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SCIENCE AND THE PRACTICE OF WILDLIFE MANAGEMENT

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Abstract: This essay explains the need for wildlife management as scientific experiments to achieve reliable knowledge (Romesburg 1981) and emphasizes that science and management are not alternative processes. I explain the rationale behind the scientific method, the construction of hypotheses and their predictions, and how to test them with manipulations available through the management of wildlife. The scale of wildlife management programs makes them suitable for scientific experimentation (Macnab 1983). Problems such as population regulation and predator-prey interactions are used to show that theory is needed to develop proper predictions.

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“Nothing is so like as eggs; yet no one, on account of this appearing similarity, expects the same taste and relish in all of them.”

David Hume (1758). *An Enquiry concerning Human Understanding*.

There is a perception among many in agencies who deal with the day to day practice of wildlife management at the local level that scientific research is an activity separate from that of management. I suggest, however, that research and management are really the same thing. Management without application of the scientific approach inevitably leads to mismanagement, and I illustrate this with examples that address some of the major problems in wildlife management. Wildlife research also suffers from the absence of the scientific method (Romesburg 1981).

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SCIENTIFIC STATEMENTS

A scientific statement is one which can be tested and disproved. If it cannot potentially be disproved than that statement falls into the realm of religious belief. Such beliefs have no place in a scientific decision-making process for management, because they involve value judgments, subjectivity, bias, and dogma.

A good example of an untestable statement (i.e., belief) is Gause's Principle of Competitive Exclusion (Gause 1934), which is variously stated along the lines of "no two species can live in the same niche, and if they attempt to do so one will exclude the other through competition."

The problem here is that whatever outcome is observed can be taken to support the principle: either exclusion is observed (a predicted outcome) or coexistence occurs which can always be attributed to some difference in niche—also predicted by the principle. The true test of Gause's Principle is to show that 2 niches are identical, but therein lies the problem: one can never show that 2 things are identical because one is always open to the criticism that some other factor has been overlooked which makes the niches different. This difficulty was neatly illustrated, if unintentionally, by Gause himself. A putative disproof of the principle was published by Ayala (1969, 1970) who kept 2 species of *Drosophila* in coexistence in bottles for a long period. Gause (1970) countered that there were, most likely, 2 different habitats in that situation and, therefore, 2 niches—the principle remained extant. In short we cannot think of a disproof of the principle and, therefore, it is not a scientific statement, and not useful to us for practical purposes.

HYPOTHESIS FORMATION

Romesburg (1981) pointed out that much wildlife knowledge is untested hypotheses about patterns in nature. The scientific method employs a strict logical procedure which starts with the construction of hypotheses, i.e., testable statements. Such statements describe how we suppose that bit of the world works. If this sup-

position is wrong, then there must be 1 or more alternative ideas (i.e., hypotheses) that can replace it. The reason we set up all scientific investigation to test simple hypotheses is that we cannot describe every little component of the world, let alone understand them. We have to simplify things by forming general rules (hypotheses) which we can then use to make predictions for the future, and upon which we base management decisions. However, we do not know whether these rules or hypotheses are correct, only that previous competing ones provided less explanation and so became extinct. We must, therefore, continue to test current hypotheses in case they are wrong, because if we assume a hypothesis is correct when, in fact, it is not, then a management decision based upon it also will be wrong.

The quotation from the Scottish natural philosopher, David Hume, makes the point that those who have worked in the tropics know only too well: one would be rash to assume the hypothesis that "all eggs taste good" is correct on the basis of past experience, i.e., the many good eggs eaten previously. One is keenly interested in finding out whether the eggs bought from the local market will disprove the hypothesis, to the extent that elaborate tests are invented, such as floating eggs in water to see if they are bad—it is in one's interest to be skeptical because a mistake has unfortunate consequences.

To illustrate the above argument, let us take a hypothetical study on the diet of black-tailed deer (*Odocoileus hemionus*) in British Columbia during winter. What does it tell us? Apart from what I have just described it tells us very little more. We do not know whether (1) diet preference is the same all year, (2) all black-tailed deer behave this way, (3) all deer species or, indeed all animal species employ the same rules for choosing their food. How do we get around this? We could describe every deer in every locality and do the same with every other species. Not only is this impractical, but it is also inefficient. I call this the nondeductive method.

A more elegant, efficient way of approaching the problem is to define a rule beforehand that describes how animals choose their food. A simple rule could be that animals choose all food types equally. This is our first hypothesis. The alternative is that they do not choose food types equally. Note that the first question is whether animals choose foods; we do not assume that they do and proceed on that basis. If they do

not select food types, we have not wasted time in investigating the cause of something that does not exist. We need investigate no further. On the other hand, if our study finds they do select foods, we can say the first hypothesis is not supported as much as the alternative, which becomes the new rule. Then we ask what the basis is for unequal choice. To examine this we now need a new rule, for example that animals prefer high nitrogen foods. Again we may find it is incorrect because some high nitrogen foods are not eaten.

In this way a set of rules with varying generality evolves. This, the hypothetico-deductive (H-D) method, is equivalent to the "strong inference" approach of Platt (1964) (also see Nichols 1991). If the study is not done in the context of these rules (hypotheses), then it is of little use because it is unrelated to other studies. Failure to use the H-D method in the past has been a feature of many studies of animal diets in wildlife ecology. Robbins (1983), for example, emphasizes that very little has been learned from the many hundreds of diet studies (erroneously called "food habit" studies).

Returning to the example of deer diets, a counter argument may sometimes be raised by a local management agency that is interested only in the diet of a particular group of deer to manage that habitat; other studies are of no consequence. The answer to this, of course, is that the specific study may not have been necessary in the first place if previous studies had addressed general hypotheses, so that a reasonable prediction of habitat and diet could have been made for this specific case. The personnel and funds could then have been devoted better to testing the outcome of the management instead. The approach of our hypothetical local agency is that of the inefficient and expensive nondeductive method.

Finally, I return to the comment made earlier that current hypotheses have not been shown to be true, only that they have not been disproved. Unfortunately, this has sometimes been forgotten in wildlife ecology, particularly when hypotheses have been around for a long time. By frequent reiteration of the hypothesis it appears "true," and so there is no longer any need to test it. At this point the hypothesis has been transformed into dogma. One example of dogma is the oft-repeated statement that lungworms carried by white-tailed deer (*Odocoileus virginianus*) are the cause of declines in moose

(*Alces alces*) populations, a hypothesis not yet supported by fact (Nudds 1990). Another example of dogma occurs in plant–herbivore studies where the presence of invader type plants (Dyksterhuis 1949, Smith 1979) is assumed to indicate overgrazing (Macnab 1985). One should remember that, in science, most golden rules have proven, in the end, to be erroneous.

PREDICTIONS FROM HYPOTHESES

It is important to identify the correct predictions that follow from a hypothesis. Many of the major problems in wildlife management stem from a misunderstanding of hypotheses, and incorrect or irrelevant predictions. The example of deer diets is simple, and the predictions are straightforward. But many hypotheses cannot be adequately described with words, and must either be set up graphically or mathematically. The predictions from these are sometimes far from obvious—good examples are those that concern carrying capacity, overgrazing, intra-specific competition, and regulation of prey by predators. Simplistic verbal descriptions of these processes have led in the past to incorrect predictions—and mistakes in wildlife management.

Therefore, wildlife managers need to understand relevant ecological theory so that they can make appropriate predictions about the result of their management programs. There is still a perception, however, that theoretical ecologists are divorced from reality and that practical ecologists (here I refer to wildlife managers) have no need to understand theory. The first point is debatable, the second is incorrect (Fretwell 1972, Nudds 1979). Some of the best applied ecology textbooks (Watt 1968, Holling 1978, Walters 1986) are also among the best theoretical works in ecology and wildlife management.

SCIENTIFIC EXPERIMENTATION

Hypotheses are tested by making specific observations that are critical to the predictions. Here the word experiment is used in a general sense to mean a test of predictions and can be thought of in 2 ways, mensurative and manipulative (Hurlbert 1984, Eberhardt and Thomas 1991). The mensurative experiment predicts a set of observations under certain conditions which are usually not under our control. No manipulations are carried out and the hypothesis stands or falls on the basis of the observa-

tions. An example of this approach is the prediction of Otterman (1974) and Otterman et al. (1975) that overgrazing and denudation of vegetation in northern Africa should result in a change of weather patterns and a progressive decline in rainfall (the anthropogenic hypothesis). The prediction for nonovergrazed areas of Africa, the control, is that such areas should not show such a trend in rainfall. An alternative hypothesis (Nicholson 1986) stated that the droughts of northern Africa were part of a continent-wide change in meteorology. The prediction that follows from this is that all areas of Africa should show the same decline in rainfall. Trends in rainfall during the 20 years since 1972 when Otterman first produced his hypothesis, show a consistent decline in northern Africa but no change in nearby eastern Africa (Sinclair and Fryxell 1985, Sinclair and Wells 1989), thus contradicting the meteorological hypothesis, while strengthening the anthropogenic hypothesis. In conclusion, it was possible to test the anthropogenic hypothesis through observation; the importance of this test and its result is that, potentially, there may be a way to manage the north African ecosystems, as opposed to accepting the alternative view that the situation is out of control because of climate.

In contrast to mensurative, the manipulative experiment tests predictions by altering a component of the system, say population density, in one area and compares the outcome with a control area where no manipulation is carried out. All other components of the system are held constant to the best of our ability. This approach may lead to less ambiguous results, but on the scale of wildlife ecosystems it is often viewed as impractical: controlled and replicated experiments can only be carried out on a small scale (usually a few hectares) and, therefore, may not be particularly relevant to large scale wildlife systems.

There are 2 answers to this objection. First, small scale experiments often do apply to large scale events (Schoener 1986). Secondly, we can address the large scale directly by making use of the manipulations of wildlife management as scientific experiments (Macnab 1983). In many cases management results in manipulations over a large area, examples being predator control, herbivore reductions, or prescribed burning. These manipulations can be used as good experiments if properly designed; one needs (1) to obtain information before, during, and after

they occur and (2) to compare the results with a similar unmanipulated area which forms the control. Two important points emerge from this. First, scientific measurements are needed throughout management operations (managers must either understand the scientific method or be under scientific guidance). Second, entire systems must not be manipulated; some parts must be left as controls.

This approach can be extended to unintentional manipulations or even to natural experiments beyond our influence. For example, national parks are areas (sometimes on a large scale) where human interference is at a minimum (or should be) and can be used as baseline controls for a large number of manipulations outside these areas (Sinclair 1983). What is needed is a system whereby long-term data on the main components of ecosystems are collected (for example trends in vegetation, animal populations, etc.). Unfortunately, such a system is not in place in any national park in the world, so these parks are not living up to their mandate.

Natural experiments are usually ones which occur unexpectedly. However, they can be used to explore large-scale ecosystem dynamics that would otherwise be beyond us. Examples of such natural experiments are the reinvasion of grey wolves (*Canis lupus*) in Banff National Park, Canada, after an absence of 40 years (Huggard 1991) (this is an introduction experiment of a predator into its natural habitat and provides a valuable precursor to the introduction of wolves into Yellowstone National Park); the expansion of wood bison (*Bison bison*) into its original range in the Northwest Territories, Canada (Gates and Larter 1990); the wild fires of Yellowstone National Park (Romme and Despain 1989, Schullery 1989); and the eradication of the rinderpest virus in Serengeti National Park, Tanzania, causing the eruption of the major ungulate species (Sinclair 1979).

Both of these approaches—mensurative and manipulative—have to address the need for replicate measurements. If we have only 1 experimental result and 1 control, then any differences we obtain may have occurred by chance. We need to repeat these results to satisfy ourselves, through appropriate statistics, that chance has played a part at a sufficiently low probability. The planned and controlled manipulations can usually accommodate a replicate design, although we must be careful that we have true replicates and not subsamples or pseudo-

replicates (Eberhardt 1976, Hurlbert 1984). But how do we obtain replicates using other approaches? Many wildlife management manipulations such as predator removals or herbivore stocking densities can be altered without much extra cost so that several smaller areas rather than 1 large one are altered. In other cases, the manipulations are so widespread that they affect several systems that may constitute replicates (Eberhardt 1988). For example, the rinderpest removal in East Africa covered several, unconnected ungulate populations so that the effects on each could be viewed separately (Sinclair 1977).

However, there are many occasions when there is no possibility of obtaining a replicate situation: the trend in aridity in northern Africa is an example. Nevertheless, it would be unwise to treat the results from these situations as invalid or unpublishable, and certainly incorrect not to study them. The wise strategy here would be to publish the result with the caveat that one must wait for future opportunities to repeat the observations. If a phenomenon is not studied on the grounds of lack of replicates, then one is always in the position of single replicates in the present because of missed opportunities in the past; many ecosystem-scale phenomena would remain unstudied under this policy. Eberhardt and Thomas (1991) expand on these approaches.

THE REGULATION OF ANIMAL POPULATIONS

The topic of population regulation is an example where theory has been misunderstood, and this has led to confusion of terms, inappropriate research, and erroneous management. Even a quick scanning of the wildlife literature provides examples where the terms limitation, regulation, and control are used not only interchangeably, but also to mean different things. The confusion is so great that many of the papers appear meaningless and require careful interpretation.

In fact, the above terms do mean different things, and to understand them we must understand theory. A detailed explanation is given in Sinclair (1989), but the main points are (1) populations must have some theoretical equilibrium density (labeled K as in the logistic equation) which they tend towards (even if random fluctuations prevent them from reaching it); (2) this tendency towards equilibrium is brought about by density-dependent mortality or repro-

duction, where density dependence is defined as the proportional increase in mortality (or decrease in reproduction) as a population increases; (3) a population is "regulated" if it experiences density-dependent mortality (the cause of the density dependence is the "regulating factor"); and (4) the factors that set the position of the equilibrium density are called "limiting factors." Because both density-independent and density-dependent factors set the equilibrium point, we must conclude that all mortalities, whatever the cause, "limit" the population. In summary, "limitation" refers to the position of the equilibrium, while "regulation" refers to the processes that bring the population back to the equilibrium. (The term "control" has no well-defined meaning except in the sense of biological control of pests.)

The implications of these meanings are (1) any question which asks whether a population is limited is trivial because all mortalities are limiting, and (2) conclusions about the regulation of a population must be based either on perturbation experiments to observe whether or not populations return to their original density, or on the demonstration of density dependence. Without either of these, regulation is not demonstrated.

What is the significance of this for wildlife management? First, limiting factors are interesting only if they are responsible for the major year to year fluctuations; these may be manipulated to set the equilibrium. Secondly, the important factors for management are those regulating the population, because they are the ones that determine the long-term viability of the population; appropriate research is needed to identify them.

In summary, I have used this topic of regulation to illustrate that a misunderstanding of the theory has led to both a confusion of terms and, in many cases, a research design that is uninformative for managers; these cases either describe limitation, which is of little value, or they refer to regulation without presenting the essential evidence either to demonstrate or disprove it.

DO PREDATORS REGULATE THEIR PREY?

All of the problems I have discussed above apply to this question, but there are some additional ones. Again, we must first turn to theory to understand predation (Ricklefs 1979:618, Sin-

clair 1989, Sinclair et al. 1990). Because of the functional and numerical responses of predator populations, the predatory effects on prey are usually inversely density dependent over a large range of prey densities; i.e., they destabilize the prey population causing it either to crash or erupt. Hence, predation is often nonregulatory.

However, in some cases predators might cause density-dependent mortality at low prey densities and, potentially, regulate the prey population. In addition, predators can sometimes regulate prey at low densities, although they are nonregulatory at high prey densities. (Note that in both cases predators are limiting the population, because without the predators the prey population density would be higher still.) The implication is that predators might cause prey populations to exist at 2 very different densities and to exhibit what are called multiple stable states. This has consequences for understanding carrying capacity and overpopulation (Caughley 1981, Sinclair 1981, Macnab 1985).

With this understanding, we can now make the proper predictions to answer our question. Where the only evidence available to us is prey density, we can demonstrate "regulation" by predators in a predator removal experiment, if (1) the prey population increases and (2) if it does not return to its previous level when predator numbers are allowed to regain their previous level. Demonstration of (1) alone is insufficient because prey populations will increase whether or not predators are regulating. By itself, it is a demonstration of the trivial case of limitation. Because most predator removal experiments are confined to demonstrating such an increase, they tell us nothing about the regulatory capacity of predators, although many claim such.

Predator regulation can also be demonstrated if a prey population at high numbers is artificially reduced, for example by culling, in the presence of predators, and the prey fail to increase again at the cessation of culling. An interesting example of this occurred when wildebeest (*Connochaetes taurinus*) were culled in Kruger National Park, South Africa (Smuts 1978). This scenario is consistent with the hypothesis that predators regulated prey at the lower density but not at the higher one.

So far we have used changes in mean density (i.e., stable state) as evidence for predator regulation. A further prediction for regulation is that the mortality caused by predators is density

dependent. This would require either that we manipulate prey density artificially or we wait for it to change naturally.

It has not been necessary to refer to the terms "additive" or "compensatory" mortality. The reason is that the causes of mortality—lack of resources and predation—always occur simultaneously, and hence it is misleading to consider them as alternatives (McNamara and Houston 1987).

The question of predator regulation illustrates many of the aspects of scientific methodology: (1) a knowledge of theory is needed to understand the complex action of predators; (2) the predictions about whether predators regulate prey populations are not intuitively obvious; and (3) these predictions require a complex, rather than simplified, experimental methodology that could be achieved from the manipulations of wildlife management programs.

CONCLUSION

The main points that emerge from this discussion are, first, that some form of experimentation is needed to further understanding of wildlife ecosystems. Second, the scale of these experiments usually precludes the standard controlled design, but many wildlife management operations can be used as good experiments provided that they are monitored scientifically and compared with controls. Third, proper scientific monitoring requires a knowledge of what predictions are being tested, and hence an understanding of the theory that underlies these predictions. It follows that wildlife management requires a scientific approach, and conversely the science of wildlife ecology requires management to carry out experiments.

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COPING WITH UNCERTAINTY IN WILDLIFE BIOLOGY

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Abstract: A decade after Romesburg admonished wildlife biologists to establish and test hypotheses to gain more "reliable knowledge," we have added an incentive to bring rigor to our science. Wildlife biologists are finding themselves defending their science against often savage criticism. At least 2 factors are central to producing solid, defensible science: (1) the rigorous application of scientific methods and (2) the development of clear operational definitions for terminology. The hypothetico-deductive (H-D) process, in the form of statistical tests of hypotheses based on experimental data, is hailed as the superior means of acquiring strong inference and reliable knowledge. Results from experimental studies, however, are seldom available, and most management decisions are made on the basis of incomplete information. We argue that even in the absence of experimental information, the H-D process can and should be used. All management plans and conservation strategies have properties that can be stated as falsifiable hypotheses and can be subjected to testing with empirical information and with predictions from ecological theory and population simulation models. The development of explicit operational definitions for key concepts used in wildlife science—particularly terms that recur in legislation, standards, and guidelines—is a necessary accompaniment. Conservation management and planning schemes based on the H-D process and framed with unequivocal terminology will allow us to produce wildlife science that is credible, defensible, and reliable.

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Wildlife biologists face a new and exceedingly challenging era. No longer is wildlife science a lonely enterprise carried out on distant landscapes. No longer do wildlife biologists write on natural histories and population trends for an audience consisting only of other wildlife biologists. And, no longer are the results of wildlife

studies relegated to moldering stacks in specialty libraries. In just a few short years wildlife biologists have been swept up into public debates and taken from the status of sequestered experts to that of key players. Wildlife biologists and their colleagues in forestry, range sciences, and conservation biology have been drawn into the