huffaker, 1965), and it seems likely that food limitation cannot be demonstrated adequately without some kind of experimentation.

A final point needs to be made regarding these two premises. The conclusion that herbivores are not food limited because they do not deplete the vegetation clearly could apply only to those herbivore species in a given area which are capable of depleting the green matter; it says nothing of the many other herbivores which do not have this capacity. These include the pollen, nectar, seed and fruit eaters, and some of the plant sucking species, gall-formers, etc., and probably some populations which feed directly on the green parts. That is, this conclusion does not apply to the herbivores as a whole trophic level (if there is such a thing) but applies only to a segment of the herbivores. A consequence of this is that, unless predators "as a group" feed exclusively on this segment of herbivores (which is untrue), then step (5) of the argument on page 220 does not necessarily follow. That is, predators "as a group" need not be food limited.

The formal structure and internal consistency of the argument in Hairston et al. are also open to criticism. First, food limitation appears to have been used in different ways with reference to herbivores and to carnivores. Thus it was concluded that herbivores are not food limited because the green plants are not depleted, but by analogous logic it can be concluded that carnivores are not food limited since herbivores apparently are seldom eaten out by their predators. This conclusion is exactly contrary to one of the major conclusions in Hairston et al. Secondly, it is not clear from the paper if the conclusions apply to populations or to trophic levels. This is a crucial aspect of the paper, and will be discussed in the next section.

Finally, we can challenge the conclusions on methodological grounds. The paper, by its deductive nature, can state only a hypothesis, not a conclusion; it cannot state laws, but only suggest possible explanations. It is suggested here that, in its present form, the hypothesis formulated should be rejected for the following reason. A widely accepted criterion of a scientific hypothesis is its *falsifiability* (Popper, 1957; 1961); unless it is possible in principle to test an idea, i.e., make some observation or experiment which could conceivably *disprove* it, it must be rejected or restated. Thus the truth or falsity of a hypothesis cannot be inferred in any way from its material origin. That is, *conclusions* of the paper cannot be accepted on the basis of the premises, logic, and internal consistency alone, even if these are all sound, since the premises cannot be exhaustive in the absence of a complete knowledge of the natural world.

We must ask of the paper, then, what predictions it makes or leads to, and can we subject these predictions to test by observation or experiment? Three kinds of studies have to be considered as possible tests: studies on (1) single populations, (2) groups of populations, or (3) trophic levels, and I will deal with these in sequence. First, it has been pointed out by Hairston (1964) that the idea cannot be tested with reference to single instances of population control, that is, single contrary instances do not refute the idea. Thus it is agreed that the first type of test is unacceptable. Secondly, there is the suggestion that the conclusions are true of herbivores, carnivores, etc. in general. For example, the authors make the following statements: "The remaining general method of herbivore control is...," "although rigorous proof that herbivores are generally controlled by preda- is lacking...," "the usual condition is for populations of herbivores not to be limited by their food supply," and "demonstrate a pattern of population control in many communities...." How do we establish such a general pattern or trend? Does this require that, say, 75% or 80% of all herbivores, or of all herbivore species, are predator limited; or conversely, how many contrary instances are necessary to refute the hypothesis? Clearly the idea as stated in the paper provides no criteria for judging it in this way, and the second kind of test also is not appropriate. This second type of test also includes studies of groups of populations smaller than trophic levels, for example the dominant producers or those herbivores capable of depleting the vegetation. But such tests concern hypotheses about the group defined, and are not tests of ideas about a trophic level.

Finally we are left with the possibility of testing if the conclusions hold for trophic levels "as a whole" and this requires an examination of the nature of trophic levels. Unlike populations, trophic levels are ill-defined and have no distinguishable lateral limits; in addition tens of thousands of insect species, for example, live in more than one trophic level either simultaneously or at different stages of their life histories. Thus trophic levels exist only as abstractions, and unlike populations they have no empirically measurable properties or parameters. In fact, organisms exist in populations and it is doubtful that nature is organized around the trophic level with regard to the processes involved in the limitation numbers. To test a hypothesis about a trophic level "as a whole," and not about a subset of it such as the dominant species, one must be able to identify the unit or some of its measurable attributes. Thus the last type of test is also inappropriate since the trophic level does not exist as an observable or experimental unit over the time span necessary for studying the limitation of numbers. It is suggested then that the idea, while it may serve as a basis for interesting polemic or as a stimulus to more rigorous formulations along these lines, is not amenable to testing and should be rejected as a useful hypothesis, at least in its present form.

This last section of the argument is treated in detail as it is a fundamental area of disagreement. I suggest that unless "as a whole" means all populations in a given group or populations "in general" in that group, then the statements are untestable, and tests of types (1) and (2), outlined above, are irrelevant to such statements. Just as contrary evidence from a subset of a trophic level is insufficient to reject a hypothesis about the trophic level, so confirmatory evidence from a subset cannot constitute a check or test of the hypothesis. Perhaps an example will best illustrate this point. The original paper points out that, in climax terrestrial communities, organic debris does not accumulate as fossil fuel. It states further that although some decomposer populations may be limited below their food supply by, for example, predation or behavioral or physiological mechanisms, other populations must eat up the "left-over" food. It is concluded that the "group as a whole remains food limited." I suggest on the contrary, that, given appropriate experimental evidence, we could conclude only that those "other" populations were food limited, that the remainder were limited in some other way, and that no meaningful hypothesis could be reached about the method of limitation of the organisms in the group "as a whole."

Some general methodological implications

The remainder of this paper is not a critique of Hairston et al., but is a presentation of some ideas which arose from the critique and its implications.

The particular instance of the non-testable idea which has been criticized here (if it is such an instance) is not unique in ecology, and such ideas seem to arise from attempts to reach statements about a broad range of undefined phenomena before statements about recognizable classes of events are achieved. Some ways in which a modification of the idea in Hairston et al. could be made testable have implications for much of theoretical ecology. Several steps are necessary. First, *operational* definitions of food limitation, predator limitation, and weather limitation are necessary. That is, those observations or experimental outcomes which will be accepted as necessary and sufficient evidence of each mode of limitation must be outlined before the observations and experiments are done. For example, food limitation might be demonstrated by a decrease in reproductive rate, an increase in mortality due to malnutrition, and a sustained increase in density following directly from artificial increase of the food supply. Secondly, the unit of study must be defined. It might be, for example, a single population or a group of populations of a recognizable type, etc. Finally, some criterion for rejection of the hypothesis must be presented. For example, to test the statements about a general method of control in Hairston et al., if 25% of the species in the group were not limited in the postulated manner then the hypothesis could be rejected.

Finally, a problem which has become apparent in the present paper must be discussed, for it is present in several areas of theoretical ecology. It is the problem of definition, and it is more than a mere semantic one. Together with the idea of testability, the *kind* of definition used is central to a rigorous approach in ecology; and the failings of ecologists in these two areas have led directly to the present non-rigorous state of some areas of the discipline. That the experimental approach is important in empirical ecology has come to be accepted; but also theories in ecology must have implicit in them their experimental test, and this is not generally true at present. The rather notorious semantic arguments in ecology about definitions have arisen from this deficiency, as has the situation where a large part of the "checking" of ideas, and much theoretical controversy evolve around *a posteriori* analysis of data. Such data usually are open to varying interpretations which cannot be resolved partly because, of course, the authors cannot agree on definitions, and partly because the data are analyzed *a posteriori* and were not collected in such a way as to test rigorously any particular *a priori* hypothesis. The worst kind of definition in this respect is one which refers only to some concept or abstraction from reality, since this kind is particularly susceptible to diverse interpretation in the face of real data.

The resolution of theoretical problems can come only by recourse to crucial experiments or observations designed to test rigorously stated hypotheses. Ecological hypotheses will be testable (i.e., disprovable) in this way only when the definitions incorporated in them are operational definitions.

SUMMARY

The paper by Hairston et al. (1960) is examined critically with regard to its premises, logic and internal consistency, and its methodology. It is suggested that, either as conclusions or hypotheses, the major points made in the paper are not acceptable. In the present paper the importance of testability and of operational definitions in ecological hypotheses are stressed.

ACKNOWLEDGMENTS

I am grateful to the staff and graduate students in the University of Michigan Ecology group for helpful discussions, and most particularly to Professors Hairston, Smith, and Slobodkin, who, although not in agreement with them, showed great patience and tolerance in listening to my arguments. Dr. Charles Krebs kindly read and criticized the manuscript, and Dr. Joseph Connell provided valuable discussion.

LITERATURE CITED

Andrewartha, H. G., and L. C. Birch. 1954. The distribution and abundance of animals. Univ. Chicago Press, Chicago. 782 p.

Beck, S. D. 1965. Resistance of plants to insects. Ann. Rev. Entomol. 10:207–232.

Chitty, D. H. 1960. Population processes in the vole and their relevance to general theory. Can. J. Zool. 38:99–113.

Dixon, A. F. G. 1963. Reproductive activity of the sycamore aphid, *Drepanosiphum platanoides* (Schr.) (Hemiptera, Aphididae). J. Anim. Ecol. 32:33–48.

Eisenberg, R. M. 1965. The regulation of density in a natural population of the pond snail, *Lymnaea elodes*. Ph.D. Thesis, Univ. Michigan.

Hairston, N. G. 1964. Studies on the organization of animal communities. J. Anim. Ecol. 33 (Suppl.):227–239.

Hairston, N. G., F. E. Smith, and L. B. Slobodkin. 1960. Community structure, population control, and competition. Amer. Natur. 94:421–425.

Hazen, W. E. 1964. Readings in population and community ecology. Saunders, Philadelphia. 388 p.

Huffaker, C. B. 1965. Population levels regulated by competition for food under different conditioning aspects of dispersion and density-unrelated stress. Bull. Ecol. Soc. Amer. 46:42.

Kormondy, E. J. 1965. Readings in ecology. Prentice Hall Inc., New Jersey. 219 p.

Mayr, E. 1963. Animal species and evolution. Belknap, Cambridge. 797 p.

Murdoch, W. W. 1966. Aspects of the population dynamics of some marsh Carabidae. J. Anim. Ecol. (In press).

Painter, R. H. 1951. Insect resistance in crop plants. Macmillan, New York.

Popper, K. R. 1957. Science, a personal report. *In* C. A. Mace [ed.], British Philosophy in the mid-century. Humanities Press, New York.

———. 1961. The logic of scientific discovery. Science Editions Inc., New York. (A translation of Logik der Forschung, 1935.)

Wellington, W. G. 1960. Qualitative changes in natural populations during changes in abundance. Can. J. Zool. 38:289–314.

A REPLY TO DR. MURDOCH

We wish to thank the editors of *The American Naturalist* for inviting us to reply to Dr. Murdoch's paper. In spite of an extensive exchange of views with him, we remain in complete disagreement. We could, of course, present counter arguments, but we feel that little purpose would be served by our doing so. Readers who found the original paper convincing will find it easy to refute Dr. Murdoch's assertions for themselves; those who disagreed with us initially will doubtless continue to disagree, regardless of any arguments that we might present. It is clear that observation and experimentation, rather than argument, will eventually resolve the question.

NELSON G. HAIRSTON, DEPARTMENT OF ZOOLOGY
FREDERICK E. SMITH, DEPARTMENT OF WILDLIFE AND FISHERIES
THE UNIVERSITY OF MICHIGAN