Spotted Owl Research: A Quarter Century of Contributions to Education, Ornithology, Ecology, and Wildlife Management

Author: Gutiérrez, R. J.

Source: The Condor, 110(4) : 792-798

Published By: American Ornithological Society

URL: https://doi.org/10.1525/cond.2008.8615

COMMENTARY

The Condor 110(4):792–798

SPOTTED OWL RESEARCH: A QUARTER CENTURY OF CONTRIBUTIONS TO EDUCATION, ORNITHOLOGY, ECOLOGY, AND WILDLIFE MANAGEMENT

R. J. Gutiérrez[1]

Department of Fisheries, Wildlife, and Conservation Biology, University of Minnesota, St. Paul, Minnesota 55108

Abstract. A great deal of research has been devoted to the study of the Spotted Owl (*Strix occidentalis*), particularly over the past quarter century. The problems faced by scientists working to achieve conservation of this species have required the development of new approaches and methods in data analysis, scientific inference, and conservation planning. Moreover, the substantial depth of information gathered during Spotted Owl studies provides an extensive platform upon which new ideas and methods can be tested and developed. Some of these advances are discussed in this paper. These contributions show that the study of the Spotted Owl has resulted in information and methods that are not only specific to the owl and its conservation but also are broadly relevant to ornithologists, ecologists, and wildlife managers.

Key words: *conservation planning, scientific contributions, Spotted Owl*, Strix occidentalis.

Investigaciones sobre *Strix occidentalis*: Un Cuarto de Siglo de Contribuciones a la Educación, Ornitología, Ecología y Manejo de Fauna

Resumen. Se ha dedicado mucho esfuerzo al estudio de *Strix occidentalis*, especialmente durante este último cuarto de siglo. Los problemas a los cuales los investigadores han tenido que enfrentarse para lograr la conservación de esta especie han requerido del desarrollo de nuevas aproximaciones y métodos para el análisis de datos, la inferencia estadística y el planeamiento en conservación. Además, la profundidad substancial de la información colectada a partir de los estudios sobre *S. occidentalis*, ha generado una plataforma extensa sobre la cual pueden probarse nuevas ideas o desarrollarse nuevos métodos. Algunos de estos avances son discutidos en este artículo. Estas contribuciones muestran que el estudio de *S. occidentalis* ha generado información y métodos que no son sólo específicos para esta especie y su conservación, sino que también son de amplia relevancia para ornitólogos, ecólogos y el manejo de fauna.

The Spotted Owl (*Strix occidentalis*) has assumed a symbolic position for the conservation of North American birds and their habitats because it is at the center of a debate about conservation of endangered species in general, and old-growth forests in particular (Simberloff 1987, Thomas et al. 1990, Gutiérrez et al. 1995). As a result, much research has been devoted to understanding its ecology in order to provide the scientific basis for credible conservation plans (Gutiérrez et al. 1995). The strong applied nature and single-species focus of this research has the potential, I believe, to overshadow its general application to ornithology and ecology. The perception that conservation-oriented research is not contributing substantively to general ecological theory or application is not limited to Spotted Owl research (Caughley 1994). Under Caughley's framework, most conservation research (and much of Spotted Owl research) has been conducted under the "declining-population paradigm," which is, according to him, of little theoretical interest (Caughley 1994:215). Indeed, the overarching funding constraint on the majority of Spotted Owl research is that it must first serve a utilitarian purpose (provide credible scientific information for conservation decisions) rather than advance general knowledge or theory. Good conservation requires appropriate and perceptive hypotheses about how systems or species will respond to management. Many management approaches require novel scientific approaches to test these hypotheses or to conduct monitoring, and have indirect or direct relevance to ecological theory regardless of how such management is labeled or characterized. Moreover, the Spotted Owl's association with forests having high economic value requires both rigorous and prudent scientific research because of the potential economic, social, political, and conservation costs associated with management decisions (Simberloff 1987, Thomas and Verner 1992, Forest Ecosystem Management Team 1993).

Throughout the past quarter century, there has been a pervasive atmosphere of antagonism toward scientific results from owl research by special-interest groups (Murphy and Noon 1991). This challenges researchers to avoid being distracted by criticisms of their research by such groups while pursuing the best applied science. Ironically, this contentious environment has led to more-defensible results and to the development of methods that not only served the objective of Spotted Owl management, but also contributed more broadly to the fields of ornithology, ecology, and wildlife management. Although the extent of empirical research on Spotted Owls is well known (Gutiérrez et al. 1995, Noon and Franklin et al. 2002), I present here some general contributions that Spotted Owl research has made to student education, ornithology, ecology, and conservation. Many of these contributions have broad general applications, and while their initial development was motivated by specific Spotted Owl problems, such contributions would likely have been developed at a

Manuscript received 29 April 2008; accepted 4 October 2008.
[1]E-mail: gutie012@umn.edu

The Condor, Vol. 110, Number 4, pages 792–798. ISSN 0010-5422, electronic ISSN 1938-5129. DOI: 10.1525/cond.2008.8615

later date. Yet, they were certainly given impetus by Spotted Owl conservation needs. In this paper, my goal is to illustrate how research on Spotted Owls has a much greater application beyond the owl and should therefore be of interest to both ornithologists and vertebrate ecologists.

I restrict my comments to the period 1983–2007 because it approximates the modern era of Spotted Owl research, the beginning of which is signified by seminal papers on the owl (Forsman 1983, Forsman et al. 1984). Noon and Franklin (2002) provide a brief but excellent summary of the historical contributions and the potential of Spotted Owl studies to contribute to population dynamics and conservation. They also provide the legal and political context that has framed Spotted Owl conservation and advocate the search for causal mechanisms (e.g., experiments) underlying observed life-history patterns. Thus, I will not duplicate their fine effort, but rather, I provide additional context to their paper.

SPECIFIC CONTRIBUTIONS TO EDUCATION, ORNITHOLOGY, ECOLOGY, AND WILDLIFE MANAGEMENT

NATURAL HISTORY AND STUDENT EDUCATION

Much natural history information has been gathered on Spotted Owls in the past quarter century because this information (e.g., habitat use, home range size) is necessary for management plans (e.g., silvicultural prescriptions, reserve design). The sheer amount of owl research has been a function of the enormous economic and political pressure surrounding the listing of the owl as a threatened species and the need to develop robust and credible conservation plans, which have resulted in profound changes in rates of logging and land conserved in the western United States (Thomas et al. 1990, U.S. Department of the Interior 1990, 1993, Verner et al. 1992, Forest Ecosystem Management Assessment Team 1993, Gutiérrez et al. 1995, 1996). Through 2007, there has been a minimum of 1533 unpublished governmental-agency or other project reports on the Spotted Owl or its management, of which 95% were from the past quarter century. Similarly, there has been a minimum of 531 peer-reviewed papers published during the same time period. I believe that there have been at least five important catalysts that led to an increase in the rate of research and publication: (1) the uncertainty about the habitat requirements and population status of Spotted Owls (U.S. Department of Agriculture 1988, U.S. Department of the Interior 1990, Verner et al. 1992); (2) the potential impact of Spotted Owl conservation on logging (Forest Ecosystem Management Assessment Team 1993, Thomas et al. 1993); (3) a scientific symposium held under the auspices of the Cooper Ornithological Society in 1984 (Gutiérrez and Carey 1985); (4) key conservation plans mandated, by the United States Congress, to be scientifically credible (Thomas et al. 1990, Verner et al. 1992); and (5) the listing of the Northern and Mexican Spotted Owls (*S. o. caurina*, and *S. o. lucida*, respectively) as federally threatened subspecies (U.S. Department of the Interior 1990, 1993).

The attention devoted to each subspecies is probably a function of its relative economic importance (i.e., the timber value of trees is highest in the range of the Northern Spotted Owl and lower in the ranges of the California [*S. o. occidentalis*] and Mexican Spotted Owls) and the length of time that there has been concern about a subspecies' status. The distribution of peer-reviewed papers supports my speculation, with approximately 37% of papers devoted primarily to Northern Spotted Owls, 20% to the other two subspecies, and 43% of remaining papers devoted either to general Spotted Owl topics or to all three subspecies collectively. In addition, papers on natural history are most represented in the literature ($n = 145$, 27%), followed by those on population dynamics ($n = 94$, 18%), management ($n = 90$, 17%), and policy or law ($n = 76$, 14%), with 24% ($n = 126$) devoted to all other topics.

The emphasis on basic ecological (natural history) information is appropriate because it provides the foundation for management plans. Such information helps prevent "silly mistakes" (Caughley and Gunn 1996) when creating management plans, although this has not always happened with Spotted Owls. For example, economic and political considerations strongly influenced Northern Spotted Owl conservation until the species was finally listed as threatened (Thomas and Verner 1992), leading to "silly mistakes" in management strategies (e.g., size for habitat reserves in initial conservation plans were below the minimum known home-range sizes of Spotted Owls; U.S. Department of Agriculture 1988). Subsequent to the failure of early conservation plans for the Northern Spotted Owl, the most relevant and recent natural-history information has been integrated into all subsequent management plans and listing decisions (Thomas et al. 1990, U.S. Department of the Interior 1990, 1993, Verner et al. 1992, Forest Ecosystem Management Assessment Team 1993, Gutiérrez et al. 1996).

An important attribute of many Spotted Owl natural history studies, not easily discerned from a casual reading of the literature, is that they are either components of much larger studies or studies replicated by geography, by time, and by subspecies. These designs are necessary to answer more complex questions about habitat ecology or to assess the link between owl population dynamics and habitat (Franklin et al. 2000). Because these designs are complex, they require substantial data gathered at different scales. Spotted Owl studies are among the few species-level studies that have the data to support such complex analyses (Franklin et al. 2000, 2004, Seamans 2005, Anthony et al. 2006). Identification of scale-dependent habitat selection is essential to designing conservation plans for Spotted Owls because the economics associated with incorrect management guidelines can be substantial. Moreover, with replicated studies, patterns can be revealed in the absence of experimental studies, based on a "strength of evidence" approach (Goldstein and Goldstein 1978, Beyers 1998, Noon and Franklin 2002). A common frustration among Spotted Owl researchers when submitting papers is that reviewers often do not see or understand the broader context of these replicate studies of habitat, home range, or other natural-history attributes. It is a paradoxical irony that the foundation of science is repeatability, but that novelty, not repeatability, is a publication priority in ornithology and ecology. Nevertheless, in the absence of critical experiments (Noon and Franklin 2002), these replicated studies have provided the generality needed to support rangewide conservation plans and provide the strength of evidence (repeatability) to withstand legal challenges. These individual natural-history studies are often completed by graduate students and frequently provide important covariates that have been used in studies that assess the influence of habitat on population dynamics (Franklin et al. 2000, Seamans 2005). Thus, research on the Spotted Owl illustrates the importance of replicated studies throughout the range of a species when the conservation of that species is contentious, experiments are lacking, and experiments are prohibitively expensive.

Many management questions are ideally suited to graduate-student research. To that end, students have earned a minimum of 58 M.Sc. and eight Ph.D. degrees studying Spotted Owls. All but three of these have been completed since 1983. This graduate research has spanned a gamut of topics from behavior to population dynamics. The role of students in Spotted Owl research has been critical because their research has provided important building blocks for conservation plans or for more complex analyses (e.g., development of accurate habitat maps and habitat analyses that aid in the development of model covariates). For example, graduate students studying Spotted Owls under my direction have developed their own habitat (vegetation) maps because existing federal agency maps were not sufficiently accurate for habitat assessments. We then used these student-generated maps to develop habitat covariates for analyses (Seamans and Gutiérrez 2007). Many M.Sc. degree students studying Spotted Owls also have pursued Ph.D. degrees in ornithology or wildlife ecology, so it is clear that the study of Spotted Owls has facilitated the development of a cadre of future ornithologists and wildlife ecologists at different entry levels.

SYSTEMATICS

The first major Spotted Owl management plan was predicated on the "50–500 genetics rule" (this idea suggests that about 50–500 individuals are needed to maintain evolutionary potential in a population) popular in conservation biology at the time (Franklin 1980, U.S. Department of Agriculture 1988). This premise was questioned by Barrowclough and Coats (1985), who thought that owl population dynamics was a more critical issue. Nevertheless, both the genetic variability and systematic relationships of Spotted Owls have assumed positions of controversy. Thus, the need to resolve or clarify Spotted Owl systematics stimulated research (Barrowclough and Gutiérrez 1990, Barrowclough et al. 1999, 2005, 2006, Haig et al. 2004), which provided this clarification. Yet misinterpretation of the results of Barrowclough and Gutiérrez (1990) and Haig et al. (2004) allowed an opportunity by special-interest groups, through the public media, to obfuscate the owl's phylogenetic relationships. Regardless, the work accomplished in Barrowclough's lab provided the sequencing primers (i.e., the foundation) for these systematic studies and other genetic studies of Spotted Owls and other *Strix* species. The study of conservation genetics is important and is considered frequently in endangered-species issues, sometimes unwisely (Zink 2004); the Spotted Owl research provides a good example of the utility of genetic data when conservation is contentious.

HABITAT RELATIONSHIPS

There have been more studies published on the habitat relationships of Spotted Owls than on any other species of raptor (Lõhmus 2004). Most of these studies were motivated as a result of concern over the effects of logging on the owl's habitat throughout its varied, large geographic range. There was also a great deal of political and economic pressure to find conditions where owls were not associated with mature and old-growth forests in order to provide evidence that the owl was "adaptable" to loss of habitat. Replicated studies provided the strength of evidence to support early findings that Spotted Owls were habitat specialists that used either old forests or structurally complex forests (Thomas et al. 1990, Verner et al. 1992).

Habitat studies also provided the foundation for attempts to link habitat conditions with demographic parameters (Franklin et al. 2000). Habitat and demographic parameters had not been previously integrated at such large scales for any endangered species. Franklin et al. (2000) developed a novel method of assessing the relationships between demography and habitat selection using a metric called "habitat fitness potential." This metric employed a Leslie matrix where the individual elements were the survival and reproduction of owls within particular territories linked to habitat conditions within that territory. The sedentary nature and strong territoriality of Spotted Owls, combined with the development of excellent techniques for assessing survival and reproduction (two critical components of fitness), made it an ideal species for evaluating the linkages between habitat and fitness.

One long-recognized problem with attempts to link habitat covariates with vital rates of Spotted Owls (or any other species) is that such linkages are conditional on a particular bird occupying a specific site, which places substantial limitation on analysis (sample size) because birds can move or die. This limitation was recognized early in Spotted Owl studies and motivated the development of analytical approaches based on occupancy of sites. Occupancy analysis was conditional only on a site having been occupied at least once by an owl during a study. Thus, rates of site occupancy (or extinction and colonization rates of sites) could be used to assess the relationship between these parameters and habitat conditions within Spotted Owl territories. So we now have analytic approaches that focus on individual animals (capture-recapture), integrated across the habitats that they use, and on sites or habitats (occupancy), integrated across the various individuals that may use them through time. Because of high site fidelity in Spotted Owls, birds and sites are certainly not viewed as biologically independent. Yet conditional on this biological dependence, we can still draw strong inferences about survival of birds and about bird occupancy dynamics of sites using these two classes of models.

In addition, Spotted Owls and other species are often monitored by vocal detection during standardized surveys (Franklin et al. 1996). Such presence-absence information has been used by ecologists for over a century, but the problem of imperfect detection had been largely ignored (MacKenzie et al. 2006). Thus, a formal analytical structure for such occupancy data was needed. In the late 1980s, independent efforts by Azuma et al. (1990), J. D. Nichols (U.S. Geological Survey, pers. comm.), K. H. Pollock (North Carolina State University), and others led to development of the first occupancy models for Spotted Owls in response to monitoring requirements for Spotted Owls by federal agencies. Subsequently, D. I. MacKenzie (Proteus Wildlife Research Consultants) and his coworkers expanded the applications of occupancy models (MacKenzie et al. 2002, 2003, 2006). Occupancy models have been used to examine Spotted Owl habitat relationships, effects of Barred Owls (*S. varia*) on Spotted Owls, and the effect of logging on dispersal (Olsen et al. 2005, Seamans 2005, Seamans and Gutiérrez 2007), but they could be used for any species that can be detected by its vocalizations or other evidence of presence. Finally, occupancy models are being extended to multistate conditions (i.e., occupancy models that consider additional information or "states" besides whether a site or habitat is occupied or unoccupied, such as unoccupied, occupied with no production of young, and occupied with successful reproduction), motivated by the uncertainty in reproduction outcomes of Spotted Owl assessments, but again, they have widespread application (Nichols et al. 2007, MacKenzie et al. in press). Many important advances like the development of occupancy models, which were partly motivated by the needs of Spotted Owl conservation, almost certainly would have been developed at some other time because they have widespread application to many species and problems in ecology, ornithology, and wildlife management (MacKenzie et al. 2006). However, the immediate need, stimulated by management and policy concerns for the Spotted Owl, helped motivate their development more quickly.

POPULATION DYNAMICS

The population status of the owl and the methods by which Spotted Owl population dynamics are assessed continues to be hotly debated despite some of the most rigorous mark-recapture studies ever conducted (see Boyce et al. 2005 and Loehle et al. 2005 as examples of criticism of Spotted Owl population analyses). Thus, it is not surprising that owl population studies have been at the forefront of extremely important analytical advances that have general benefit to studies of animal populations.

Following the listing of the Northern Spotted Owl as a threatened species, the United States Secretaries of Agriculture and the Interior requested that a workshop be convened in 1993 to examine all extant Spotted Owl population data (Forsman et al. 1996). This was the first of five meta-analyses of Spotted Owl population data conducted between 1993 and 2006 (Forsman et al. 1996, Franklin et al. 1999, 2004, Anthony et al. 2006, Blakesley et al. 2006). Although, mark-recapture theory and methodology were well developed, it became apparent during the first Spotted Owl workshop that the sheer quantity and complexity of the mark-recapture data were an impediment to modeling efficiently the many a priori hypotheses that could be considered in an analysis. Program SURGE was one of the programs used at the first meta-analysis (Pradel et al. 1990), which illustrated this problem (Forsman et al. 1996). Thus, G. C. White (Colorado State University) developed a "front-end" program to SURGE that facilitated the input of Spotted Owl data into SURGE. This program was the origin of Program MARK (White and Burnham 1999, G. C. White, pers. comm.). White (pers. comm.) would have developed MARK eventually because of a fundamental need for a comprehensive program to analyze population data. Program MARK has enjoyed exponential growth in its use, and it has been made freely available by White (at <http://welcome.warnercnr.colostate.edu/~gwhite/mark/mark.htm>). Spotted Owl researchers also contributed to the development of MARK through beta testing of some of the first iterations of the program (A. B. Franklin, Colorado State University, pers. comm.). The Spotted Owl meta-analyses also have served as beta-testing platforms.

At the 1993 meta-analysis workshop, Spotted Owl trends were estimated using a Leslie projection matrix based on the estimates of stage-specific reproductive and survival rates of birds (Franklin et al. 1996). However, it was recognized during the workshop that estimates of the finite rate of population change using the projection method (denoted here as λ_{pm}) could be biased because juvenile owls were known to emigrate from study areas (Gutiérrez et al. 1985, Miller et al. 1997). Thus, Burnham et al. (1996) attempted to correct for this potential bias using estimates of juvenile emigration rates derived from radio-telemetry studies. Despite the attempt to correct this potential bias, the projection-based trend analysis was criticized. This criticism was relevant not only to Spotted Owls but also to all studies of species where the study area was of finite size and where dispersal occurred (Barrowclough 1978, Zimmerman et al. 2007). As a result, one of the participants of the workshop, J. D. Nichols (U. S. Geological Survey), sponsored a postdoctoral researcher whose research objective was to develop a solution to overcome this problem. The solution was the development of a reverse time-series Jolly-Seber estimator, which also would have broad general application to studies of population trends (Pradel 1996). This estimator (denoted λ_{RJS}) has been used in all owl meta-analyses subsequent to 1993. The estimator was not a panacea for understanding trends because the underlying reasons for changes in numbers of owls on a study area were obscured (Franklin et al. 2004), but it did overcome the bias of undetected emigration rates of owls. To overcome this lack of biological insight, work was initiated to partition the contributions of emigration and immigration to λ_{RJS} (Nichols et al. 2000). In addition, investigation of possible bias in this estimator was motivated entirely by the Northern Spotted Owl data (Hines and Nichols 2002). Again, these inference methods were stimulated in part by the immediate needs of Spotted Owl researchers but have extensive potential application for estimation of population trends for animals that can be counted accurately on study areas.

Another problem, encountered by scientists working on recovery of the Mexican Spotted Owl was how to monitor trends of this spatially extensive metapopulation. The solution was to sample a large number of quadrats using mark-recapture and combine the resulting data into a single estimator. This estimator was developed by Bowden et al. (2003) and also has important applications to ecology and conservation of metapopulations.

Although inferences attributable to various owl trend analyses or estimation results have been carefully presented in most owl papers because of the concern that vested interests have in the results of these analyses, the meaning of λ, the finite rate of population change, was opaque to the general public. Thus, Franklin et al. (2004) developed a unique metric called "realized change" (Δ_t), which represented the proportion of the population size in the first year that remained in each subsequent year. It was a simple, relative measure of the change in the population from the beginning to the end of a study.

WILDIFE MANAGEMENT AND CONSERVATION PLANNING

The conservation of the Spotted Owl began as a specific wildlife-management problem but quickly expanded to broader conservation issues. Its iconic significance is obvious because it is rare in conservation annals that the United States Congress demands a credible conservation plan for a species. Such was the case with the Northern Spotted Owl when Congress commissioned a "scientifically credible" plan for its conservation (Interagency Scientific Committee [ISC]; Thomas et al. 1990). This demand was made because prior plans were challenged in court as inadequate to protect the owl. Such inadequacy likely contributed to the listing of the Northern Spotted Owl as an endangered species (U.S. Department of the Interior 1990). The resulting ISC plan made three major contributions to conservation planning: (1) the plan was premised on testing a priori biological hypotheses about the owl; (2) individual-based models were developed based on owl ecology and population theory to guide the development of a land-allocation strategy; and (3) the conservation strategy itself was considered a falsifiable hypothesis (Thomas et al. 1990, Noon and McKelvey 1996). This approach set a standard for conservation plans because of its clarity, rigor, adherence to scientific principles, and its persistence following many political and legal challenges (Noon and McKelvey 1996).

The ISC plan also became the foundation for all subsequent conservation plans for owls and Pacific Northwest forests (Noon and McKelvey [1996] provided an extensive review of the ISC and its link to the Northwest Forest Plan [U.S. Department of Agriculture and U.S. Department of the Interior 1994]). The ISC plan was developed at the same time the owl was listed as threatened, so the first Northern Spotted Owl recovery team reviewed the ISC conservation strategy and adopted it with some minor modifications (U.S. Department of the Interior 1992). This team produced a draft recovery plan for the Northern Spotted Owl (U.S. Department of the Interior 1992), which was never accepted because it became entangled by politics (i.e., change of national political administrations in Washington, DC.). Nevertheless, one conservation aspect that was developed within that plan was a brief exposition of the contribution that a Spotted Owl recovery strategy would make to conservation of other wildlife and forests in the Pacific Northwest. This draft recovery plan illustrated both the need to protect the owl and the concern that more values were at stake in this regionwide conservation issue. As part of his presidential campaign, President Clinton pledged to resolve the controversy that for years surrounded the conservation of ancient forests of the Pacific Northwest and the Spotted Owl. He fulfilled his pledge by supporting the development of the Pacific Northwest Forest Plan, which was a comprehensive plan to conserve all biological values (vertebrates, forests, watersheds, and ecosystems) within the Pacific Northwest forests (U.S. Department of Agriculture and U.S. Department of the Interior 1994). A scientific analysis team provided a comprehensive assessment and recommendations for many issues surround such an ambitious endeavor (Forest Ecosystem Management Assessment Team 1993, Thomas et al. 1993). Spotted Owls were but one component of that plan, yet they were a critical one because they gave impetus to the design of the final strategy through the ISC process. Further, an integral part of the Pacific Northwest plan was an "effectiveness monitoring plan" for the owl. This monitoring plan depended on the long-term owl mark-recapture studies described above. So in the case of the Northern Spotted Owl, a single species conservation plan evolved into a multidimensional conservation plan, yet the latter is still partly dependent on the former through "effectiveness monitoring." As Noon and McKelvey (1996) note, the scientific rigor and transparent process that resulted in the creation of these plans have set a standard that has been robust to legal and political challenges. Hence, they serve as a model for conservation action for all wildlife and forests.

An alternative but equally novel conservation plan was developed for the California Spotted Owl (Verner et al. 1992). This was a habitat-based rather than a reserve-based strategy like the Northern Spotted Owl plan. This plan was different from the ISC plan because there was greater uncertainty about the response of owls to current habitat conditions, its population status, and its nearly continuous spatial distribution in the Sierra Nevada, California. However, like the ISC, this plan was predicated on scientific credibility. I think these divergent plans also provided a measure of credibility to the public and the government that a rigorous scientific process for considering conservation strategies could result in different approaches for the same species (i.e., the differences demonstrated that the plans were not simply "land grabs" by environmentalists, as had been suggested by some special interest groups).

CONFLICT RESOLUTION IN SCIENCE

The first Spotted Owl meta-analysis was beset by conflict when one modeler representing a special-interest group criticized the methods, yet left the analysis workshop without either debating the criticism or providing an alternative approach (Anderson et al. 1999). A second participant withdrew his data after observing and disagreeing with the results of the analysis. Consequently, Anderson et al. (1999) developed a protocol to avoid such conflicts in future Spotted Owl meta-analyses. This protocol has been used with great success in all subsequent meta-analyses because it establishes a priori guidelines for discussion, procedures, level of rigor, transparency of data, accuracy of data, analyses, and other details relevant to an entire analytical process (Franklin et al. 2004:appendix 2). While this protocol was developed to serve the needs of Spotted Owl meta-analyses, it is general to all analyses of collective data where the results are likely to be controversial or subject to external debate. Moreover, the wide distribution of the owl and similarity of management challenges for their conservation across their range facilitated an exceptional degree of cooperation and synergism among many scientists. Scientists working on Spotted Owls collectively embraced the emerging analytical paradigm of model selection based on likelihood estimation (Burnham et al. 1996), which served to elevate the rigor of Spotted Owl studies as well as to enhance inference from analyses. Using model selection does not provide the underlying mechanisms for Spotted Owl responses as advocated by Noon and Franklin (2002), but it can establish a stronger foundation for designing experiments than would have been possible using classic inferential statistics. The meta-analyses described above, the adoption of a model selection paradigm, and the ability to resolve conflicts among scientists taken together serves as an exemplary model for conservation science and wildlife management.

POTENTIAL FOR FUTURE CONTRIBUTIONS OF OWL RESEARCH

The attention the Spotted Owl has received because of its use of old forests and the decline of some of its populations has led to substantial research to support conservation planning. Spotted Owl population studies are the most intensive ever to be conducted on an endangered species. Despite this solid foundation of information, almost everything discovered about Spotted Owls has been challenged in some way. A cottage industry has developed to find weaknesses in these research results, and the research environment occasionally has been acrimonious. Paradoxically, this seemingly tense situation has led to the development of much stronger analytical methods to remove criticism and make inferences stronger. Many of these methods and results have widespread application to ornithology, ecology, and wildlife management.

I believe that ornithologists and ecologists would be well served to monitor the Spotted Owl literature because of emerging developments. In the future, I expect that new methods and approaches will arise from the study of Spotted Owls because the substantial data thus far collected on the species provides an extensive data platform for examining new methodologies and analyses, which will ultimately be useful for testing many ecological and theoretical ideas. For example, the Northern Spotted Owl population studies are both enormous and long term, with 14 studies (some up to 23 years in length) recording 32 054 recaptures of 11 432 banded birds over nearly 30 000 km^2 of area (Anthony et al. 2006). The beauty of the Spotted Owl data is that they have been rigorously and synchronously collected over vast areas with an emphasis on precisely estimating fitness parameters (survival and reproduction), so they will continue to lend themselves well to testing ecological theory and to developing new analytical methods of interest to many scientists.

ACKNOWLEDGMENTS

I thank Luke George for inviting me to present parts of this paper at the 2005 Cooper Ornithological Society meeting. David Dobkin suggested I develop my presentation as a formal paper, and I appreciate his patience in allowing me time to write it. My 30 past and present graduate students who have worked on Spotted Owls have been a constant source of enjoyment and stimulation. Lorelle Berkeley, Laura Erickson, and Casey Phillips managed literature databases and read drafts of this paper. Martin Raphael and an anonymous reviewer provided helpful reviews of the paper. I am grateful to my long time collaborators, George Barrowclough, Alan Franklin, Gary White, Jim Nichols, Mark Seamans, and Guthrie Zimmerman for sharing many ideas and discussions over the past several decades. Jim Nichols provided helpful comments on drafts of this paper.

LITERATURE CITED

Anderson, D. R., K. P. Burnham, A. B. Franklin, R. J. Gutiérrez, E. D. Forsman, R. G. Anthony, and T. M. Shenk. 1999. A protocol for conflict resolution in analyzing empirical data related to natural resource controversies. Wildlife Society Bulletin 27:1050–1058.

Anthony, R. G., E. D. Forsman, A. B. Franklin, D. R. Anderson, K. P. Burnham, G. C. White, C. J. Schwarz, J. D. Nichols, J. E. Hines, G. S. Olson, S. H. Ackers, L. S. Andrews, B. L. Biswell, P. C. Carlson, L. V. Diller, K. M. Dugger, K. E. Fehring, T. L. Fleming, R. P. Gerhardt, S. A. Gremel, R. J. Gutiérrez, P. J. Happe, D. R. Herter, J. M. Higley, R. B. Horn, L. L. Irwin, P. J. Loschl, J. A. Reid, and S. G. Sovern. 2006. Status and trends in demography of northern Spotted Owls, 1985–2003. Wildlife Monographs 163.

Azuma, D. L., J. A. Baldwin, and B. R. Noon. 1990. Estimating the occupancy of Spotted Owl habitat areas by sampling and adjusting for bias. USDA Forest Service General Technical Report PSW-124.

Barrowclough, G. F. 1978. Sampling bias in dispersal studies based on finite area. Bird Banding 49:333–341.

Barrowclough, G. F., and S. L. Coats. 1985. The demography and population genetics of owls, with special reference to the conservation of the Spotted Owl (*Strix occidentalis*), p. 74–85. *In* R. J. Gutiérrez and A. B. Carey [eds.], Ecology and management of the Spotted Owl in the Pacific Northwest. USDA Forest Service General Technical Report PNW–185.

Barrowclough, G. F., and R. J. Gutiérrez. 1990. Genetic variation and differentiation in the Spotted Owl (*Strix occidentalis*). Auk 107:737–744.

Barrowclough G. F., J. G. Groth, L. A. Mertz, R. J. Gutiérrez. 2005. Genetic structure, introgression, and a narrow hybrid zone between Northern and California Spotted Owls (*Strix occidentalis*). Molecular Ecology 13:1911–1922.

Barrowclough G. F., J. G. Groth, L. A. Mertz, R. J. Gutiérrez. 2006. Genetic structure of Mexican Spotted Owl (*Strix occidentalis lucida*) populations in a fragmented landscape. Auk 123: 1090–1102.

Barrowclough, G. F., R. J. Gutiérrez, and J. G. Groth. 1999. Genetic structure of Spotted Owl populations based on mitochondrial DNA sequences. Evolution 53:919–931.

Beyers, D. W. 1998. Causal inference in environmental impact studies. Journal of the North American Benthological Society 17:367–373.

Blakesley, J. A., D. Anderson, and D. Noon. 2006. Breeding dispersal in the California Spotted Owl. Condor 108:71–81.

Bowden, D. C., G. C. White, A. B. Franklin, and J. L. Ganey. 2003. Estimating population size with correlated sampling unit estimates. Journal of Wildlife Management 67:1–10.

Boyce, M. S., L. L. Irwin, and R. Barker. 2005. Demographic meta-analysis: synthesizing vital rates for Spotted Owls. Journal of Applied Ecology 42:38–49.

Burnham K. P., D. R. Anderson, and G. C. White. 1996. Meta-analysis of vital rates of the Northern Spotted Owl. Studies in Avian Biology 17:92–101.

Caughley, G. 1994. Directions in conservation biology. Journal of Animal Ecology 63:215–244.

Caughley, G., and A. Gunn. 1996. Conservation biology in theory and practice. Blackwell Science, Cambridge, MA.

Forest Ecosystem Management Assessment Team [U. S. Department of Agriculture, Forest Service, U.S. Fish and Wildlife Service, National Oceanic and Atmospheric Administration, National Marine Fisheries Service, National Park Service, Bureau of Land Management, and Environmental Protection Agency]. 1993. Forest ecosystem management: an ecological, economic, and social assessment. Report of the Forest Ecosystem Management Assessment Team. Portland, OR.

Forsman, E. D. 1983. Methods and materials for locating and studying spotted owls. USDA Forest Service General Technical Report PNW-162.

Forsman E. D., S. DeStefano, M. G. Raphael, and R. J. Gutiérrez. 1996. Demography of the Northern Spotted Owl. Studies in Avian Biology 17.

Forsman, E. D., E. C. Meslow, and H. M. Wight. 1984. Distribution and biology of the Spotted Owl in Oregon. Wildlife Monographs 87.

Franklin, A. B., D. R. Anderson, E. D. Forsman, K. P. Burnham, and F. W. Wagner. 1996. Methods for collecting and analyzing demographic data on the Northern Spotted Owl. Studies in Avian Biology 17:12–20.

Franklin, A. B., D. R. Anderson, R. J. Gutiérrez, and K. P. Burnham. 2000. Climate, habitat quality, and fitness in Northern Spotted Owl populations in northwestern California. Ecological Monographs 70:539–590.

Franklin, A. B., K. P. Burnham, G. C. White, R. G. Anthony, E. D. Forsman, C. Schwarz, J. D. Nichols, and J. Hines. 1999. Range-wide status and trends in Northern Spotted Owl populations. Colorado Cooperative Fish and Wildlife Research Unit, Colorado State University, Fort Collins, CO.

Franklin, A. B., R. J. Gutiérrez, J. D. Nichols, M. E. Seamans, G. C. White, G. S. Zimmerman, J. E. Hines, T. E. Munton, W. S. LaHaye, J. A. Blakesley, G. N. Steger, B. R. Noon, D. W. H. Shaw, J. J. Keane, T. L. McDonald, and S. Britting. 2004. Population dynamics of the California Spotted Owl (*Strix occidentalis occidentalis*): a meta-analysis. Ornithological Monographs 54:1–55.

Franklin, I. R. 1980. Evolutionary change in small populations, p. 135–149. *In* M. E. Soulé and B. A. Wilcox [eds.], Conservation biology, an evolutionary-ecological perspective. Sinauer Associates, Sunderland, MA.

Goldstein, M., and I. F. Goldstein. 1978. How we know: an exploration of the scientific process. Da Capo Press, New York.

Gutiérrez, R. J., and A. B. Carey [eds.]. 1985. Ecology and management of the Spotted Owl in the Pacific Northwest. USDA Forest Service General Technical Report PNW-185.

Gutiérrez, R. J., E. D. Forsman, A. B. Franklin, and E. C. Meslow. 1996. History and demographic studies in the management of the Spotted Owl. Studies in Avian Biology 17:6–11.

Gutiérrez, R. J., A. B. Franklin, and W. S. LaHaye. 1995. Spotted Owl (*Strix occidentalis*). *In* A. Poole and F. Gill [eds.], The birds of North America, No. 179. The Academy of Natural Sciences, Philadelphia, PA, and The American Ornithologists' Union, Washington, DC.

Gutiérrez, R. J., A. B. Franklin, W. LaHaye, V. J. Meretsky, and J. P. Ward. 1985. Juvenile Spotted Owl dispersal in northwestern California: preliminary results. *In*: R. J. Gutierrez and A. B. Carey, [eds.], Ecology and management of the Spotted Owl in the Pacific Northwest. USDA Forest Service General Technical Report PNW-185:60–65.

Haig, S. M., T. D. Mullins, E. D. Forsman. 2004. Subspecific relationships and genetic structure in the Spotted Owl. Conservation Genetics 5:683–705.

Hines, J. E., and J. D. Nichols. 2002. Investigations of potential bias in the estimation of lambda using Pradel's (1996) model for capture-recapture data. Journal of Applied Statistics 29:573–587.

Loehle, C., L. Irwin, D. Rock, and S. Rock. 2005. Are survival rates for northern Spotted Owls biased? Canadian Journal of Zoology 83:1386–1390.

Lõhmus, A. 2004. Raptor habitat studies—the state of the art, p. 279–296. *In* R. D. Chancellor and B. U. Meyburg [eds.], Raptors worldwide. Proceedings of the VI World Conference on Birds of Prey and Owls, Budapest, Hungary.

MacKenzie D. I., J. D. Nichols, J. E. Hines, M. G. Knutson, and A. B. Franklin. 2003. Estimating site occupancy, colonization and local extinction when a species is detected imperfectly. Ecology 84:2200–2207.

MacKenzie D. I., J. D. Nichols, G. B. Lachman, S. Droege, J. A. Royle, and C. A. Langtimm. 2002. Estimating site occupancy rates when detection probabilities are less than one. Ecology 83:2248–2255.

MacKenzie, D. I., J. D. Nichols, J. A. Royle, K. H. Pollock, L. L. Bailey, and J. E. Hines. 2006. Occupancy estimation and modeling. Elsevier, Burlington, MA.

MacKenzie, D. I., J. D. Nichols, M. E. Seamans, and R. J. Gutiérrez. In press. Dynamic models for problems of species occurrence with multiple states. Ecology.

Miller, G. S., R. J. Small, and E. C. Meslow. 1997. Habitat selection by spotted owls during natal dispersal in Western Oregon. Journal of Wildlife Management 61:140–150.

Murphy, D. D., and B. R. Noon. 1991. Coping with uncertainty in wildlife biology. Journal of Wildlife Management 55:773–782.

Nichols, J. D., J. E. Hines, J.-D. Lebreton, and R. Pradel. 2000. Estimation of contributions to population growth: a reverse-time capture-recapture approach. Ecology 81:3362–3376.

Nichols, J. D., J. E. Hines, D. I. Mackenzie, M. E. Seamans, and R. J. Gutiérrez. 2007. Occupancy estimation and modeling with multiple states and state uncertainty. Ecology 88:1395–1400.

Noon, B. R., and A. B. Franklin. 2002. Scientific research and the Spotted Owl (*Strix occidentalis*): opportunities for major contributions to avian population ecology. Auk 119:311–320.

Noon, B. R., and K. S. McKelvey. 1996. Management of the Spotted Owl: a case study in conservation biology. Annual Review of Ecology and Systematics 27:135–162.

Olson, G. S., R. G. Anthony, E. D. Forsman, S. H. Ackers, P. J. Loschl, J. A. Reid, K. M. Dugger, E. M. Glenn, and W. J. Ripple. 2005. Modeling of site occupancy dynamics for Northern Spotted Owls, with emphasis on the effects of Barred Owls. Journal of Wildlife Management 69:918–932.

Pradel, R. 1996. Utilization of capture-mark-recapture for the study of recruitment and population growth rate. Biometrics 52: 703–709.

Pradel, R. J., J. Clobert, and J. D. Leberton. 1990. Recent developments for the analysis of multiple capture-recapture data sets: an example using two Blue Tit populations. Ring 13:193–204.

Seamans, M. E. 2005. Population ecology of the California Spotted Owl in the central Sierra Nevada. Ph.D. dissertation, University of Minnesota, St. Paul, MN.

Seamans, M. E., and R. J. Gutiérrez. 2007. Habitat selection in a changing environment: the relationship between habitat alteration and spotted owl territory occupancy and breeding dispersal. Condor 109:566–576.

Simberloff, D. 1987. The Spotted Owl fracas: mixing academic, applied and political ecology. Ecology 68:766–772.

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: a report of the interagency scientific committee to address the conservation of the Northern Spotted Owl. U.S. Department of Agriculture and U.S. Department of the Interior, Portland, OR.

Thomas, J. W., M. G. Raphael, R. G. Anthony, E. D. Forsman, A. G. Gunderson, R. S. Holthausen, B. G. Marcot, G. H. Reeves, J. R. Sedell, and D. M. Solis. 1993. Viability assessments and management considerations for species associated with late-successional and old-growth forests of the Pacific Northwest: the report of the scientific analysis team. USDA Forest Service, National Forest System, Forest Service Research, Portland, OR.

Thomas, J. W. and J. Verner. 1992. Accommodation with socioeconomic factors under the endangered species act—more than meets the eye. Transactions of the 57th North American Wildlife and Natural Resources Conference 57:627–641.

U.S. Department of Agriculture. 1988. Final supplement to the environmental impact statement for an amendment to the Pacific Northwest regional guide. 2 Vols. USDA Forest Service, Portland, OR.

U.S. Department of Agriculture and U.S. Department of the Interior. 1994. Final supplement impact statement on management of habitat of late-successional and old-growth forest related species within the range of the Northern Spotted Owl. Vols. 1–2 and Record of Decision. USDA Forest Service and U.S. Bureau of Land Management, Portland, OR.

U.S. Department of the Interior. 1990. Endangered and threatened wildlife and plants: determination of threatened status for the Northern Spotted Owl. Federal Register 55:26114–26194.

U.S. Department of the Interior. 1992. Recovery plan for the Northern Spotted Owl: draft. U.S. Department of Interior, Portland, OR.

U.S. Department of the Interior. 1993. Endangered and threatened wildlife and plants; final rule to list the Mexican Spotted Owl as a threatened species. Federal Register 58:14248–14271.

Verner, J., K. S. McKelvey, B. R. Noon, R. J. Gutiérrez, G. I. Gould Jr., and T. W. Beck [eds.]. 1992. The California Spotted Owl: a technical assessment of its current status. USDA Forest Service General Technical Report PSW-113.

White, G. C., and K. P. Burnham. 1999. Program MARK: survival estimation from populations of marked animals. Bird Study 46: S120–S138.

Zimmerman, G. S., R. J. Gutiérrez, and W. S. LaHaye. 2007. Finite study areas and vital rates: sampling effects on estimates of Spotted Owl survival and population trends. Journal of Applied Ecology 44:963–971.

Zink, R. 2004. The role of subspecies in obscuring avian biological diversity and misleading conservation policy. Proceedings of the Royal Society of London Series B 271:561–564.