

- SCHOENER, T. W. 1986. Mechanistic approaches to community ecology: a new reductionism? *Am. Zool.* 26:81-106.
- SCHULLERY, P. 1989. The fires and fire policy. *BioScience* 39:686-694.
- SINCLAIR, A. R. E. 1977. *The African Buffalo*. Univ. Chicago Press, Ill. 355pp.
- _____. 1979. Dynamics of the Serengeti ecosystem: process and pattern. Pages 1-30 in A. R. E. Sinclair and M. Norton-Griffiths, eds. *Serengeti: dynamics of an ecosystem*. Univ. Chicago Press, Ill.
- _____. 1981. Environmental carrying capacity and the evidence for overabundance. Pages 247-257 in P. A. Jewell, S. Holt, and D. Hart, eds. *Problems in management of locally abundant wild mammals*. Academic Press, New York, N.Y.
- _____. 1983. Management of conservation areas as ecological baseline controls. Pages 13-22 in R. N. Owen-Smith, ed. *Management of large mammals in African conservation areas*. Haum, Pretoria.
- _____. 1989. Population regulation in animals. Pages 197-241 in J. M. Cherrett, ed. *Ecological concepts*. Blackwell Scientific Publ., Oxford, U.K.
- _____. AND J. M. FRYXELL. 1985. The Sahel of Africa: ecology of a disaster. *Can. J. Zool.* 63: 987-994.
- _____, P. D. OLSEN, AND T. D. REDHEAD. 1990. Can predators regulate small mammal populations?: evidence from house mouse outbreaks in Australia. *Oikos* 59:382-392.
- _____, AND M. P. WELLS. 1989. Population growth and the poverty cycle in Africa: colliding ecological and economic processes? Pages 439-484 in D. Pimentel and C. W. Hall, eds. *Food and natural resources*. Academic Press, New York, N.Y.
- SMITH, E. L. 1979. Evaluation of the range condition concept. *Rangelands* 1:52-54.
- SMUTS, G. L. 1978. Interrelations between predators, prey and their environment. *BioScience* 28: 316-320.
- WALTERS, C. 1986. *Adaptive management of renewable resources*. MacMillan, New York, N.Y. 374pp.
- WATT, K. E. F. 1968. *Ecology and resource management*. McGraw-Hill, New York, N.Y. 450pp.

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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

land-use decision-making process and have been required to defend the merits of their field studies in a heretofore foreign venue.

Land use policy has become big news-with big economic consequences and even bigger political stakes. Environmental organizations have filed appeals of virtually every National Forest Plan that has been completed in the past several years. Management plans for populations of bison (*Bison bison*) and elk (*Cervus elaphus*) that migrate through Yellowstone National Park have been challenged in federal courts by hunters and those with livestock interests. Congress commissioned a rare cooperative effort among the U.S. Forest Service, U.S. Fish and Wildlife Service, Bureau of Land Management, and National Park Service that produced a plan to save the threatened northern spotted owl (*Strix occidentalis*). The list goes on. In an increasingly litigious society, even wilderness is not free of contention or beyond the reach of the courtroom. We may not welcome them, but lawyers are joining us in the stacks of our biology libraries.

Now, a decade after Romesburg (1981) admonished us to establish and test hypotheses to gain more "reliable knowledge," that is, to do better wildlife biology, we have an added incentive to bring rigor to our science. Wildlife biologists are finding themselves defending their science against often savage criticism. Our definitions of "threatened" and "endangered," our monitoring data, our population estimates, our inferences regarding the decline of native populations will be scrutinized by the timber industry, livestock associations, mining interests, environmental organizations, and other interest groups with particular policy agendas. These groups will employ lawyers and consultant scientists to seek flaws and weaknesses in our definitions, our analyses, and our products. And in those cases in which no obvious flaws exist, critics will note how little we actually know. They will exaggerate and misconstrue the inherent, inevitable uncertainty that accompanies our best scientific efforts.

The disquieting experience of having one's scientific work subject to challenge in a legal proceeding is one that many wildlife biologists will soon face. However, we can and should prepare for that kind of scrutiny. At least 2 factors are central to producing science that is credible, defensible, and repeatable. These factors produce science that can be used to con-

struct clear and explicit planning products, be they defined reserve boundaries, recovery plans for endangered species, or land management strategies that meet multiple-use objectives.

The first requisite element is the rigorous application of the scientific method, not only in the process of gathering and analyzing data and communicating results, but also in the process of applying those data and results to land use planning and wildlife management. Second is the development of clear operational definitions for crucial terminology that recurs in legislation, standards, and guidelines. Good science is rendered worthless when it is delivered to meet vague goals that are phrased as abstract biological concepts. The most thorough population viability analysis, for example, cannot be brought to bear in reserve design unless viability is explicitly defined. Here, we discuss both the application of scientific method and the use of clear, precise terminology as interactive, critical elements of good, defensible science.

SCIENTIFIC METHOD

For an expert witness to be assertive but downright wrong is usually received by judge and jury more positively than is an honest assessment of the uncertainty that specific facts convey. As scientists, we have been trained (or, better, should have been trained) to treat facts with doubt, a circumstance that lawyers seize upon and exploit to their great advantage. Lawyers have little trouble establishing that biologists are uncertain about their analyses and products, and in a court of law, that is tantamount to an indictment. But, of course, uncertainty is the *raison d'etre* of science. The pursuits of wildlife biologists, conservation biologists, and other biologists are (or, again, should be) linked by the application of scientific method in experimentation, synthesis, and application. Each should seek to reduce levels of uncertainty associated with conclusions used in the practical application of their science by subjecting explicit alternative hypotheses to rigorous tests. The hypothetico-deductive process, as this has been called, is hailed as the superior means of acquiring strong inference and reliable knowledge (see Platt 1964). Yet, the tradition of weak inference, induction, and retrodution remains well entrenched in wildlife and associated sciences.

Why are wildlife biologists and their brethren in other applied population-level disciplines, such

as conservation biology, such strange bedfellows with the hypothetico-deductive method? For largely the same reasons that prompted Romesburg (1981) to write his piece a decade ago (see also Murphy 1990). For one, the targets of study by wildlife biologists are usually large, mobile, often gregarious species that exhibit complex behaviors and can be widely distributed across highly diverse landscapes that typically have been logged, grazed, cultivated, drained, roaded, and beset by introduced species in environments that are inherently variable. This study arena, at least superficially, appears terribly opaque to systematic, rigorous experimental design.

The importance of the hypothetico-deductive process in conducting the best possible wildlife biology has been argued-in a series of provocative and introspective presentations that have shaken the foundations of the discipline (e.g., Romesburg 1981, 1989; Bailey 1982; Macnab 1983; Gavin 1989; Peek 1989; Wagner 1989; Keppie 1990). This healthy housekeeping should yet result in a better wildlife science, as increasing numbers of workers trade in correlative experimentation and retroductive analysis for more robust techniques that will yield more reliable results. This process will take time, however, as veterans retool and as new training produces a cohort of biologists weaned on hypothetico-deductive methods. Unfortunately, meeting the challenge of gaining more reliable knowledge is not the only hurdle; translating that knowledge into defensible management prescriptions and policy is itself no small task. Not surprisingly, that translation-in the form of reserve design and management planning-has been historically subject to even less rigor than the science upon which it has been based.

Most researchers believe the best application of the hypothetico-deductive process to be in the form of statistical tests of hypotheses based on data derived from direct experimentation with treatment and control units. This approach provides tests with high power and reduces Type II error probabilities. However, results from experimental studies are generally not available, and most management decisions are made on the basis of incomplete information drawn from disparate sources. Even in the absence of experimental information, we believe that the hypothetico-deductive method can and should be used. Essentially, all management plans have properties that can be stated as falsifiable hy-

potheses, which then may be subjected to testing with existing empirical information and theoretical predictions.

In 1989 Congress responded to mounting political pressure from environmentalists and the timber industry by directing the land management agencies to convene an Interagency Spotted Owl Scientific Committee (ISC) to produce a "scientifically credible" strategy to conserve the northern spotted owl. The experience of the ISC clearly showed that lawyers pay particular attention to how scientific information is used in conservation planning. The development of a strategy for the northern spotted owl, and its defense before Congress and in depositions to lawyers for environmental groups and the timber industry, provide an enlightening example of how procedures grounded in the hypothetico-deductive method can be used in conservation planning.

Our experience on the ISC suggests that lawyers do not understand how science is done. They perceive that we do science like criminals build successful alibis. Alibis are built of evidence that must stand in total, akin to a structure built from so many metaphorical bricks. The structure, it is often argued, is no stronger than the weakest brick used in its construction. The lawyer's job is then to find that weak brick and, in doing so, bring down the structure. In other words, lawyers view our conservation plans as having been built from bricks of data. Such plans would thus be as weak as the weakest data or empirical generalizations used to construct them. Such plans, they argue, are fatally flawed given a paucity of observations, a poorly constructed theoretical model, or even a calculation error.

What biologists actually do-or should do-to bring science to conservation planning is quite different. Biologists do not construct conclusions from data; they construct hypotheses that are tested with data. A conservation plan is not built from bricks of hard data, but is loosely constructed with pertinent information on distributions, abundances, natural history observations, and habitat associations. The resultant structure is tested with statistical analysis of empirical data, predictions from ecological theory and population models, and inferences drawn from studies of related species. In essence, we fling bricks of data at a structure-our plan, our hypothesis-as a means of identifying its weaknesses. Drawing inference from the results of these tests, we adjust and reshape the structure

to strengthen it. The testing process continues until relevant data, models, and inferences are exhausted. The conservation plan so produced is not as weak as the weakest data or softest test of its integrity—it is as strong as the strongest data or toughest test.

Conservation strategies, reserve designs, management plans, and similar applications of wildlife science that are tested with, not built from, data appear to be resistant to standard legal challenges. Such a conceptual structure shifts the burden of proof from the scientist (the defender of the plan) to the lawyer (the antagonist), and confounds the usual witness-counsel relationship. Our review of the legal literature has turned up surprisingly few references related to scientific method, and none that focus on application of hypothetico-deductive procedures in problem solving. By and large, courtroom arguments do not focus on experimental procedures, *per se*, but on the products of those experiments, for instance in drug testing and in engineering contexts. Even exhaustively critical analyses that target the process of proof and disproof, such as those in paternity suits, rarely invoke hypothesis-testing procedures.

The Northern Spotted Owl Example

The hypothetico-deductive method was used by the ISC to design a reserve system for the northern spotted owl. That straightforward process provides a particularly rich demonstration of the application of the method to the design phase of conservation planning (see Murphy and Noon 1991). A preliminary reserve design was constructed as a map that portrayed reserve boundaries describing the locations, sizes, shapes, and spacing of available habitat patches. For reserve design purposes, an assertion of a map property served as a hypothesis that was subjected to tests with information from population viability analysis. When tests failed to confirm 1 or more properties of the map-based reserve system, the system was adjusted to make it consistent with available information.

For the northern spotted owl, an intersection of 4 map layers provided the preliminary reserve design—an initial map that portrayed the maximum size and number of habitats that could be considered in a proposed reserve system. One map layer outlined the current and historical distributions of the owl. A second presented the current and historical distributions of the owl's habitats, including disturbed areas likely to re-

cover to suitable habitat in the future. A third map layer provided population size information from surveyed portions of the range of the owl and included projections of densities of owls from unsurveyed areas of similar habitat. And a fourth map layer depicted land ownership patterns. Lands not available for conservation planning purposes (in this case, lands in private ownership) were excluded from the planning process.

The intersection of these 4 map layers defined the maximum extent of a potential reserve system, a collection of habitat "polygons" or habitat conservation areas (HCA's) that varied in size, shape, and quality and were scattered as "patches" across a largely unsuitable landscape matrix. The HCA's and the owls they supported could be evaluated in the context of metapopulation theory. This initial map and its attendant properties allowed us to generate hypotheses in the context of 5 generally accepted principles of reserve design: (1) species that are well distributed across their historical geographic ranges tend to be relatively less prone to extinction; (2) population persistence increases with population size and habitat patch size; (3) habitat patches that are less internally fragmented tend to support species for longer periods than patches that are fragmented; (4) habitat patches that are sufficiently close together to allow dispersal tend to promote population persistence; and (5) habitat patches that are connected by habitat corridors, or that are set in a landscape similar to the habitat patches, will allow target species to disperse freely among patches and will tend to support a species for longer periods than habitats not so situated.

We used these principles to develop and test a number of general but explicit hypotheses. To test empirically the hypothesis that northern spotted owls, in fact, were declining in numbers and to gain insight into the probable causes of that decline, we considered data pertinent to 3 hypotheses— H_0 : spotted owl populations are not declining, H_0 : spotted owl populations do not discriminate among habitats on the basis of forest age or structure, and H_0 : habitat selected by spotted owls has not declined in extent. Given evidence of declining populations, significant habitat associations, and decline in habitat extent, the relationship between habitat area and population size was investigated by testing the hypotheses that— H_0 : no relationship exists between the size of a habitat patch and its carrying

capacity for owls, and H_0 : no relationship exists between patch size and the likelihood of continued population persistence.

How we brought data to bear on these latter hypotheses is demonstrative. Initial information to test the hypotheses was available from empirical studies of insular bird species (e.g., Jones and Diamond 1976, Diamond and May 1977, Diamond 1984, Pimm et al. 1988) and population dynamics theory (e.g., Richter-Dyn and Goel 1972, Leigh 1981, Goodman 1987). Additionally, the ISC sought to test the hypotheses with a dynamic metapopulation model developed specifically for the northern spotted owl. The basis of the dynamic model was a continuous rectangular array of HCA's that collectively occupied a fixed percentage of a simulated forested landscape. The sizes of HCA's were determined by the number of spotted owl pair sites they contained. The percent of each HCA stocked with suitable habitat was varied, with sites assigned status as suitable or unsuitable for pair occupancy. In different model runs, HCA sizes were systematically varied to evaluate the effect of local population size on population stability (Thomas et al. 1990:Appendix M). Persistence likelihood was estimated by plotting 100-year trends in mean owl pair occupancy (No. occupied sites/HCA, averaged over all HCA's) for HCA's of different sizes. Two operational criteria were established to evaluate persistence: stabilization of mean pair occupancy and stabilization occurring at >70% occupancy.

Two basic scenarios were simulated. The first scenario assumed that all sites within an HCA were suitable, and the second approximated current forest conditions in the Pacific Northwest. Given the assumption of 100% habitat suitability, the model did not predict stabilization at high occupancy levels unless HCA's were capable of supporting at least 15 pairs. Based on the more realistic assumption of 60% suitability, mean occupancy did not stabilize until HCA's were large enough to support at least 20 pairs of owls.

Model predictions, theory, and empirical studies were consistent in suggesting a significant positive relationship between habitat patch (HCA) size and carrying capacity, and between habitat patch (HCA) size and persistence likelihood. Collectively, these results allowed us to reject the null hypotheses of no relationship. In addition, results from the projection model,

structured and parameterized on the basis of extensive life history studies of northern spotted owls, directed us to establish HCA's of geographic extent adequate to support minimum populations of 20 owl pairs.

Having established relationships between habitat patch size, carrying capacity, and population persistence, we considered the likelihood of continued persistence in the face of fragmentation, employing the hypothesis- H_0 : no relationship exists between the extent of fragmentation within a patch and population persistence likelihood. And, then, to determine appropriate distances between patches, we addressed 2 hypotheses- H_0 : no relationship exists between successful dispersal of juvenile owls and distance between patches, and H_0 : no relationship exists between the spacing of habitat patches and persistence likelihood of populations. These hypotheses were tested in a similar fashion with information from empirical studies, ecological theory, and model predictions.

These and other hypotheses served to guide sequential tests of map properties resulting in a reserve system that was-where possible-designed to preserve continuous habitat patches adequate to support ≥ 20 pairs of owls. These patches were separated by ≤ 12 miles, across a landscape matrix of structurally similar habitat to facilitate interpatch dispersal. Having drawn the conclusion that dominant current methods of timber harvest are not conducive to sustaining northern spotted owl populations and recognizing the potential substantial economic and social costs that would follow implementation of an extensive reserve system in which timber harvest would be prohibited (as well as the legal requirement that management of public lands meet multiple-use objectives), the ISC sought a conservation plan that would meet explicit "acceptable" (carefully avoiding the term "minimal" here) standards for the owl. In so doing, the ISC identified and applied to the maps reserve system properties that would result in a self-sustaining population of owls with a high likelihood of persistence to 100 years. These reserve system properties were supported by empirical field data from northern spotted owl studies, conclusions drawn from explicit models of owl population dynamics, and studies of other bird species in insular or otherwise patchy habitats.

Importantly, the iterative process of hypothesis testing provided a basis for the elimination

of some habitat areas from the preliminary reserve map (which included all available habitat) with acceptable cost to the persistence of the species, thus enhancing the likelihood of the plan being adopted. In essence, the ISC used hypothesis-testing procedures to edit the original habitat polygons into a smaller subset, ultimately producing a justifiable reserve design. Although the conservation strategy is not a unique solution to the challenge posed to the ISC by Congress, it is internally consistent, repeatable, and defensible-criteria that meet the mandate of "scientific credibility."

Because the habitat used most frequently by the northern spotted owl appears to be that with structural characteristics of mature or old-growth forest (that is, habitat left unaltered but for natural processes), the reserve design strategy for the owl promises to be the most important management planning exercise for that species. Clearly, not all wildlife species and their habitats are best managed with simple habitat preservation; many require direct manipulation of habitat features or intervention in response to demographic trends to meet conservation or other management goals. Wildlife management in such contexts can also benefit greatly from the application of scientific method, and can provide an additional defense against the "prove it" demands of those who attempt to discredit the scientific process because of its inherent uncertainty. This is accomplished by implementing flexible management programs cast in an adaptive context (Holling 1978, Walters 1986). Such frameworks explicitly acknowledge uncertainty and provide a process for incorporating new information into management strategies. Adaptive management can provide a reliable assessment of management programs, provide new ecological information in the process of assessment, and, if warranted, use the new information to modify existing plans. The same iterative process described above should be employed. The map of habitat polygons that is sequentially adjusted to produce a reserve design consistent with available evidence is an analog of a preliminary management plan, the prescriptions of which can be adjusted to make them consistent with information accrued from management, research, and monitoring.

Under this application of the hypothetico-deductive process, monitoring programs may be viewed as sets of ongoing experiments that are

specifically designed to differentiate among alternative management options (Murphy 1990, Noss 1990, Walters and Holling 1990). Management plans are developed using existing scientific information in much the same way that preliminary reserve designs are constructed. Management planning should incorporate an understanding of population dynamics and should identify the environmental factors thought to affect those dynamics. Management responses should be based on predictions of changing environmental conditions. These predictions thus can serve as testable hypotheses that direct the acquisition of new data from basic research and, most importantly, from monitoring. Monitoring, especially, is used to test the implicit biological assumptions underlying our management plans. Hence, monitoring should be a hypothesis-testing exercise that, through time, allows management to be improved as alternative management responses (hypotheses) are excluded. Adaptive management is the endeavor in which wildlife biologists have most systematically employed hypothetico-deductive method to gain reliable knowledge (Holling 1978, Romesburg 1981, Macnab 1983, Walters 1986, Eberhardt 1988).

RELIABLE TERMINOLOGY

Uncertainty in the wildlife sciences is not limited to the scientific process itself, but extends to the basic terminology we use to pose our questions and state our conclusions. Wildlife biologists, conservation biologists, and other applied ecologists regularly use vague, abstract, and nonquantifiable nomenclature. If 10 biologists were asked to define a single term commonly used in wildlife science, they likely would invoke 10 different definitions. This is more than a problem of semantics. Much of the characteristically vague nomenclature that pervades wildlife biology is directly derived from federal regulations, for example the National Environmental Policy Act (1969), the Endangered Species Act (1973), the National Forest Management Act (1976), and the federal codes that followed these Acts. Legal definitions for a wide array of terms-for threatened and endangered species, critical habitat, habitat conservation plans, multiple use, sustained yield, diversity, viable populations, management indicator species, environmental impact-provide the only

guidelines for determining whether a given regulation has been followed. Confoundingly, among the data most often used to test hypotheses employed in conservation planning are those drawn from population viability analyses, a loosely defined set of scientific criteria involving analysis of empirical data and theoretical models which are characterized by vague and ambiguous terms.

While the lack of precision and clarity in legal-scientific terminology causes short-term problems in decision-making, the real harm is realized over the long term. Precious time and resources are spent in courtroom haggles over the threatened status of a given population or the degree of viability ensured by a management plan, the contents of which were, unclearly, mandated by legislative language in the first place. Today's conservation planning is handicapped by limited funding, rapidly expanding human populations, and increasing conflicts between wildlife and other values. Attempts by antagonists to highlight the uncertainties inherent in science and to discredit scientific conclusions and recommendations are made easier when we are forced to defend our methods without clear, precise, and generally accepted definitions of the major biological concepts and terms that we are legally mandated to address. To redress this problem we must first acknowledge that the wildlife biology profession has a history of sloppy terminology. We must also admit to the difficulties in creating universally acceptable definitions for many terms. These difficulties, however, do not excuse us from our obligation to provide operational definitions of the commonly used terms on which our science-and its defendability-depend.

This point is best illustrated by example. The designation of critical habitat for a federally listed threatened or endangered species is required by the Endangered Species Act. The Act (Section 3, 5(A) ii) defines critical habitat as "the specific areas within the geographic range occupied by the species, at the time it is listed . . . on which are found those physical or biological features (I) essential to the conservation of the species and (II) which may require special management considerations or protection." Section 50 CFR 424.12 specifies that "critical habitat" is to include "(1) space for individual and population growth, and for normal behavior; (2) food, water, air, light, minerals or other nutri-

tional or physiological requirements; (3) cover or shelter; (4) sites for breeding, reproduction, rearing of offspring, germination or seed dispersal; and generally (5) habitats that are protected from disturbance or are representative of the historic geographical and ecological distributions of the species."

These generic definitions are vague enough to encompass all aspects of the habitat in which a species resides, and they provide no specific guidance for differentiation between habitat in general and the presumed subset that is "critical habitat." When the Act is applied to particular species on real landscapes, the need for greater precision and clarity in this definition is obvious, since "critical habitat" not only determines the footprint within which species protection measures operate, but also restricts human activities, which in turn, typically sets the stage for debates on the placement of such boundaries on maps.

That it is imperative for wildlife biologists to be concerned about the reliability of empirical data, the clarity of nomenclature, and the judicious application of scientific methods to species management is illustrated by the consequences of designating critical habitat for the northern spotted owl. In April 1991, the U.S. Fish and Wildlife Service proposed that >5 million hectares of federally owned land be formally designated as critical habitat. If approved by the agency, the designation could restrict timber harvest, with substantial short-term economic effects and predictable adverse reaction from communities dependent upon the timber industry. Opponents of the proposal immediately mounted a vigorous attack on the empirical data and the scientific processes used to designate the type and amount of critical habitat in an attempt to discredit the scientific bases of the conservation proposal. To withstand such attacks, the U.S. Fish and Wildlife Service must have in place definitions of terms, reliable empirical data, and inferences based on acceptable scientific methods. Because the best available scientific information is often incomplete-the relationships between habitat structure and composition, and population stability and persistence, are poorly known for almost all species-the definition of critical habitat must be clear and specific and must suggest qualitative, evaluative criteria.

The definition of critical habitat is also a challenge, because independently the terms "habi-

tat" and "critical" have never been precisely defined. The biological literature includes a long history of ambiguous and vague definitions of habitat, few of which would survive cross-examination in the courtroom. Those definitions of habitat range from "an animal's address" (Elton 1927) to "an ecological feature that has a certain homogeneity with respect to the sorts of environments it might provide for animals" (Andrewartha and Birch 1984). Two areas of pervasive confusion are the distinction between the terms "niche" and "habitat" (Whittaker et al. 1973, 1975; Carey 1980), and whether the term "habitat" should have synecological (Carey 1980) or autecological (James et al. 1984) context. Although we do not wish to contribute to this debate, it is clear that in the context of the Endangered Species Act, habitat has an autecological restriction. We believe that this clarification—"habitat [refers] to [the species] distributional response to environmental factors at different points in the landscape" (Whittaker et al. 1975)—best addresses the intent of the Act, and specifically acknowledges that, for many species, habitat requirements vary geographically. This specificity in the definition of habitat is required for the effective, defensible application of science to conservation.

Yet, developing a clear definition of habitat might be viewed as easy when compared to developing a precise definition of the subset of that habitat that should be deemed "critical" for species survival. "Critical" implies a turning point of sorts, the imminence of decisive change of condition accompanied by considerable risk. But, risk of extinction of a target species very well may be a continuous rather than a threshold phenomenon. In addition, in the context of species management, the term critical implicitly incorporates the concept of population viability; "critical," therefore, must be defined in terms of life history requirements for survival and reproduction. Critical habitat certainly ought to be habitat that, assuming certain risks, can provide for long-term population viability. In turn, viability implies a balance between birth and death rates and is best defined in terms of a biologically measurable parameter—the finite population growth rate (λ)—which over the long term must be ≥ 1.0 . Of course, a rate ≥ 1.0 cannot be assured (or for that matter sustained): it is a function of birth and death rates—random variables, usually with unknown probabilities

subject to stochastic demographic and environmental events.

For most wildlife species, the association between a habitat used by a species and the expected value of its birth and death rates provides a clear criterion for the classification of critical habitat. Only the subset of habitats that, on the average, result in stable or increasing populations would qualify as critical habitat. And even with such a simplification, wildlife biologists must admit to a high degree of uncertainty vis-a-vis critical habitat for most species—almost none of the thousands of studies of animal selection and use of habitat to date have related habitat variation to variation in fitness parameters. The environmental factors that affect persistence likelihoods of species are even less amenable to quantification and less yet to designation, and they must be determined on a case-by-case basis. Ultimately, the factors included will be limited by our understanding of the life history requirements of a given species and our ability to designate the relevant factors on maps. For all species, critical habitat, therefore, must be liberally defined geographically. Critical habitat must be designated throughout the range of a species to spread the risk of extinction due to simultaneous catastrophic, extinction-causing events. While waiting for the results of more detailed studies, critical habitat may need to be defined simply as habitat in which successful reproduction occurs. Failure to act because of incomplete information is imprudent, as loss of critical habitat in the interim may jeopardize future conservation efforts.

Once an operational definition of "critical habitat" is agreed upon and the spatial distribution of populations and risk-spreading are considered, we are obligated in each case to address the uncertainty associated with the efficacy of the designated habitat. In an iterative process of revision, population trends must be monitored and habitat-specific estimates of fitness parameters (birth and death rates) must be made in a hypothetico-deductive framework. Research studies designed to provide that firm empirical foundation for our terminology will be largely experimental. The results of explicit tests of the null hypothesis that no relationship exists between habitat variation and variation in fitness components, for example, will provide the empirical basis for defining "critical habitat." Estimates of the association between hab-

itat and fitness components provide insights into the evolutionary bases of a species' habitat requirements—the information that is needed for effective management, and the designation of critical habitat.

CONCLUSION

The provocative application of the hypothetico-deductive process to conservation planning through successive map iterations, the implementation of hypotheses-driven monitoring protocols in rigorous adaptive management schemes, and the development of explicit operational definitions for key concepts used in wildlife science will all contribute greatly to the production of wildlife science that is credible, defensible, and, to use Romesburg's (1981) succinct descriptor, reliable. These features of a better wildlife science depend on greater precision in all aspects of our science. Even clarification of our nomenclature will demand accurate assessment of the relationship between species life history requirements and population persistence likelihood which, in turn, will demand a much greater focus on experimental studies that test explicit hypotheses concerning ecological processes. Our terminology and our planning products will pass muster only if they share a firm foundation in empirical data and ecological theory, and are strengthened by the framework of a deductive methodology.

LITERATURE CITED

- ANDREWARTHA, H. G., AND L. C. BIRCH. 1984. The ecological web. Univ. Chicago Press, Ill. 506pp.
- BAILEY, J. A. 1982. Implications of "muddling through" for wildlife management. *Wildl. Soc. Bull.* 10:363-369.
- CAREY, A. B. 1980. Multivariate analysis of niche, habitat, and ecotope. Pages 104-113 in *The use of multivariate statistics in the study of wildlife habitat*. U.S. Dep. Agr. Gen. Tech. Rep. RM-87.
- DIAMOND, J. M. 1984. "Normal" extinctions of island populations. Pages 191-196 in M. H. Nitecki, ed. *Extinctions*. Univ. Chicago Press, Ill.
- _____, AND R. M. MAY. 1977. Species turnover rates on islands: dependence on census interval. *Science* 197:266-270.
- EBERHARDT, L. L. 1988. Testing hypotheses about populations. *J. Wildl. Manage.* 52:50-56.
- ELTON, C. 1927. *Animal ecology*. Sigwick and Jackson, London. 300pp.
- GAVIN, T. A. 1989. What's wrong with the questions we ask in wildlife research? *Wildl. Soc. Bull.* 17:345-350.
- GOODMAN, D. 1987. The demography of chance extinction. Pages 11-34 in M. E. Soule, ed. *Viable populations for conservation*. Cambridge Univ. Press, Cambridge, U.K.
- HOLLING, C. S., editor. 1978. *Adaptive environmental assessment and management*. John Wiley & Sons, New York, N.Y. 377pp.
- JAMES, F. C., R. F. JOHNSON, N. O. WAMER, G. J. NIEMI, AND W. J. BOECKLEN. 1984. The Grennellian niche of the wood thrush. *Am. Nat.* 124:17-30.
- JONES, H. L., AND J. M. DIAMOND. 1976. Short-time-base studies of turnover in breeding bird populations on the California Channel Islands. *Condor* 78:526-549.
- KEPPIE, D. M. 1990. To improve graduate student research in wildlife education. *Wildl. Soc. Bull.* 18:453-458.
- KLOPFER, P. H. 1969. *Habitats and territories: a study of the use of space by animals*. Basic Books, Inc., New York, N.Y. 117pp.
- LEIGH, E. G. 1981. The average lifetime of a population in a varying environment. *J. Theoretical Biol.* 90:213-239.
- MACNAB, J. 1983. Wildlife management as scientific experimentation. *Wildl. Soc. Bull.* 11:397-401.
- MATTER, W. J., AND R. W. MANNAN. 1989. More on gaining reliable knowledge: a comment. *J. Wildl. Manage.* 53:1172-1176.
- MURPHY, D. D. 1990. Conservation biology and scientific method. *Conser. Biol.* 4:203-204.
- _____, AND B. R. NOON. 1991. Integrating scientific methods with habitat conservation planning: reserve design for the northern spotted owl. *Ecol. Appl.*: In Press.
- NOSS, R. 1990. Indicators for monitoring biodiversity: a hierarchical approach. *Conser. Biol.* 4:355-364.
- PEEK, J. M. 1989. A look at wildlife education in the United States. *Wildl. Soc. Bull.* 17:361-365.
- PIMM, S. L., H. L. JONES, AND J. DIAMOND. 1988. On the risk of extinction. *Am. Nat.* 132:757-785.
- PLATT, J. R. 1964. Strong inference. *Science* 146:347-353.
- RICHTER-DYIN, N., AND N. S. GOEL. 1972. On the extinction of a colonizing species. *Theoretical Population Biol.* 3:406-433.
- ROMESBURG, H. C. 1981. Wildlife science: gaining reliable knowledge. *J. Wildl. Manage.* 45:293-313.
- _____, 1989. More on gaining reliable knowledge: a reply. *J. Wildl. Manage.* 53:1177-1180.
- THOMAS, J. W., E. D. FORSMAN, J. B. LINT, E. C. MESLOW, B. R. NOON, AND J. VERNER. 1990. *A conservation strategy for the northern spotted owl*. Interagency Scientific Committee to Address the Conservation of the Northern Spotted Owl. U.S. For. Serv., U.S. Bur. Land Manage., U.S. Fish Wildl. Serv., and Nat. Park Serv., Portland, Ore. 427pp.
- WAGNER, F. H. 1989. American wildlife management at the crossroads. *Wildl. Soc. Bull.* 17:354-360.
- WALTERS, C. J. 1986. Adaptive management of

- renewable resources. MacMillan Publ. Co., New York, N.Y. 374pp.
- _____, AND C. S. HOLLING. 1990. Large-scale management experiments and learning by doing. *Ecology* 71:2060-2068.
- WHITTAKER, R. H., S. A. LEVIN, AND R. B. ROOT. 1973. Niche, habitat, and ecotope. *Am. Nat.* 107: 321-338.
- _____, _____, AND _____. 1975. On the reasons for distinguishing "niche, habitat, and ecotope." *Am. Nat.* 109:479-482.

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WILDLIFE PARASITISM, SCIENCE, AND MANAGEMENT POLICY

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Abstract: Wildlife managers lack a scientifically sound basis from which to formulate management policy regarding many host-parasite interactions. One contributing factor to this problem is the paucity of hypothetical-deductive (H-D) research concerning the ecological consequences of host-parasite interactions. A comparison of justifications used for wildlife brucellosis management policy in Wood Buffalo National Park (NP) (Canada) and the Greater Yellowstone Area (U.S.) demonstrates how perspective (with or without science) can drive policy formation. If wildlife scientists consistently used the H-D method to gather reliable knowledge pertinent to an ecological perspective of wildlife brucellosis (or other host-parasite interactions), their contribution toward the formation of disease management policy would be more significant. In situations where disease management must commence prior to the completion of manipulative experiments (which admittedly can be difficult to apply with free-roaming wildlife), adaptive resource management, as suggested by Walters (1986), could profitably be used to test hypotheses.

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Romesburg's (1981) argument that medical science's quest for reliable knowledge is like that of wildlife science (Nichols 1991) can be extended by illustrating how medical *practice* is analogous to wildlife management and policy making—the practice portion of wildlife science. In both fields, practitioners are trained to translate science into practice. Practitioners commonly collect information or observations, hypothesize (diagnose) the cause, and collect more data aimed at narrowing the list of differential diagnoses to a definitive one. If a medical problem is serious enough, however, treatment of the most likely causes frequently evolves while results of further testing are pending.

I argue that wildlife policy makers and managers who must deal with disease issues often apply such techniques. They, like medical practitioners, assume that (1) doing something that might be beneficial is better than doing nothing when the facts are unclear and the problem appears to be critical, (2) as long as a treatment is expected to cause no harm it might as well be tried, and (3) because visible action in the face of conspicuous disease demonstrates one's

good intentions, it has inherent merit. Veterinary practitioners often summarize this concept by stating that "it is better to wonder why the animal lived than know why it died." I maintain that, while it might be appropriate for a rural veterinarian to utilize a blitz of therapeutic remedies to treat a critically ill horse while awaiting diagnostic test results, it is rarely appropriate for wildlife policy makers and managers to implement sweeping disease management programs prior to testing specific hypotheses about whether diseases have the ecological consequences they are frequently assumed to have. Most wildlife-parasite interactions, for instance, might not need to be considered emergencies demanding action before facts are collected. At the very least, "management" should be effected as experimentation to test hypotheses about the effects of diseases. (See Nichols [1991], Sinclair [1991], and Murphy and Noon [1991] regarding adaptive resource management.)

I use current controversies about management policy for brucellosis in wildlife in the Greater Yellowstone Area (Yellowstone NP, Grand Teton NP, and thousands of hectares of