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USE, INTERPRETATION, AND IMPLICATIONS OF DEMOGRAPHIC ANALYSES OF NORTHERN SPOTTED OWL POPULATIONS

MARTIN G. RAPHAEL, ROBERT G. ANTHONY, STEPHEN DESTEFANO,
ERIC D. FORSMAN, ALAN B. FRANKLIN, RICHARD HOLTHAUSEN,
E. CHARLES MESLOW, AND BARRY R. NOON

INTRODUCTION

Demographic analyses of Northern Spotted Owl (*Strix occidentalis caurina*) populations have generated much discussion and debate among scientists, conservationists, managers, and representatives of the timber industry (Gutiérrez et al. *this volume*). The results of these analyses appear clear: populations of territorial adult female Northern Spotted Owls have been in decline for the past 8–10 years, and the rate of decline is accelerating (Burnham et al. *this volume*). Debate, however, has focused on at least three topics: (1) analysis and interpretation of results (reliability of the data, analytical techniques involved, potential biases, and, interpretation of the results); (2) the relationship between demography and habitat alteration; and (3) given the results of this research, the implications for land management.

Our objectives are to discuss the uses and limitations of demographic data for the management of spotted owl populations, provide additional interpretations of the spotted owl demographic data from a management perspective, and make recommendations for additional analyses and future monitoring efforts. We also will attempt to link inferences from demographic analyses to habitat management.

USES OF DEMOGRAPHIC DATA

ROLE OF DEMOGRAPHIC DATA IN UNDERSTANDING POPULATION ECOLOGY

Studies of population ecology of terrestrial vertebrates show that demographic parameters of populations can be affected by an array of environmental variables, including weather; abundance, availability and quality of food and breeding sites; plant-herbivore and predator-prey interactions; rates of emigration and immigration; and habitat quality. These and other factors may act additively or synergistically on populations. In the case of the Northern Spotted Owl, extensive and intensive alteration of late-seral forests, perhaps in conjunction with other variables, has likely played a significant role in the demography of the species during the last century. Obtaining a better understanding of relationships between population growth or stability in relation to habitat conditions is one of the key goals in population research (Van Horne 1983, Vickery et al. 1992a,b, Conroy 1993).

Mark-recapture or mark-recovery techniques have been used to correlate survival with habitat types where birds were either marked or recaptured (Conroy 1993). Other studies attempted to correlate survival with food supply (Koenig and Mumme 1987, Estes 1990, Dinerstein and Price 1991, Marzluff and Balda 1992) or water (Heitmeyer and Fredrickson 1981, Cowardin et al. 1985, Raveling and Heitmeyer 1989). Relationships between survival and reproduction and the dispersion or availability of resources (e.g., wetlands) have also been examined (Rotella and Ratti 1992, Thompson and Fritzell 1989).

Among raptors, availability of nest sites and prey, and territoriality may act to regulate populations (Newton 1976). Newton (1986) documented a relationship among population levels, reproductive success, and habitat quality for the European Sparrowhawk (*Accipiter nisus*) during long-term studies in England. Higher quality habitats were occupied by nesting pairs in all or most years. As numbers of breeders rose, however, lower quality habitats were occupied, until ultimately the breeding population was limited. Raptors also show numerical and functional responses based on abundance of prey (Newton 1976, Adamcik et al. 1978). Red-tailed Hawks (*Buteo jamaicensis*), which tend to be prey generalists, however, showed functional (high nestling mortality), but not numerical responses to fluctuations in hare populations (Adamcik et al. 1979).

Although many studies have examined correlations between food supply and survival rates or reproductive rates of birds (e.g., Wilson et al. 1986, Koenig and Mumme 1987, Marzluff and Balda 1992, Taylor et al. 1992,) there are few examples where demographic parameters have been linked with habitat amount, distribution, or quality at the nest-site or landscape level. Methods have been proposed that utilize resighting data from radiotelemetry studies to assess relationships between survival rates and habitat (Conroy 1993). Although these methods are relatively new and untested in field studies, they appear to offer some promise for assessing relationships between habitat conditions and survival.

DETERMINATION OF RECOVERY AND DELISTING

Delisting of endangered or threatened species by the U.S. Fish and Wildlife Service has generally been based on numeric goals for population abundances rather than on changes in basic demographic rates. A recent example is the delisting of the gray whale (*Eschrichtius glaucus*), now relatively common along the Pacific Coast after being nearly eradicated by over-harvest in the late 1800's. However, demographic data could be used as a more reliable indicator of population trend and status. For example, the recovery plan for the desert tortoise (*Gopherus agassizi*) included a requirement that the population must exhibit a statistically significant upward trend or remain stationary for at least 25 years before delisting would be considered (USDI 1994). The draft recovery plan for the Northern Spotted Owl proposed the use of demographic data to assess recovery (USDI 1992a).

INTERPRETATION OF EXISTING NORTHERN SPOTTED OWL DATA

Burnham et al. (*this volume*) synthesized results from 11 large scale Spotted Owl demography studies in a meta-analysis and estimated an average rate of population decline of 4.5% per year (with a 95% confidence interval of 0.6% to 8.4%) after adjusting estimates of juvenile survival for permanent emigration. Based on this analysis, Burnham et al. (*this volume*) concluded that the finite rate of population change (λ) was probably <1.0 for the population of territorial females, based on the years of study (see Franklin et al. *this volume*). The most parsimonious statistical model in a meta-analysis of adult survival indicated adult female survival rates were declining over time (Burnham et al. *this volume*). Based on this finding, the rate of population decline was apparently accelerating during the period of study.

Although the meta-analysis conducted by Burnham et al. (*this volume*) indicated an overall decline in survival rates of adult females, estimated rates of adult survival varied among individual study areas. The best capture-recapture models identified in the individual study areas indicated declining linear trends in adult survival in some areas, constant rates of adult survival in other areas, and non-linear trends in others. However, the individual studies were unable to achieve the same statistical power to detect underlying trends as the meta-analysis.

MODEL-BASED VERSUS SURVEY-BASED ESTIMATES OF POPULATION TREND

The conclusion by Burnham et al. (*this volume*) that the territorial owl population was declining has been controversial because (1) estimates of population trend from counts of owls (derived from annual surveys of the population of owls within density study areas) do not clearly demonstrate a population decline (Thomas et al. 1993a); and (2) estimates of λ may be biased low because of bias in survival rates (Bart 1995a; Forsman et al. *this volume*). However, other factors (see below) may result in positive biases in estimates of λ.

It is not surprising that survey-based estimates of trends in owl numbers deviate from estimates based on capture-recapture models of population growth rates for long-lived species experiencing rapid declines in habitat. The empirical estimate of population stability from counts of owls does not directly account for the number of additions (births) and losses (deaths) in a population. For example, by this measure of growth a population whose death rate far exceeded its birth rate could appear stable if it was maintained by recruits from the local population of nonbreeding owls (floaters), by outside immigration, or both (see Franklin 1992).

In contrast, estimates of λ from capture-recapture models are functions of survival rates and *in situ* recruitment (birth rates). These model-based estimates are particularly useful because they are capable of discriminating a subpopulation on a study area that appears stable due to recruitment from outside the study area from one that is inherently stable due to a balance between birth and death rates. For the Northern Spotted Owl, we are specifically interested in whether a local population is stable ($\lambda \geq 1.0$) in the absence of immigration/emigration dynamics.

Another factor contributing to the disparity between density and model-based estimates of population trend is the response of the territorial component of the owl population to habitat loss. During periods of rapid decline in amounts of late-successional forests, owls were presumably displaced from previously occupied habitats (Forsman et al. 1984, Forsman 1988). Many of these individuals did not die immediately, but became nonterritorial floaters or replaced territorial owls that in turn became floaters. Such circumstances could result in "packing" of adult owls into the remaining suitable habitat and this could lead to decreased reproductive and survival rates of territorial owls. Therefore, one might expect to infer declining populations ($\lambda < 1.0$) from demographic studies under circumstances of density-induced declines in survival and reproduction.

LIMITATIONS AND POTENTIAL BIASES OF DEMOGRAPHIC DATA

Demographic analyses are subject to potential biases depending on the assumptions on which they are based and the reliability of parameter estimates. Interpretation of demographic results may also be limited to certain geographic segments of the population because the study areas may be small in comparison to the geographic range of a species or parts of the species' range may not be adequately represented. These considerations are important in the interpretation of the demographic characteristics of Northern Spotted Owl.

At least seven simulation models of spotted owl populations have been developed (see Lande 1988; Noon and Biles 1990; Lamberson et al. 1992, 1994; Carroll and Lamberson 1993; Bart 1995a), and one of these is a spatially explicit population model (McKelvey et al. 1992). These simulation models have suggested alternative scenarios for the dynamics of spotted owl populations. The models by Lande (1988) and Noon and Biles (1990) are most comparable to the demographic analyses here because they are deterministic models based on Lotka-Leslie methods. Bart (1995a) used a stochastic simulation model to evaluate the effects of errors in estimates of reproductive and survival rates on estimates of the annual rate of population change.

WHAT SEGMENT OF THE POPULATION DOES THE CAPTURE-RECAPTURE MODEL REPRESENT?

There is disagreement as to whether an inference about rate of population change applies to only the territorial population (Anderson and Burnham 1992; Franklin et al. *this volume*; Burnham et al. *this volume*) or the entire population (Bart 1995a) of Spotted Owls. Because data on reproductive rates and estimates of adult survival are collected from territorial owls, Anderson and Burnham (1992) and Burnham et al. (*this volume*) contend that the annual rate of population change refers to only the territorial segment of the population. In contrast, Bart (1995a) has suggested that the results pertain to the entire population because of the exchange of owls between the territorial and floater components. However, how floaters contribute to or regulate spotted owl population dynamics is unknown. Whereas floaters have been incidentally observed in spotted owl populations (Franklin 1992), certain conditions must be met for floaters to have a substantial regulatory capacity in population dynamics (see Klomp 1972, Patterson 1980, Sinclair 1989).

Although it is not entirely clear which segment of the population is represented by the demographic results, we believe the results in Burnham et al. (*this volume*) and the other papers in this volume primarily represent the dynamics of the territorial population when survival rates are adjusted for permanent emigration (see below). However, some of the data used in the Lotka-Leslie models to estimate λ were collected from juvenile owls who have been part of the nonbreeding segment of the population. For example, of 1,169 juvenile owls banded on four study areas (H.J. Andrews, Olympic Peninsula, Siuslaw National Forest, Southern Oregon), 145 (12%) were reobserved; 58 (40%) were resighted for the first time 1 year after banding; 54 (37%) 2 years after banding; 25 (17%) 3 years after banding; 6 (4%) 4 years after banding; and 2 (1%) 5 years after banding. Approximately 60% of the banded and resighted juveniles were not observed for 2 or more years after banding. Presumably these individuals were either part of the nonterritorial population for this period of time or they temporarily emigrated to another territorial population. Obviously, we know little about the fate of banded juveniles (only 12% have been reobserved) and when they do appear in the territorial population, they may show up 2–5 years after they are banded. These facts tend to make interpretations of λ less certain, but the key here is that only the territorial birds breed. The question is whether these birds are replacing themselves. If not, the population, as a whole, will decline in the long run.

PROJECTION OF POPULATION CHANGES

As indicated by Burnham et al. (*this volume*), the results from the demographic analyses apply only to the years during which data on reproductive rates and survival were collected. Forecasts of future population trends depend on assumptions (1) that the population would maintain a stable age distribution and (2) rates of survival and reproduction would remain the same as the period when these data were collected. Because these assumptions are not valid for Spotted Owl populations (Burnham et al. *this volume*), forecasting into the past or future more than several years beyond the period of data collection is risky. Even predictions 2–3 years into the future will be biased if rates of reproduction or survival change considerably, although such forecasts are obviously more defensible than long-term forecasts.

POTENTIAL BIASES

Lambda (λ) is estimated as a function of birth and death rates; therefore, the reliability of any estimated rate of population change reflects the bias and precision of these estimates. These potential biases include violation of any assumptions of the underlying Lotka-Leslie model, as well as biased estimation of reproductive rates, survival rates, the influence of senescence on survival and reproductive rates, the effects of emigration of juveniles and adults from study areas, and longevity of studies.

Assumptions of the Lotka-Leslie model

Violations of the assumptions of the Lotka-Leslie model may create biases in the estimate of λ (see Franklin et al. *this volume*), but the degree and direction of bias varies considerably among the different assumptions. Calculation of λ from an eigenanalysis of the projection matrix (see Caswell 1989) assumes a stable age (stage) distribution if inferences are extended to forecasting trends (see Franklin et al. *this volume*). This is not a problem if inferences are limited to projections because convergence to a stable distribution is asymptotically exponential (Caswell 1989:70). If the vital rates vary stochastically, or are time-dependent, then the assumption of a stable stage distribution is invalid. To date, all calculations of λ for spotted owls have been based on mean (i.e., constant) values of the vital rates (Burnham et al. *this volume*).

Falsely invoking the assumption that birth and death rates are constant over time in the analysis of owl demographic data would lead to an overestimate of λ. Adult female survival rate has shown a significant negative time trend (Burnham et al. *this volume*), thus this assumption is clearly violated. If the annual rate of population change varies with time, then growth of that population is described by the product of a sequence of projection matrices. In the special case of independent matrices (i.e., independent environments), population growth rate is equivalent to the dominant eigenvalue (λ) of the projection matrix based on mean values for the vital rates (Tuljapurkar 1982). However, under time-dependent or stochastic conditions, the average growth rate of the population may be a misleading indicator of population stability. This occurs because the distribution of population sizes from time-varying projection matrices is approximately lognormal (Tuljapurkar and Orzack 1980). A property of lognormal distributions is that the modal population size will always be smaller than that based on the mean values of the vital rates (Gerrodette et al. 1985). Thus, the actual growth rate of any single population with time-varying rates is always ≤ the growth rate estimated from mean values of the projection matrices (Cohen et al. 1983). However, the magnitude of the positive bias arising from annual variation in survival or reproductive rates appears to be small (Noon and Biles 1990).

Duration of studies

Shorter study duration may underestimate survival. For example, survival rates of juvenile owls (Burnham et al. *this volume*) were higher for the 6 long-term ($\bar{x} = 0.334$, SE = 0.027) versus 5 short-term ($\bar{x} = 0.208$, SE = 0.047) study areas ($t = 3.26$, $P = 0.011$). Estimates of adult survival rates did not differ between long-term and short-term studies (USDA and USDI 1994a, Burnham et al. *this volume*). These differences in the estimates of juvenile survival for long-term versus short-term studies resulted in higher mean values of λ for the six long term ($\bar{x} = 0.952$, SE = 0.040) versus five short term ($\bar{x} = 0.894$, SE = 0.041) study areas ($t = 2.36$, $P = 0.043$). We offer three possible explanations for these differences in survival rates for long-term versus short-term studies: (1) survival rates may have actually decreased during the later years; (2) longer study duration provided better estimates of survival, particularly for juveniles; or (3) survival rates differed between the geographic areas represented by the sets of long-term and short-term study areas. Both point estimates of juvenile survival rates and their standard errors may be particularly sensitive to duration of studies because it takes a number of years for juveniles to appear in the territorial population. Because banded adults are most often territorial and have high resighting probabilities, their survival estimates are much less sensitive to study duration (USDA and USDI 1994a, Burnham et al. *this volume*).

Senescence

A decrease in survival and/or reproductive rates in older owls will overestimate survival and reproductive rates and result in an inflated estimate of λ. The particular form of the age-specific survival and reproductive rates used in the demographic analyses assumed that senescence was not occurring. Anderson et al. (1990), Noon and Biles (1990), and Bart (1995a) simulated the effects of senescence on the estimates of λ. Bart (1995a) found that moderate senescence may cause an overestimate in λ by as much as 0.02. Noon and Biles (1990) found the effects of senescence to be most pronounced when adult survival rates were high, juvenile survival rates were low, and values of λ were >0.7. The effects of senescence at ages <21 years of age were dramatic, so failure to account for senescence could result in significant overestimates of λ. The extent to which senescence occurs in owl populations is unknown, so the magnitude of the potential bias is unknown at present.

Estimation of reproductive rates

The estimation of reproductive rates may be biased in several ways. First, death of some young owls may occur prior to detection, leading to an underestimate of fecundity (but an overestimate of survival rates of juveniles). Second, most of the demographic studies did not include pairs of owls in fecundity estimates unless the age of the female was known. The majority of pairs in which age of females was unknown were pairs that appeared to produce no young and that could not be located enough times to confirm the age and identity of the female. Exclusion of these females from the estimates of fecundity may have caused a positive bias in estimates of fecundity (Reid et al. *this volume*). Third, Bart and Robson (1992: 9) showed that λ may be overestimated by as much as 0.027, assuming nonterritorial female owls comprise up to about 30% of the population but are not observed. However, we believe the inferences from λ apply primarily to the territorial female component of owl populations (Franklin et al. *this volume*) so the influence of this potential bias is probably not great.

Permanent emigration and estimates of survival

Another potential bias is permanent emigration of juveniles or adults which would result in underestimates of juvenile survival rates. The Cormack-Jolly-Seber estimates (Pollock et al. 1990) of survival cannot discriminate between undetected emigrants and individuals that have died (see Franklin et al. *this volume*). To the extent that banded owls emigrate, survive at least one year, and are never observed again, Cormack-Jolly-Seber models will underestimate survival rates on local study areas. As a result, estimates of λ will be biased low.

Based on the results of radio-telemetry studies, undetected emigration of banded juvenile owls, followed by their subsequent survival, occurs frequently (Forsman personal communication). The bias in survival estimates of juveniles caused by such movements is probably greater for study areas that are relatively isolated (e.g., H.J. Andrews in the Oregon Cascades) versus study areas that are surrounded by other study areas. In larger or more contiguous study areas (e.g., Oregon Coast Range), emigrating owls are more readily detected. Burnham et al. (*this volume*) recognized the potential bias in estimates of juvenile survival and computed the necessary rates of juvenile survival to result in $\lambda = 1.0$, given the estimates of other vital rates. They found that juvenile survival and emigration must be in the range of 0.57 and 0.51, respectively, for owl populations to be stationary. Both of these rates are substantially greater than the actual rates estimated on most of the study areas, but a juvenile emigration rate of 0.60 was reported from the Olympic study area (Forsman et al. *this volume*). Although the estimates of emigration rates were based on small samples from only two years of data, they do suggest that, in some years and on some areas, rates of emigration were relatively high. It is clear, however, that rates of emigration estimated from one year of telemetry data will not be adequate for long-term estimates of permanent emigration. It is likely, for example, that some proportion of juveniles that emigrate during their first year of life will continue to move around (i.e., disperse [Miller 1989]) and will eventually be detected when they acquire territories. In these cases, emigration will be temporary, and the negative bias on estimated juvenile survival will be reduced when they reappear as territorial adults.

Permanent emigration by adult owls appears to be infrequent. However, even occasional permanent emigration by adults is an important consideration because model estimates of λ are especially sensitive to changes in survival rates of adults (Lande 1988, Noon and Biles 1990). Therefore, a relatively small, negative bias in estimates of adult survival due to emigration could cause underestimates of λ. Telemetry studies of adult owls have indicated some emigration, and this may have an influence on estimates of adult survival on study areas that are isolated from other study areas (Thrailkill et al. *this volume,* Wagner et al. *this volume*).

Net effect of the potential biases on estimates of λ

Bart (1995a) evaluated the potential biases on λ from permanent emigration and senescence with a stochastic simulation model. Bart suggested that the results of the spotted owl demographic analyses may have underestimated λ by 0.03 to 0.13. We believe his results should be viewed cautiously because some of his assumptions do not reflect the field situation. For example, his simulations estimated the extreme bias in λ only when it was assumed that neither senescence nor overestimation of fecundity rates were occurring. Including these factors would increase the estimate of λ, which would counter the negative biases of permanent emigration. Also, the most important source of bias in estimates of λ in Bart's simulations was the proportion of sites monitored, which affected the estimation of emigration rates. For example, he assumed that the proportion of territories that were monitored in each study area was 0.2 or 0.4 in the first year of marking and increased linearly to 0.8 in the fifth year. He also assumed that any bird that left the study area had a recapture probability of 0. His assumed proportion of sites monitored is lower than actual proportions in most demographic study areas, and there is no support for the assumption that the proportion monitored increases linearly with time or that recapture probability is 0 when birds leave the area. In fact, in the present demographic studies, many emigrants are recaptured after they leave study areas. Collectively, we believe these assumptions may have led to an extreme estimate of the negative bias in λ.

As discussed previously, estimates of λ are probably most affected by the negative bias in the estimate of juvenile survival. However, Burnham et al. (*this volume*) adjusted their estimate of juvenile survival to account for emigration followed by survival. Permanent emigration of adult owls is rare. Therefore, we believe the most current estimates of λ for spotted owls (Burnham et al. *this volume*) have largely addressed Bart's (1995a) concern.

From the above it should be obvious that there are both positive and negative biases that may effect estimates of λ, but the relative magnitude of these biases are currently unknown. This is likely to be a lively topic of research and debate in the future.

Applicability to the Range-wide Population

The Spotted Owl demographic studies reported in this volume were initiated by different researchers and agencies with little coordinated effort to ensure equal representation of the different ecological provinces within the range of the owl. For example, there are two study areas in the western Cascades of Oregon, whereas there are no demographic studies in the western Washington Cascades, eastern Oregon Cascades, western Washington lowlands, or the California Cascades. In contrast, there are seven demographic study areas in the Coast Range and Klamath Provinces of western Oregon and northern California. The eastern Washington Cascades is well represented by two demographic studies. Until studies and data are available from other areas, it is unknown if the existing data adequately represent the dynamics of the entire population. However, the current studies encompass a large portion of the Northern Spotted Owl's geographic range in the United States (Franklin et al. *this volume*).

Inferences from a Heterogeneous Population

An additional problem that may complicate interpretation of the demographic data is the extent to which inferences from estimates of λ apply to heterogeneous subpopulations consisting of a mixture of source and sink territories. We believe this is an important issue. Virtually all extensive studies of lifetime reproductive success among birds, for example, have shown that relatively few individuals in a population produce most of the offspring (see Newton 1979), and this has been observed among Spotted Owls as well (Verner et al. 1992b:74). Spotted Owl subpopulations in the study areas also may be heterogeneous because the amount and distribution of suitable habitat remaining and the degree of habitat fragmentation varies considerably over the owl's range. The overall estimate of λ for a heterogeneous subpopulation is a weighted average with the weights determined by the relative numbers of the source and sink territories in the sample. Various combinations of source and sink proportions could yield a weighted estimate of $\lambda < 1.0$ even though a portion of the subpopulation may be stable or increasing.

If one could partition a population into its source and sink components, it is obvious that the long-term dynamics (assuming constant vital rates) in a deterministic analysis is determined by the persistence of the source component of the population. The problem of drawing the correct biological inference (population is declining, stable, or increasing), however, is not this easily addressed. For example, consider the case where the source component of the population is small and the vital rates are time-dependent. Estimates of λ based on mean values of the vital rates could have a substantial positive bias (Cohen et al. 1983), and the researcher could incorrectly infer a stable or growing population.

Given the above, valid insights into the persistence likelihood of a heterogeneous population must come from analyzing other relevant factors—for example, the smallest source population size or number of source territories needed for local stability. As described by Lamberson et al. (1994), the threshold number of territories may be determined by considering the limits of demographic and environmental stochasticity and the spatial distribution of breeding pairs. At a larger geographic scale, overall persistence of a population may be determined by the number and spatial distribution of locally stable source populations. The latter constraint is imposed by rare, catastrophic events that require many local populations, widely dispersed, so that adverse effects are not experienced simultaneously by all local populations.

Is the Current Level of Habitat Fragmentation Beyond the Extinction Threshold?

Based on their interpretation of the Burnham et al. (1994b) report, some prominent scientists and conservation groups have suggested that the

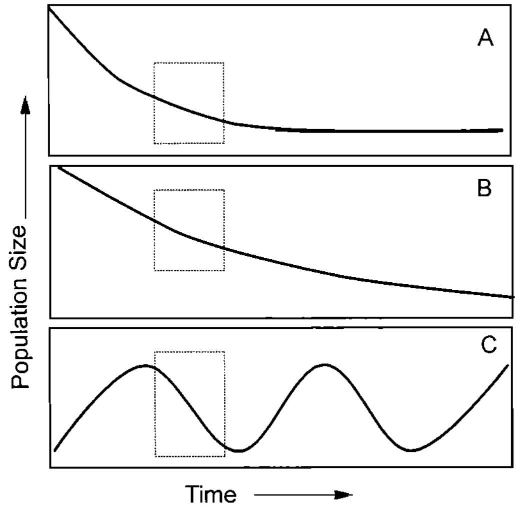

FIGURE 1. Graphic representation of three hypothetical scenarios for Northern Spotted Owl populations. Dashed boxes represent plausible periods when declining populations were detected by current studies. Explanation of scenarios is in text.

declining adult survival rate may indicate a population that has passed a persistence threshold and is declining toward extinction. Consistent with this interpretation would be the observation that populations are declining more rapidly than the rate of habitat loss (Lande 1987, Lamberson et al. 1992). Accelerating rates of population decline might also suggest that a threshold had been passed.

The assumption that the Spotted Owl will reach an eventual positive, stable equilibrium in the context of a continuing overall decline in carrying capacity requires the demographic rates of the territorial owls in the remaining habitat be relatively unaffected by habitat losses occurring elsewhere. Under this scenario, the population is in decline largely because juveniles cannot find territorial vacancies and the rate of juvenile survival is depressed. As the amount and distribution of habitat stops declining or increases, juvenile survival rate will increase and the population will approach an equilibrium. Simulation studies (Raphael et al. 1994) support this scenario. Under these conditions, however, the decline in population cannot exceed the rate of habitat loss and will generally lag behind it (Lamberson et al. 1992).

The evidence provided by papers in this volume support the hypothesis that Northern Spotted Owl populations are declining across a large proportion of their range and that adult survival is also declining. Since these declines have been documented only over the last 5–10 years, which is less than the average generation length of spotted owls, forecasting the future is difficult. A number of scenarios can be suggested concerning the future fate of Spotted Owl populations:

1. *Northern Spotted Owl populations will decline but reach an equilibrium at some lower population level (Fig. 1A).* If habitat across the range of the Spotted Owl stabilizes at some equilibrium amount and configuration, Spotted Owl populations will eventually reach an equilibrium and remain stable at a lower population size. This hypothesis assumes (1) survival rates are density dependent and will show a compensatory increase as population densities decline, and/or (2) survival and reproductive rates increase as the amount and quality of habitat within home ranges in reserved areas increases.

2. *Northern Spotted Owl populations will continue to decline to extinction (Fig. 1B).* There are at least 3 ways this could arise: (1) current habitat loss and fragmentation is so severe that Spotted Owl populations have passed a persistence threshold arising from difficulties in finding suitable territories and mates (Lande 1988); (2) habitat quality has been so depressed that birth and survival rates will not support a stable population; or (3) populations are so small as to be inescapably vulnerable to stochastic extinction events. For all these scenarios, the overall owl population will continue to decline to extinction at some unknown rate and over some unknown period of time.

3. *Observed declines in Northern Spotted Owl populations are part of a natural, long-term fluctuation in numbers (Fig. 1C).* Observed declines are a result of natural fluctuations in numbers that are unrelated to the amount and distribution of suitable habitat, and the present studies have merely estimated population trends during a transient period of natural decline. We do not view this as a plausible scenario.

The management plans proposed by Thomas et al. (1990), USDI (1992b), and USDA and USDI (1994a) all assumed that scenario 2 had not occurred and that scenario 1 was a likely outcome once a condition of no-net-loss of habitat was reached. Researchers have attempted to discriminate among these scenarios with sophisticated computer projections (Lamberson et al. 1992,1994; McKelvey et al. 1992; Raphael et al. 1994; Holthausen et al., 1995). However, these models are characterized by simplifying assumptions, uncertainty in parameter estimates, and unknown aspects of spotted owl behavior. Therefore, continued monitoring of spotted owl population trends with demographic analyses and monitoring of changes in amount and distribution of habitat is a prudent approach to discriminate among these possible outcomes.

RECOMMENDATIONS FOR ADDITIONAL ANALYSES

Modifying Demographic Study Areas

Design criteria

Given the legal and social significance of the status and trend of Spotted Owl populations and the high cost of obtaining demographic information, agencies should strive to acquire reliable, range-wide information on the status of owl populations. With limited funding, it is important to determine the most efficient study design that will meet this objective. We are aware of 17 different studies, including the 11 described in this volume. Because of the biases and other limitations cited above, we believe the current design of the program of demographic studies can and should be improved.

Several factors should be considered. First, if inferences are to apply to the entire geographic range of the Northern Spotted Owl, the demographic study areas must be more representative of range-wide conditions. As discussed above, some physiographic provinces are omitted and others are well represented by current study areas. Other important environmental criteria for study area selection and design should include habitat quality (for example, representation of all relevant elevation zones, forest composition, and structural features), large-scale land ownership patterns, and land allocations (proportions of wilderness, national parks, and other large areas withdrawn from timber cutting, as well as lands available for timber cutting).

Second, each study area should be large enough to reduce the biases in estimates of juvenile and adult survival due to undetected emigration (Franklin et al. 1990). Not only size, but shape of study area should be reexamined. Some of the areas are long and narrow (e.g., Siskiyou), some include a collection of small, scattered sites (e.g., northwestern California), and some are surrounded by other study areas; these irregular shapes likely exacerbate emigration biases (see Franklin et al. *this volume*). Ideally, study areas should be shaped to minimize the ratio of edge to area.

In addition, many of the current study areas are not surveyed with equal effort over their entire extent. As a result, banded birds, especially juveniles, may emigrate to unsurveyed sites within the study area where they may survive but not be reobserved. If study areas were consolidated to reduce such effects, more reliable inferences might be obtained.

Finally, we recommend use of radio-telemetry to estimate rates of emigration and survival of juvenile and adult owls on a larger sample of study areas. Although labor-intensive and expensive, such studies appear to be the only feasible way to evaluate the effects of emigration on estimates of survival from capture-recapture studies.

Selection criteria

Several additional considerations are relevant in deciding whether to drop or add demographic study areas. First, certain study areas may be critical to understanding dynamics of isolated or unique owl populations, such as on the Olympic Peninsula. Second, some study areas offer opportunities for integration with other ongoing efforts, such as Adaptive Management Areas (Thomas et al. 1993*b*) where demographic response of owls to silvicultural techniques might be tested using carefully designed experiments. Study duration also should be considered, with retention of longer-term studies a high priority. We recommend development of a screening process to evaluate each current study area against the above criteria to assess the value of the information they provide. Such screening should be undertaken by knowledgeable but objective scientists.

Role of Demographic Studies in Monitoring

At present, the ongoing demographic studies are the basis of the regional monitoring strategy for the Northern Spotted Owl. It is unlikely that a single measure of population status will be accepted by all parties so estimates of parallel changes in related factors will raise confidence in estimated population trends. Other components of a regional monitoring strategy could include monitoring trend in amount and pattern (size, shape, and arrangement) of habitat over time, monitoring density of territorial owls, and conducting periodic large-scale surveys or counts to estimate changes in abundance (USDI 1992b). Each of these is discussed below.

Habitat trend

Loss of habitat due to logging and other disturbance is usually cited as the fundamental cause of declining populations of the Northern Spotted Owl (Anderson et al. 1990, Thomas et al. 1990, Murphy and Noon 1992). We believe that any plan must monitor trends in the amount and distribution of suitable habitat. Ideally, these habitat data will cover all ownerships, perhaps using remotely sensed information. Given these data, relationships between status and trend of owl populations can be tested against trends in habitat attributes. Evidence that net loss of habitat is no longer occurring will be critical in delisting the owl as a threatened species.

Local density studies

Estimates of population trend based on complete surveys of selected study areas may be an important element of a monitoring strategy. Such surveys on density study areas are an ongoing component of many of the studies reported in this volume (see Franklin et al. *this volume*). Direct estimates of density, in conjunction with model-based results of demographic analyses, may strengthen a monitoring program.

Regional surveys or density estimates

The Northern Spotted Owl recovery team recommended a large-scale survey to estimate population size and trend (USDI 1992b). Various designs of such a survey have been suggested, including call counts at a sample of several thousand stations with single visits (USDI 1992b) and randomly selected quadrats with multiple visits (Noon et al. 1993; Holthausen et al. 1995, Seaman et al., unpublished data). The former design might yield a yearly estimate of relative abundance, whereas the latter might yield a yearly density estimate. The latter technique has the advantage that multiple visits can be used to estimate sighting probability, but is more costly than the former method. Both approaches suffer from bias associated with use of calls to elicit responses from owls. If biases can be understood or sufficiently reduced, it may be possible to directly estimate the annual rate of population change from the ratio of populations from one year to the next where estimates of population sizes are estimated from density studies and regional surveys, using open- or closed-population mark-recapture estimators (Noon et al. 1993).

The major advantage of a regional survey is that it provides a robust means to validate inferences from the demographic studies. With an adequate design, regional surveys can yield broad statistical inferences, and can directly estimate population trend and provide information on the geographic distribution of owls. The demographic studies would continue to provide independent estimates of trends and provide essential information on the processes responsible for these trends.

LINKING DEMOGRAPHIC ANALYSES TO HABITAT

Importance of habitat relationships

Limitations on the extrapolation of demographic data into the future have both research and management implications. Controversy over Northern Spotted Owls focuses on the future status of the owl population, and management efforts focus on the future status of owl populations under different habitat management scenarios. Thus, while demographic information may be useful in determining the past and current status of populations, it has not been very helpful in resolving questions about the future effects of current management decisions.

To improve the formulation of testable hypotheses, management is increasingly turning to simulation models (Raphael et al. 1994, Holthausen et al. 1995). The simulation models that are most germane to management questions are those that link population attributes (density, birth and death rates) to habitat conditions, and thus base future population performance on projected future habitat conditions (e.g., McKelvey et al. 1992). An improved understanding of the relationship between habitat and population performance is essential to the use of simulation models in the formulation of hypotheses and the refinement of habitat management plans. Unless we can test responses of demographic parameters to habitat condition, management plans are no better than our hypotheses.

Simulation models are useful for testing assumptions or assessing relative risk to populations under alternative scenarios. However, limitations of these models must be clearly understood. As discussed by Holthausen et al. (1995), simulation results are entirely dependent on the structure of the model, its underlying assumptions, and the input data supplied to them. These models are inevitably a simplification of reality and do not take into account the myriad interactions that influence real populations.

EXISTING INFORMATION

To date, demographic studies have yielded only limited information on relationships between variation in the vital rates and habitat. Such relationships are currently being studied at a number of scales including the nest site, the home range, and larger areas encompassing entire local populations. At the scale of individual territories, occupancy, fecundity, and persistence of owls on territories have been significantly correlated with amounts of suitable habitat in the territories (Thomas et al. 1990, Lehmkuhl and Raphael 1993, Bart 1995b). At a larger scale, fecundity of breeding pairs and survival of adults have been correlated with percent habitat in variously-sized areas that included individual or multiple nest sites of pairs (Bart and Forsman 1992, Bart 1995b). Finally, at the scale of entire demographic study areas, Raphael et al. (unpublished data) found no correlations between average habitat conditions on study areas and rates of fecundity and survival estimated for those study areas. The lack of association at this scale may result from selective use of higher-quality sites. Spotted Owls have been shown to select home ranges where superior habitat conditions are located so that habitat within home ranges is of higher quality than the average conditions on the larger landscape (Ripple et al. 1991, Lehmkuhl and Raphael 1993). Alternatively, the lack of correlation between vital rates and habitat may indicate that the amount and distribution of habitat is not limiting population processes and vital rates.

Results of these studies, and a consideration of the ways that owls use habitat, suggest the following scale-dependent relationships between habitat and demography: (1) studies at scales smaller than individual home ranges may provide some insight about patterns of occupancy, but cannot reveal relationships of habitat conditions to actual population performance; (2) studies at the scale of individual home ranges are most likely to reveal relationships of population performance to habitat if such relationships exist; and (3) studies completed at landscape scales may mask relationships of population performance to habitat unless habitat conditions and prey abundance are homogeneously distributed within study areas.

We conclude that the relationships between habitat and demographics may be most significant at the scale of individual home ranges. This is the scale at which such relationships have been modeled in recent computer simulations reported by McKelvey et al. (1992) and Raphael et al. (1994).

Analytical technique

The parameters of most interest in an analysis of habitat effects on population performance are fecundity, juvenile survival, and adult survival. Persistence of birds on home ranges is of less interest, but may be used to provide insight into survival if capture history information is not available. To associate these parameters with habitat at the scale of individual home ranges, it is necessary to determine the area within which habitat should be measured. Ideally, radio telemetry would be used to determine the actual boundaries of pair home ranges, and habitat would then be measured within those boundaries. In practice, using radio telemetry for a large number of owls is impractical, too expensive, and potentially disruptive to the owls. Therefore, circles chosen to represent mean home range sizes of territorial pairs in the geographic area being studied should be drawn around nest sites and used as surrogates for true home ranges. Circles are clearly crude approximations for actual home ranges, but when sample sizes of homes ranges are large, the circles provide a reasonable approximation of conditions within home ranges (Lehmkuhl and Raphael 1993).

Fecundity and persistence on home ranges

The relationships between demography and habitat variation at the scale of a home range can most readily be estimated for fecundity and persistence on territories (e.g., Bart 1995b). The habitat parameter used by Bart was the percent suitable habitat within single or multiple home range-sized areas. Where areas were large enough to include more than one home range, they were chosen based on homogeneity of habitat conditions. Habitat was used either as a continuous variable, allowing correlation (Bart 1995b), or as a categorical variable, allowing investigation for significant differences among categories (Bart and Forsman 1992). Utility of the results for simulation modeling is probably enhanced by treating habitat as a continuous variable.

Survival

Determining the relationship between habitat and survival is the most difficult. Survival values estimated in the demographic studies are the result of the capture-recapture histories of hundreds of owls (Franklin et al. *this volume*). Raphael et al. (unpublished data) attempted to relate habitat to survival on entire demographic study areas, but found little correlation. The lack of pattern may have been a consequence of scale—the areas actually used by individual owls are much smaller and may be different from the overall conditions of the study areas—or lack of variation in survival among areas. At smaller scales, habitat variables can be attached to individual or groups of capture histories using a number of modeling approaches (Lebreton et al. 1992, Conroy 1993, Skalski et al. 1993). The demographic studies reported in this volume provide large sample sizes and may allow detection of even moderate differences in habitat configuration provided such variation is present within study areas. A meta-analysis incorporating study areas would be the strongest approach.

EPILOGUE

To develop a comprehensive management plan for the Northern Spotted Owl and other species associated with older forests, the Clinton administration convened an interagency team of scientists, managers, and technicians in 1993 and instructed them to develop a series of options for management of federal lands within the range of the Northern Spotted Owl. Collectively referred to as the Forest Ecosystem Management Assessment Team (FEMAT), this team proposed

10 different options, ranging from a plan that would have followed the forest plans in effect at that time, to a plan that would have allowed no future harvest of mature or old-growth forests on federal lands (Thomas et al. 1993b). After reviewing the options, the President instructed the federal agencies to adopt an intermediate option (Alternative 9) that would protect large areas of mature and old-growth forest, but that would also allow some harvest of older forests.

The President's proposed plan was almost immediately challenged in federal court by industry and environmental groups who argued, respectively, that the plan was illegal and that it was not adequate to protect the spotted owl and other wildlife. The interpretation of the demographic data described in this series of papers played a central role in this litigation. The government was convinced that the available demographic data indicated a declining owl population and that this decline called for conservation of much of the owl's remaining habitat.

We have discussed at length the potential biases associated with parameter estimation using mark-recapture methods, and limits to inference from the analysis of the parameterized projection matrices. Despite remaining uncertainty, these methods are the best currently available and provide the most reliable insights into the population dynamics of wild animal populations. The methods do not provide exact rates of population change. We believe, however, that the estimated direction of change for the Spotted Owl, decline, is reliable; the magnitude of this decline remains in question. Further, a probable mechanism causing the population decline can be described: extensive loss and fragmentation of an estimated 80% of late-seral stage forest within the last 40 years (Bolsinger and Waddall 1993). Therefore, conservation efforts (Thomas et al. 1990) and changes in land management (Thomas et al. 1993b) are clearly justified by the results of the Spotted Owl demographic studies.

Finally, we believe it is critical to continue to monitor the owl population over time to document the response of the population to future changes in the amount and distribution of suitable habitat. In this context, we believe the demographic studies will continue to provide a foundation for our understanding of the status and trend of the Northern Spotted Owl.

SUMMARY

Ongoing demographic studies have played a leading role in estimating the status and trend of populations of the Northern Spotted Owl. Interpreting results of these studies is controversial because of debate about the reliability of the data and the analytical techniques used. In this paper we discuss the uses of demographic data, outline some of the potential biases in estimates of demographic parameters, and suggest ways to reduce biases. Major sources of bias include permanent emigration of juveniles (marked birds that leave the area, survive at least a year, and remain undetected), senescence, estimates of reproductive rates, and study duration. Biases can be either positive or negative. Although we know the direction of bias associated with each source, the net effect of these biases on the estimated rate of population change, λ, remains difficult to assess, and further work is needed to better understand their cumulative effect. We recommend modifications to the current study designs to reduce biases and to ensure a better representation of range-wide habitat conditions. We believe the ongoing demographic studies are a key to understanding the relationship of the owls to variation in habitat and to change in amount and distribution of habitat, and that these studies are a major component of a long-term monitoring strategy. A priority for future research is to establish relationships between fitness and habitat conditions measured at different scales, and to synthesize these results across the individual home ranges.

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