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OVERVIEW

SCIENTIFIC RESEARCH AND THE SPOTTED OWL (*STRIX OCCIDENTALIS*): OPPORTUNITIES FOR MAJOR CONTRIBUTIONS TO AVIAN POPULATION ECOLOGY

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Among all avian research programs, results from investigations into the ecology, behavior, life history, and demography of Spotted Owls (*Strix occidentalis*) may have had the single greatest effect on land-use policy in the United States. The reasons for that are simple: in general, throughout their ranges, populations of all three subspecies of Spotted Owl—Northern, California, and Mexican—require large areas associated with large, old trees, that have high economic value (Simberloff 1987, Yaffee 1994). In truth, motivation for that long-term, intensive research program has been driven as much by legal and political concerns as scientific interest. Legal concerns stem from a mandate to comply with federal environmental laws such as the National Forest Management Act and the Endangered Species Act—legislation that compels federal land management agencies to maintain the viability of all vertebrate species. Intense political interest is an inescapable consequence of large-scale conservation programs with extensive economic effects.

Much has been written, from both positive and negative perspectives, on the conservation significance of Spotted Owl research findings (Noon and Murphy 1997). Our objectives in this article are not to review that literature or revisit the controversies, but rather to focus on the scientific importance of the research. In brief, Spotted Owl researchers have contributed to advances in the field of conservation biology in many ways including topics in reserve design (Murphy and Noon 1992, Lamberson et al. 1994, Noon and McKelvey 1996a), population viability analyses (Lande 1988, White 2000), metapopulation theory (Lande 1987, LaHaye et al. 1994, Noon and McKelvey 1996b), individual-based models (McKelvey et al. 1993, Dunning et al. 1995), analysis of space-use (Bingham and Noon 1997, Carey and Peeler 1995), trend analysis (Burnham et al. 1996, Franklin et al. 1999), and the interface between science and the formulation of public policy (Murphy and Noon 1991, Noon and Murphy 1997).

General ecology and life history.—Our discussion will only briefly summarize what is known of the ecology and life history of Spotted Owls because numerous federal management plans address Spotted Owls (e.g. Thomas et al. 1990; U.S. Department of Agriculture 1992; U.S. Department of Agriculture et al. 1993; U.S. Department of the Interior 1992, 1995; Verner et al. 1992) and thorough reviews of the owl's ecology and life history have been published (e.g. Gutiérrez and Carey 1985, Gutiérrez et al. 1995). Spotted Owls are medium-sized owls (450–850 g) occupying primarily coniferous forests in mountainous regions of western North America and Mexico (Gutiérrez et al. 1995). In general, they are nonmigratory, but there is some evidence for short-term altitudinal migrations in winter in some populations of California Spotted Owls (Verner et al. 1992). Pairs of Spotted Owls generally occupy large home ranges (up to 3500 ha for Northern Spotted Owls in Washington State), but home-range size varies widely within and among the three subspecies (Gutiérrez et al. 1995). Variation in home-range size is associated with vegetation community type, amount of old-growth forest (Forsman et al. 1984, Carey et al. 1992), and variations in the primary prey species (Zabel et al. 1995). Even though there have apparently been large decreases in the abundance of Spotted Owl since the late 1800s, the current geographic distribution of all three subspecies appears to be similar to their historic distribution (Gutiérrez 1994).

Most observations of habitat use for Spotted Owls are associated with some component of old-growth or late seral forest. In the vast ma-

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jority of habitat-use studies, Spotted Owls have been found to use forests with greater structural complexity and older age than random sites for nesting and roosting behaviors (studies reviewed in Thomas et al. 1990; U.S. Department of the Interior 1992, 1995; Verner et al. 1992). Old-growth stands having large-diameter trees with cavities and broken tops are most often correlated with the location of nest sites. The most interesting geographic variation in habitat use is for California Spotted Owls on the western slopes of the Sierra Nevada where populations occupy mature oak woodlands at elevations below 1000 m (Verner et al. 1992) and for Mexican Spotted Owls that inhabit xeric desert canyons and older coniferous forest at higher elevations in the southwestern United States and Mexico (Ganey and Dick 1995).

Small and medium-sized mammals, primarily rodents, are the primary prey of Spotted Owls. In general, Northern Spotted Owls forage most intensely on northern flying squirrels (*Glaucomys sabrinus*) in Oregon and Washington (Carey et al. 1992) and at higher elevations in California (Verner et al. 1992). Woodrats (*Neotoma* spp.) are taken at lower elevations by both the Northern and California subspecies and at all elevations by Mexican Spotted Owls. There is some evidence that greater availability of woodrats is associated with smaller home range size in Northern and California spotted owls (Zabel et al. 1995).

Even though Spotted Owls are most often associated with late seral forest, the abundance of several preferred prey species is often greater in earlier seral stages. For example, dusky-footed woodrats (*Neotoma fuscipes*) are more common in young forest (Sakai and Noon 1993). As a consequence of that pattern of prey distribution, foraging Northern Spotted Owls in the southern portion of the geographic range may hunt disproportionately along the edges between late and early seral forest (Zabel et al. 1995, Ward et al. 1998). Ward et al. (1998) suggest that some degree of fragmentation within Northern Spotted Owl territory may provide an energetic benefit to owls by increasing that abundance of potential prey. That conjecture has recently been supported by Franklin et al. (2000) who found increased survival and reproduction in territories with high amounts of edge between late and early seral forest.

Across all three subspecies, Spotted Owls seem to follow a bet-hedging life-history strategy (Boyce 1988) with high adult survival, low and sporadic reproduction, and low recruitment rates. The life-history structure of the Spotted Owl is well known. Four age classes can be identified by plumage characteristics (Forsman 1981, Moen et al. 1991), providing a means to estimate survival and reproductive rates by age (stage) class. In general, studies have shown very similar estimates of the vital rates across all three subspecies. Age or stage-specific estimates of survival and fecundity can be used to parameterize population projection matrices with two to four distinct age (stage) classes and to project future population trajectories assuming constant vital rates (e.g. Lande 1988; Noon and Biles 1990; Seamans et al. 1999, 2001; Blakesley et al. 2001). Estimates of survival rates for Spotted Owls have been based on intensive capture–recapture studies, and fecundity rates have been estimated by determining the reproductive output of known aged birds. Spotted Owls are one of the few avian species where zero reproductive output can be estimated using field methods (Forsman 1983) such that fecundity can be estimated directly. All Spotted Owl researchers have used common methods of data collection and analysis allowing comparison across populations and subspecies (methods reviewed in Franklin et al. 1996).

Once the life-history structure has been characterized in projection matrix format, powerful analytical methods are available (Caswell 2001). For example, the dominant eigenvalue of the projection matrix (λ) is an estimate of population trend over the period of the study. The sensitivities or elasticities of the elements of the projection matrix estimate the degree to which variation in those elements affect the rate of population change (Caswell 2001). Such analyses provide insights to management and design of field studies (e.g. Noon and Biles 1990). For example, sensitivity analyses of the projection matrix have shown that population growth rate is most influenced by adult female survival rate (Lande 1988, Noon and Biles 1990). That result led to a focus on capture–recapture field methods that provided precise and unbiased estimate of adult survival rate (Franklin et al. 1996).

Eigenvector sensitivities are not necessarily indicative of the life-history attributes that have most influenced the observed dynamics of a population (Noon and Biles 1990). It is often the vital rate that is naturally most variable that has contributed most to the observed variation in population growth (Sæther and Bakke 2000). For Spotted Owls, most researchers have found fecundity to show much greater year-to-year variation than survival rate (Seamans et al. 2002, Blakesley et al. 2001, Franklin et al. 2000).

To summarize, it is clear that we currently know a great deal about the life history and ecology of Spotted Owls. In addition, common field methods and methods of analysis have allowed comparisons with and among subspecies that are seldom achieved in studies of other species. That work has provided good quantitative descriptions of natural history and yielded a large body of descriptive work that provides a solid foundation for developing alternative hypotheses in subsequent observational studies. The studies have also been relatively long-term, allowing researchers to examine the plausibility of alternative hypotheses as explanation of the observed patterns of temporal and spatial variation and population trends. In addition, examples from Spotted Owls have contributed to advances in life-history sensitivities in birds (Blakesley et al. 2001) and provided valuable data sets for quantitative ecologists to explore.

However, it also clear that until recently most Spotted Owl research has been descriptive. Researchers have described the geographic distribution, habitat relationships, area requirements, prey relationships, life-history sensitivities, and population trends of owls with great detail. Unfortunately, the mechanisms underlying the observed patterns of variation are, for the most part, unknown. Only recently have Spotted Owl researchers begun to explore causal models to better understand relationships and to seek mechanistic explanations for the patterns that have been observed (e.g. Franklin et al. 2000, Seamans et al. 2002).

Evolution of Spotted Owl Research and its Relevance to Population Ecology

Similar to many other studies in population ecology, research on Spotted Owls has proceeded in a logical sequential fashion beginning with descriptive studies of life history, behavior, and habitat ecology. Initial studies focused on characterizing the geographic distribution of the species and its general habitat associations. That work was followed by more detailed investigations into patterns of distribution within its geographic range, specific habitat relationships within these areas, estimates of minimum area requirements, and the extent of geographic variation in these patterns. Much of that work was inspired by a concern that species associated with late successional forest in the western United States may be subject to significant population declines due to high levels of timber harvest (Thomas et al. 1990, Verner et al. 1992). Such descriptive research on basic ecological and habitat relationships has proven extremely important in the development of long-term management plans on public lands for all three subspecies (Thomas et al. 1990, U.S. Department of Agriculture 2001, U.S. Department of Agriculture et al. 1993, U.S. Department of the Interior 1995, Verner et al. 1992). Those plans all specify constraints on silvicultural practices within Spotted Owl habitat and minimum areas for retention of late seral forest conditions (e.g. Bingham and Noon 1997). For the most part, those guidelines were based on information gathered from radio-tagged owls followed by estimates of home-range size and habitat use.

Concurrent with those habitat-use studies, heated debate arose over the ''true'' status and trend of Spotted Owl populations on public lands. That occurred first, and most pronounced, for Northern Spotted Owl populations that occupy forests extensively exploited for timber products. As a consequence of those controversies, research became considerably more focused on population dynamics and temporal trends. That research emphasized demographic studies and employed intensive capture–recapture methods to provide estimates of age-specific survival rates, and behavioral methods to locate reproducing owls and to estimate reproductive output (Franklin et al. 1996).

For many years, obtaining precise and accurate estimates of population trend within local populations of Spotted Owls has been the primary research agenda. That was motivated, in large part, because of the uncertainty of the status of the Spotted Owl and the potential economic consequences of listing the various subspecies under the Endangered Species Act. Though the motivation and funding for that research was not specifically addressed at advancing our knowledge of population dynamics, significant insights into the design, analysis, and interpretation of demographic studies was made. For example, during that period, significant advances in mark–recapture methods (White and Burnham 1999) and the analysis of life-history sensitivities and projection matrices were stimulated, in part, by ongoing research on Spotted Owls (e.g. Lande 1998, Mills et al. 1999).

Research on Spotted Owls has now largely moved beyond a narrow focus on estimates of population trend and begun to look for mechanistic explanations for the observed variation in reproduction, survival, recruitment, and population growth rates. Increased understanding of the behavior of dynamic populations, by itself, is sufficient justification to move in that direction. In the case of species potentially at risk of extinction, however, there is additional motivation. To intervene and arrest population declines, it is necessary to understand the factors contributing to the declines and their relative contributions to the observed dynamics. Given that information, it may then be possible to focus future manipulative experiments on a more narrowly defined set of hypothesized relationships.

The Current Research Paradigm

Adoption of the information-theoretic approach.—As research on Spotted Owls shifted from studies on natural history and habitat use to population dynamics, the analytical approach used in those observational studies shifted from null hypothesis testing to an information-theoretic approach (Burnham and Anderson 1998). That transition was largely due to collaboration among different researchers and, in the Northern Spotted Owl, the use of workshops where researchers came together and analyzed data from their study areas in a meta-analytical framework (see Anderson et al. 1999).

An information-theoretic approach avoids the numerous problems with using null hypothesis testing (see Johnson 1999, Anderson et al. 2000) and instead focuses on posing a set of multiple *a priori* research hypotheses for a particular data set, and then ranking and weighting those hypotheses to find the most plausible hypothesis given the data using an objective criterion (Anderson and Burnham 1998). These methods, an extension of likelihood theory, provide strength of evidence measures for the *a priori* set of alternative hypotheses; an advantage not possible with null hypothesis testing (Anderson et al. 2000). Additional features of that approach include multi-model inference because it is unlikely that a single model will be uniquely supported by the data; the possibility of averaging effects across competing models also exists (Anderson and Burnham 1998). In this issue, Seamans et al. (2002) provide an excellent example of the application of the information-theoretic approach.

By explicitly positing a set of competing *a priori* hypotheses that incorporate various factors known or hypothesized to be related to variation in the data, studies can explore a plausible range of hypotheses that explain the data, such as variation in owl demography and population trends. The link between statistical methods and the biology of the organism occurs through the set of *a priori* hypotheses. These begin as verbal ideas of what factors may influence the observed system, which are then translated into statistical models (Franklin et al. 2001). The competing hypotheses admit to uncertainty about causation, but remain bounded by *a priori* knowledge and experience. A key feature is that the science of the situation is done before data analysis through the formulation of the *a priori* models; it is not a ''fishing expedition'' hoping to hook a significant *P*-value, as is often done in a null hypothesis testing framework.

Focus on process variation.—In our opinion, the strength of the approaches currently being used by many Spotted Owl biologists is the mutual dependence between model formulation and prior biological knowledge. White (2000) emphasized three sources of variation in the dynamics of wild populations—temporal, spatial, and individual—as important sources of variation effecting life-history traits. Factors representing those sources of variation can be explicitly incorporated as covariates into a set of *a priori* statistical models that seek to explain variation in demographic rates of possible causal factors. Current approaches in Spotted Owl research have begun to focus on the variation of population processes (the variation in a given parameter over time and space), which requires partitioning the variance of the dependent variable (e.g. survival) into its sampling and process components (Burnham et al. 1987, White 2000). By removing variation attributable to the sampling process, subsequent statistical modeling focuses exclusively on the process component of variation (see Franklin et al. 2000, Seaman et al. 2002). In avian ecology, sampling variation has often been ignored with process variation in the system confused with total variation (Link and Nichols 1994, Gould and Nichols 1998), which positively biases estimates of temporal and spatial process variation.

Future Research Directions

The search for mechanisms.—At this point, we know a great deal about natural history, habitat-use patterns, and life-history parameters and how they vary in Spotted Owls. Morrison (2001) recently criticized studies on wildlife habitat use and selection for being mostly descriptive in nature and concentrating solely on identifying patterns of use, rather than the causes of those patterns. Mechanistic explanations for habitat use are generally lacking, a situation that makes it difficult for resource managers to understand why they must manage certain components for wildlife species. In addition, habitat is rarely considered in terms of quality (Van Horne 1983) where variation in demographic traits, such as survival and reproduction, may be explained by different habitat components. Morrison (2001) stressed (1) the need to relate habitat to population performance measures, such as fitness; (2) the need to concentrate on identifying the separate roles of critical resources for organisms; and (3) the need to identify factors constraining an organism's use of those critical resources. In general, research on wildlife–habitat relation studies need to strive for mechanistic explanations of why certain habitat components separate high-quality from low-quality habitats for key wildlife species, such as Spotted Owls. Carey (1985) and Gutiérrez (1985a) proposed five hypotheses to explain why Northern Spotted Owls may depend on older forest: availability of nest sites, favorable microclimate, avoidance of predators, prey availability, and coevolution. Thus far, none of those hypotheses has been adequately tested, although a number of studies have examined separate predictions from those hypotheses (e.g. Barrows and Barrows 1978, Barrows 1981, Johnson 1992, Ting 1998, Weathers et al. 2001).

Even with respect to observed patterns, there have been recent surprises. For example, in the Klamath physiographic province of northern California and southern Oregon, increasing evidence suggests that edges between older forest and younger seral stages (ecotones) may be important components of Northern Spotted Owl habitat quality (Zabel et al. 1995, Ward et al. 1998, Meyer et al. 1998, Thome et al. 1999, Franklin et al. 2000). Franklin et al. (2000) found that high-quality habitat for Northern Spotted Owls represented a trade-off, balancing the amount of interior older forest with ecotones to achieve optimal survival and reproductive output. The mechanism proposed for that trade-off was that older forest provided protection from predators and suitable microclimates whereas ecotones provided foraging areas for owls where prey was both abundant and available; a combination of the hypotheses initially proposed by Carey (1985) and Gutiérrez (1985a). Thus, a pattern emerged indicating the importance of ecotones for Northern Spotted Owls, but we are still forced to speculate as to why they are important. The apparent importance of ecotones in defining habitat quality for Northern Spotted Owls in northwestern California is based on long-term observational data. However, cause and effect for the suggested mechanisms behind the importance of ecotones cannot be determined without experimentation. Two of the three needs argued by Morrison (2001) for understanding wildlife–habitat relations have already been met: the relationship of habitat to population performance in the form of habitat quality, and identifying the role of critical resources. However, we still need to address the third need: identifying the mechanisms constraining Northern Spotted Owls in using one of the critical resources, in this case, ecotones.

The roles of observational data and manipulative experiments.—A legitimate question often posed by resource managers is ''do we need to know why Spotted Owls use certain resources?'' In other words, is it not sufficient to know just the patterns and not the mechanisms behind those patterns? We argue that just observing the patterns continues to fuel debates and litigation over what resources are needed to manage for Spotted Owls and why. Part of the reason for the history of disputed management plans and court cases with the Northern and Mexican spotted owls is that mechanistic explanations were lacking for why Spotted Owls used different habitats and whether those habitats were essential to maintaining viable owl populations. For example, Northern Spotted Owls achieve high densities in second-growth redwood (*Sequoia sempervirens*) forests on private lands along coastal northern California that have been managed intensively for timber production (Diller 1999). Mexican Spotted Owls occupy desert canyons that have little forested vegetation when compared to populations occupying older forests in more mesic portions of their range (Ganey and Dick 1995). Understanding why owls use those seemingly disparate areas and how well they perform in those areas would unify those seemingly paradoxical patterns.

Observational studies have served two useful purposes: (1) providing clear and explicit hypotheses that can be further examined with experiments, either as large-scale manipulative experiments or as smaller-scale experiments that test key predictions posed by a larger question; and (2) estimating variation in demographic parameters and the uncontrollable factors, such as climate, that may influence that variation. For example, the observational study on habitat quality in Northern Spotted Owls by Franklin et al. (2000) provided explicit landscape patterns in owl territories that could be tested in a large-scale manipulative experiment. However, not all understanding of mechanisms can be understood with large-scale experiments. For example, important influences such as climatic variation cannot be addressed directly with an experiment.

There are two reasons why observational studies are important to an overall understanding of Spotted Owl population dynamics. First, long-term observational studies are required to capture sufficient environmental variation and examine hypotheses on the large-scale effects of that variation on Spotted Owl populations. That type of research is slow because a period of 10–15 years is required to develop models capable of explaining effects of environmental covariates, such as climate on demographic parameters (e.g. Seamans et al. 2002). However, those models are explicit hypotheses that need further evaluation with an independent set of data collected over another 10–15 years in the same and different populations. That type of research refines the observed patterns, but remains slow because it relies on time and replicated studies for inference on causal mechanisms. In that way, it is similar to some aspects of astronomy where experiments cannot be conducted on, say, planets (the sampling unit of interest), but relies on causal inference built through repeated observations over time and replicated studies (Goldstein and Goldstein 1978) followed by the application of assembly rules as suggested by Beyers (1998). Science conducted in this manner can be strengthened (and quickened) by including well-conceived manipulative experiments designed to test certain key mechanisms believed to adequately explain the observed patterns of variation. For example, North et al. (2000) examined the effects of weather and the structure of vegetation around nests on reproductive success of California Spotted Owls and found that reproduction was negatively affected by spring precipitation and positively affected by high foliage volumes around the nest. They proposed that nest-site canopy structure protected fledglings from detrimental weather. However, there may be a number of alternative explanations that could be examined by conducting experiments centered around physiology-based questions dealing with the thermoregulatory ability of young and viability of eggs exposed under different conditions.

Summary

Research on Spotted Owls has followed a natural progression from natural history based studies to pattern description to the exploration of alternative hypotheses. The one key element still missing is the use of manipulative experiments in trying to establish cause-and-effect relationships. We are not the first to advocate the use of manipulative experiments to better understand mechanisms for Spotted Owls; Gutiérrez (1985b) advocated the use of manipulative experiments to understand the influence of timber harvesting on Spotted Owl reproduction, foraging and habitat use, whereas

Block et al. (1995) advocated experiments on the effects of prescribed fire on Mexican Spotted Owls as part of the recovery plan for this subspecies. However, manipulative experiments are rare in Spotted Owl research with some specific exceptions (Willey 1998, Delaney 1999). To address many of the issues we have discussed previously, manipulative experiments will need to be integrated into the current research program because the dearth of direct experiments has clouded the controversies surrounding the management of all three subspecies of Spotted Owl. The lack of causal models that adequately explain the observed habitat associations and area requirement of Spotted Owls impedes the implementation of effective conservation measures.

In summary, we argue that future research programs on Spotted Owls should include the following: (1) large-scale manipulative experiments, (2) continued long-term observational studies, and (3) small-scale manipulative experiments coupled with long-term observational studies.

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