

## EVALUATION OF POPULATION TREND ESTIMATES CALCULATED USING CAPTURE–RECAPTURE AND POPULATION PROJECTION METHODS<sup>1</sup>

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**Abstract.** Concern has arisen recently that Northern Spotted Owl (*Strix occidentalis*) populations may be declining faster than suspected by Spotted Owl biologists. This is based on recent estimates by the USDI of the annual rate of change in population size (i.e., population trend) calculated using capture–recapture and population projection methods. These original reports estimated change in the territorial population but used an inappropriate demographic model which did not incorporate immigration from the floater population. This approach, however, would be appropriate for estimating trend in the total population (floaters and territorial birds) if the model assumptions were met. This raises the possibility that Northern Spotted Owl populations are declining at approximately the rate reported in the USDI studies (6–8% per year) rather than at the rate previously suspected (1–3% per year).

I investigated this issue using a stochastic computer simulation in which population trends were estimated with capture–recapture and population projection methods and compared to the true population trends in the simulation. Factors that might cause bias in the trend estimate were identified and set to simulate the smallest and largest likely bias. The most important of these factors were the floater population and permanent emigration from the study site. Results showed that population trends in the simulation were underestimated by 0.03 to 0.13. Thus if the true annual rate of change in population size were 0.99 (i.e., a decline of 1%/yr), the estimate of 0.99 provided by the USDI studies would be 0.86 to 0.96. The simulations also provided new evidence, based on the past and current size of the floater population, indicating that Northern Spotted Owl populations have probably been declining at an average rate of  $\leq 3\%$  per year during the past few decades. My analysis indicates that the USDI studies should not be interpreted as providing evidence that owl populations are declining faster than previously assumed. We need careful investigation of trend estimates based on capture–recapture and demographic analyses before they are used as the basis for management decisions.

*Key words:* demography; population dynamics; Spotted Owl; *Strix occidentalis*.

### INTRODUCTION

This study addresses the issues of how rapidly Northern Spotted Owls (*Strix occidentalis*) are declining, and, more generally, of how population trends can be estimated for species in which a substantial segment of the population consists of nonterritorial individuals (“floaters”) who do not breed and are essentially undetectable on field surveys.

Northern Spotted Owls breed primarily in old-growth forests in northwestern California, western Oregon, and western Washington. They have been the subject of intense scrutiny during the past several years, much of which has focused on how rapidly their populations are decreasing. Most Spotted Owl biologists believe that the owl populations are decreasing slightly (1–3% per year), at a rate approximately equal to the rate at which old-growth is being harvested (Thomas

et al. 1993). This view was questioned recently in two reports (USDI 1990, 1992) that analyzed fecundity and resightings of color-banded owls, and concluded that Spotted Owl populations are declining much faster than had previously been suspected. The reports have been discussed extensively in government documents and have been used in court to argue that timber harvest on federal land in California, Oregon, and Washington should be sharply curtailed. The reports describe an analytic approach for estimating population trends that might be widely used, but raise several analytic and semantic problems. Deciding what trends are being estimated and how well has proven difficult. A thorough examination of the issues thus seems warranted.

The USDI reports (1990, 1992) used a standard projection equation (e.g., Caswell 1989):

$$1 = \frac{b_1 s_0}{r} + \frac{b_2 s_0 s}{r^2} + \frac{b s_0 s^2}{r^3(1 - s/r)}, \quad (1)$$

where  $b_1$ ,  $b_2$ , and  $b$  were the birth rates (number of fledglings produced) for birds of age 1 (12-mo-old), 2,

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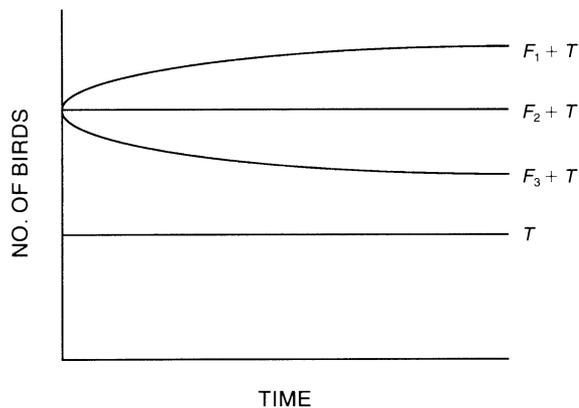


FIG. 1. Hypothetical Spotted Owl populations with the same number of territorial birds ( $T$ ) and variable dynamics with floater birds ( $F$ ). Birth and survival rates determine whether total population size increases ( $F_1 + T$ ), remains stable ( $F_2 + T$ ), or decreases ( $F_3 + T$ ) through time, but they do not affect, and thus cannot be used to estimate, trend in the number of territorial birds.

and older, respectively;  $s_0$  and  $s$  were the survival rates during the 1st yr, and subsequent years, of life; and  $r$  was the annual rate of change in population size. My notation differs slightly from that in USDI (1992).

Most young Spotted Owls enter the floater population for  $\geq 1$  yr before becoming territorial (Thomas et al. 1990). The authors of USDI (1990, 1992) argued that since these floaters are not surveyed directly,  $r$  should be interpreted as applying solely to the territorial population. Several difficulties exist with this view. First, the eigenanalysis approach that results in Eq. 1 assumes that the population is closed to movement. As a result, all surviving young enter the population and all additions to the population are from surviving young. Population size at any time,  $t + 1$ , can thus be represented as  $n(t + 1) = An(t)$  where  $A$  is the Leslie matrix of birth and survival rates. This equation has a central role in the proof of Eq. 1 (e.g., Caswell 1989:54), but it does not hold for the territorial segment of the Spotted Owl population. Most young owls do not enter the territorial segment; most additions to this segment come from nonterritorial birds. The projection equation, upon which the eigenanalysis is based, thus does not hold for territorial birds.

Second, *as long as floaters are present*, trend in the territorial segment is determined by trend in the amount of habitat suitable for territories, not by birth and survival rates. This point is easily seen by an example: the lower line in Fig. 1 depicts the territorial segment ( $T$ ) of a population. It decreases slightly, perhaps as a result of slow loss of habitat suitable for breeding territories. The three upper lines depict the trend including three hypothetical nonterritorial ( $F$ , floater) segments of the population. In one ( $F_3 + T$ ), birth and survival rates are too low to maintain the population; in one ( $F_2 + T$ ) the population is stable; and in one ( $F_1 + T$ ) birth

and survival rates are such that total population size is increasing towards a new stable point. Thus, birth and death rates in such a population determine whether and how long a nonterritorial population persists, but they have no effect on trend in the territorial population as long as nonterritorial birds are available to replace dead territorial birds in suitable habitat.

Third, empirical evidence also indicates the inappropriateness of using the projection equation to estimate trend in the territorial segment of the population. The USDI studies estimated that the population trends (i.e., annual rate of change in population size) of territorial birds on the five areas they studied varied from 0.88 to 0.93, but surveys of these territorial birds have shown that their populations were approximately stable during the study period (Thomas et al. 1993). The USDI studies investigated detection (resighting) rates of these surveys and found them to be high ( $\approx 90\%$ ) and constant during the study period. Under these conditions, the surveys provide a reliable estimate of trend (i.e., if surveys detect any constant fraction of the animals present, then the estimate of trend is unbiased). Thus reliable, empirical evidence indicates that the territorial segment of these populations was approximately stable during the study period.

Fourth, the simulations described below also show that trend in the territorial population cannot be estimated using Eq. 1. In most of the simulations, the territorial segment of the population was stable, yet the trend estimate produced by solving Eq. 1 for  $r$  was consistently below 1.0 because total population size was declining.

Although the authors of the USDI reports apparently did not intend their estimates to be applied to the whole population (floaters as well as territorial birds), the projection equation they used seems fairly well-suited to that purpose. Movements between floater and territorial owls are not a problem since birds are still within "the population." This population is under density-dependent regulation, but this does not cause significant bias in trend estimates (applied to the whole population) if estimates of the vital rates are unbiased. In this article, I investigate whether or not methods used in the USDI studies provide reasonably accurate estimates of trend in the entire population.

The analysis was somewhat complex because several sources of potential bias in the trend estimate were present. The projection equation is based on the assumptions that the birth and death rates remain constant through time (e.g., Caswell 1989). Birth rate means number of births divided by the total number of birds (not just territorial birds) in a given age class. Spotted Owl populations appear to be limited by space (USDI 1992). As population size changes, changes also occur in the proportion of birds that are floaters; this in turn affects the birth rate by changing the proportion of birds breeding. Thus the assumption that birth rates are constant through time is unlikely to be correct for Spotted

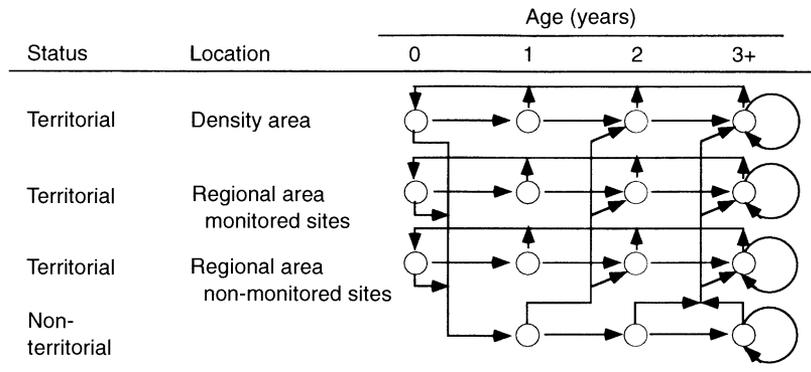


FIG. 2. Major stages and transitions in the simulation of Spotted Owl population dynamics. Territorial birds occur in three distinct areas (differing in survey efficiency) and have four age classes. Nonterritorial birds move freely between the areas but do not breed and are not detected on surveys. Arrows indicate possible transitions between stages (○). See text for description of other features of the simulation program.

Owls. The trend estimate derived from the projection equation is also based on the assumption that the population is at its stable age distribution, whereas numerous factors may drive a real population away from this condition. A further assumption is that the population is closed to movement. Emigration and immigration may cause bias in the trend estimate, though the magnitude and direction of bias depend on the specific circumstances. Finally, the USDI estimates assume a particular form of age-specific survivorship, but if some other form is actually correct, this might also cause bias in the trend estimate.

The combined effect of these potential sources of bias was difficult to determine analytically, so simulation methods were used. The overall objective was to explore the use of this approach for populations limited by space and to determine whether or not the USDI studies should revise the current belief that Spotted Owl populations are declining at the rate of  $\approx 1\text{--}3\%$  per year.

#### METHODS

The phrase “population trend” is used to mean “annual rate of change in population size,” where population refers to total population: floaters and territorial birds. If the population changes from a size of  $N_1$  at time 1 to  $N_2$  at time 2, then the trend,  $r$ , is defined as satisfying  $r^{t-1} = N_2/N_1$ , where  $t$  is the number of years between time 1 and time 2. When a series of population sizes was available, the trend was calculated using exponential regression. If  $N_t$  = population size in year  $t$ , and  $b$  = slope of the linear regression of  $\ln(N_t)$  on  $t$ , then the trend is  $\exp(b)$ . (An alternate definition of trend used by some authors is that  $r$  satisfies  $r^{t-1} = N_t/N_1$ , but I preferred to use all data, not just the first and last values, in calculating trend.) “True population trend” ( $r$ ) means the trend calculated from the population sizes in the simulation; “estimated population trend” ( $\hat{r}$ ) means the trend obtained by analyzing data

produced by the simulation using capture–recapture and population projection methods.

The analyses were carried out with a comprehensive computer program, written in True BASIC, which simulated an owl population, measured the true trend, produced a capture–recapture data set, estimated survival rates from this set of capture histories, and then estimated the population trend using Eq. 1. Major features of the simulation program are shown in Fig. 2, with additional details.

Bias was defined as the average difference, estimated trend minus true trend ( $\hat{r} - r$ ), in a series of runs. Percent bias was defined as  $(\text{bias})/(\text{true trend}) \times 100$ . Negative bias means the estimated trend tended to be smaller than the true trend; positive bias means the estimated trend tended to be larger than the true trend. Sample sizes were adjusted so that the standard error of the estimated bias was  $<0.003$  and/or the coefficient of variation of the estimated bias was  $<0.05$ . In most cases, 100 runs were sufficient to satisfy this criterion.

The simulated study area was divided into a “density” area with 30 sites (locations at which a female could nest), all of which were monitored, and a surrounding “regional” area with 60 sites, a year-specific fraction of which were monitored. The proportion of sites monitored in the regional area was set at 0.2 or 0.4 in the 1st yr of marking, and increased linearly to 0.8 in the 5th yr of marking. These values provide a reasonable range for the true values in the field studies (E. D. Forsman, *personal communication*). Once a site in the regional area was selected for inclusion in the sample, it was monitored in each subsequent year. These prescriptions were followed in the field studies reported in USDI (1992). No change in habitat occurred during the simulation.

The model simulated the female segment of an owl population during 15 yr. Males were assumed to be present as needed by females. Up to 30 age-specific birth and death rates and up to four age-specific move-

ment rates were permitted. Birds were allowed to live indefinitely; those older than 30 yr were given the same birth and survival rates as 30-yr-old birds. Birth was defined as the production of a female offspring that survived until fledging. The program required probabilities that (1) dispersing birds originating within the density area remained in the density area, moved to the regional area, or emigrated, and (2) that birds originating in the regional area remained there, moved to the density area, or emigrated. Calculation of these probabilities is described in *Emigration*. The number of birds of each age class leaving the study area as a result of dispersal equaled the number entering the study area except for a small random component. Immigrants and young birds remaining in the study area were added to the pool of floaters. Birds were chosen randomly from this pool at the end of each year to fill vacancies in the territorial population. The probability of filling a vacancy was the same for all birds of the same age class, but could vary between age classes so that older or younger birds had a competitive advantage in obtaining territories. All outcomes involving rates or proportions (e.g., births, deaths, movements, resightings) were determined stochastically. Outcomes were determined separately for each individual in the population (i.e., the model was individually based). Births were treated as a binomial random variable.

Marking and resighting rates were supplied for territorial birds and floaters in the density area, at monitored sites in the regional study area, and at non-monitored sites in the regional area. The same rates were used for marking and resighting. Marking began in year 11 (to let the age distribution stabilize), and resightings continued until year 15. The true and estimated population trends were based only on the simulation results for years 11 through 15, because the USDI studies were based on approximately five years of data.

The marking and resighting data were used to construct capture histories, which were then reduced to the form used by the capture-recapture program SURGE4 (Lebreton et al. 1992) used in the 1992 USDI report. SURGE4 was then used to obtain estimates of survival for the first year of life (from the beginning of dispersal in fall until the start of the next breeding season), and for all subsequent years. Resighting rates were year-specific, but not age-specific as in USDI (1992). Birth rates obtained from field studies and survival rates supplied by SURGE4 were used in the projection equation (Eq. 1) to estimate the population trend.

Additional details about possible sources of bias and the way the program permitted investigation of each source are provided below.

#### *Birth rates*

Birth rates were defined as the average number of female young produced per adult female (all females, not just territorial ones). I expressed this rate as  $p_i b_i^*$ , where  $p_i$  = proportion of the females of age  $i$  that were

territorial,  $b_i^*$  = the birth rate per territorial female, and  $p_i b_i^*$  thus equals the overall birth rate. The simulation program reported the  $p_i$ .

The formula for estimating annual rates of change in population size assumed that the birth rate was constant, when in fact it varies from year to year in real owl populations (USDI 1992). This variation was simulated by entering an average birth rate and then letting the program give equal probabilities to the birth rate in a particular year being zero or twice the average rate. This procedure resulted in more variation in the birth rate than has been observed in the field (Forsman, *personal communication*). The simulation thus produced an upper bound for the likely effects of variation in birth rate.

#### *Emigration*

Emigration was defined as occurring when the resighting probability for a marked bird fell to zero. Permanent emigration occurred when marked birds left the population during dispersal or settled on a non-monitored territory in the regional study area. Temporary emigration occurred when a bird entered the floater population.

All juveniles were assumed to disperse each fall. The probabilities that a dispersing juvenile emigrated, landed in the regional study area, or landed in the density area were estimated using a separate program. The density and regional portions of each of the five USDI (1990, 1992) study areas (Willow Creek, California; Medford, Roseburg, and Andrews, Oregon; and Olympic Peninsula, Washington) were delineated on maps and then stored in a computer file. Locations in the density and regional area were then chosen randomly to simulate birds beginning dispersal. A bearing was chosen at random, and a distance was chosen randomly from a set of natal dispersal distances recorded for radio-tagged juvenile Northern Spotted Owls (Thomas et al. 1990). The bearing and distance were used to determine the settling location, and the program recorded whether this location was in the density area, the regional area, or neither. Separate movement functions were constructed for males and females in each study area, and the average of the probabilities for the five study areas was used in the present analysis.

The natal dispersal data used in this analysis were collected on one of the five study areas. After this analysis was completed, additional data became available from another of the areas (the Roseburg study area). The new data set provided an opportunity to evaluate the simulation estimates of emigration rates. In the sample of radio-marked, dispersing juveniles from the Roseburg study area, 33% of nine birds emigrated from the density area, and 44% of nine birds emigrated from the regional area. The comparable numbers predicted by the simulation were 25 and 29%, respectively, suggesting that the simulation produced reasonably realistic estimates of emigration rates.

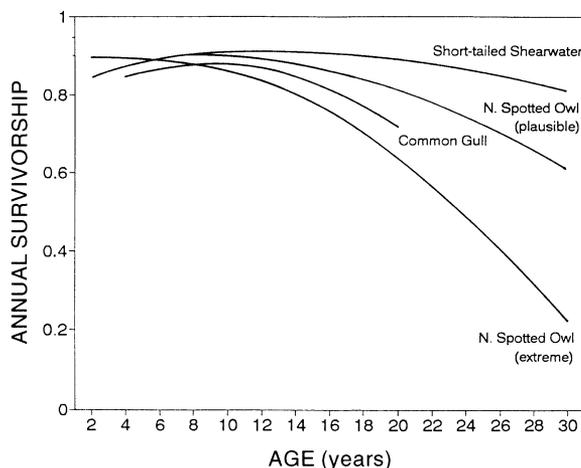


FIG. 3. Senescence in two long-lived avian species as reported by Newton (1989:Fig. 26.2, p. 459), and trends for Spotted Owl senescence used in this study.

In the simulation, a few territorial adults also dispersed after each breeding season. Values for the rate of dispersal by territorial birds were based on three data sets. The rate of emigration by radio-marked, territorial birds from the Roseburg study area in Oregon was 1% in a sample of >100 bird-years (Thomas et al. 1990:237). The comparable rate from the Willow Creek study area in California was 1.7% in a sample of 60 bird-years (Thomas et al. 1990:237). Dispersal rates were not reported in these studies, but were presumably somewhat higher than emigration rates (unless none of the dispersing birds settled within the study area). The rate of reported dispersal by color-banded, territorial birds was 5% in a sample of 200 bird-years in a study near Eugene, Oregon (J. A. Thraillkill, *personal communication*). The true dispersal rate was probably higher than 5% because birds settling outside the study area presumably had low resighting probabilities. Territory abandonment is thought to be higher among younger birds (E. D. Forsman, *personal communication*, G. S. Miller, *personal communication*). The data suggest that reasonable values for post-breeding season dispersal rates by 1-yr, and older, birds may be 5 and 2%, respectively, and that the values 10 and 4% provide reasonable upper bounds for these rates. I used these values in the simulation.

The probabilities that a dispersing, previously territorial, adult emigrated from the study area, landed in the regional study area, or landed in the density area were determined as described for juveniles except that distances dispersed were based on field data from dispersing males only. Males tend to disperse shorter distances than females (Thomas et al. 1990). The reason for using results from males only was that some evidence from marked birds suggests that adults may move shorter distances than juveniles (J. A. Thraillkill, *personal communication*, E. Forsman, *personal commu-*

TABLE 1. Population trend and proportion of birds that were floaters ( $F$ ) in the six populations of Spotted Owls investigated in the simulations. Trend = 1.00 in stable populations; trend < 1.00 in declining populations.

Population	Senescence*	Trend	Prop ( $F$ )
1	Absent	0.97	0.00
1s	Moderate	0.95	0.00
2	Absent	1.00	0.13
2s	Moderate	1.00	0.12
3	Absent	1.00	0.38
3s	Moderate	1.00	0.35

\* See Fig. 3 and Table 2.

*nication*). Too few data from adults were available to estimate the distribution of dispersal distances directly.

#### Senescence

Senescence here means a decline in survivorship or birth rate as age increases above some threshold value. No data on senescence are available for Spotted Owls, so data from other species were used. Newton (1989: Fig. 26.2, p. 459) presented trends showing the change in survivorship with age in several avian species. Two of the species (Short-tailed Shearwater, *Puffinus tenuirostris*, and Common Gull, *Larus canus*) had average survival rates in the range observed for Spotted Owls (Fig. 3). Senescence was modelled with the equation from USDI (1990) used to simulate senescence:

$$\text{senescence rate} = \alpha - \beta(\text{age} - \tau)^2,$$

where  $\alpha$ ,  $\beta$ , and  $\tau$  are constants.  $\alpha$  is the maximum value of the rate (occurring when age =  $\tau$ ), and  $\beta$  and  $\tau$  affect how quickly the rate decreases from its maximum value as the absolute difference between age and  $\tau$  increases. The same equation was used to model senescence in birth rate.

The equations were used to determine age-specific survival and birth rates, and these values were used in the simulation when senescence was present. The program also recorded the actual survival rate of birds 2, and >2, yr old and used these values to determine whether or not any bias existed in the capture-recapture estimates of survival rates.

Effects of senescence on the trend estimate were eliminated by using survival and birth rate functions with no senescence or by using the true, age-specific survival and birth rates (not estimates) in calculating the trend estimates. The latter option required expanding the equation for the population trend (Eq. 1) to permit more age-specific values for survival and birth rates.

#### Description of populations investigated

Two sets of populations were studied. The first set was constructed to facilitate investigation of the effects of different sources of bias in the trend estimate. It included six populations (Tables 1 and 2): two populations (1, 1s) which had no floaters and which were

TABLE 2. Parameters used to define average annual birth and survival rates for the first set of Spotted Owl populations investigated in the simulations.

A) SENESCENCE ABSENT								
Population*	Birth rates by age class (yr)				Survival by age class (yr)			
	0	1	2	≥3	0	1	2	≥3
1	0	0.11	0.14	0.33	0.40	0.86	0.86	0.86
2	0	0.11	0.14	0.33	0.40	0.89	0.89	0.89
3	0	0.11	0.14	0.33	0.40	0.92	0.92	0.92

B) SENESCENCE PRESENT†						
Population*	α		Other parameters‡			
	Birth rate	Survival rate	β <sub>1</sub>	β <sub>2</sub>	τ	
1s§	0.35	0.90	0.0015	0.0006	8	
2s	0.35	0.94	0.0015	0.0006	8	
3s	0.35	0.97	0.0015	0.0006	8	

\* See Table 1. Populations were 1, 2, and 3, and 1s, 2s, and 3s.  
 † Birth and survival rates for age > 1 yr were calculated with the senescence model (USDI 1990) described in text: rate =  $\alpha - \beta_1(\text{age} - \tau)^2$  for age <  $\tau$ , and rate =  $\alpha - \beta_2(\text{age} - \tau)^2$  for age  $\geq \tau$ .  
 ‡ Same values used for birth and survival rates.  
 § The survival for this population is shown in Fig. 3 as the ‘‘plausible’’ survivorship curve for Spotted Owls. Other curves have the same shape but are shifted vertically.

declining at the rate of 3–5% per year, two stable populations (2, 2s) in which 12–13% of the birds were floaters, and two stable populations (3, 3s) in which 35–38% of the birds were floaters (Tables 1 and 2). Senescence was absent in three of the populations (1, 2, 3) and present in three others (1s, 2s, 3s).

The second set of populations was constructed to facilitate estimating the combined effect of potential sources of bias in the USDI studies. This set also had six populations: two each declining at annual rates of 1, 4, and 7%. In each pair of populations, one was constructed to minimize bias in the trend estimate and the other was constructed to maximize this bias. Results were used to establish upper and lower bounds for the range within which the actual bias probably lies. The specific assumptions made in constructing these populations are discussed (see *Results*).

RESULTS

In this section, I first address the issue of whether or not the capture–recapture and projection method provides essentially unbiased estimates of trend when the estimates of the average birth and death rates are unbiased. Next, I explore the effects on the trend es-

timate of floaters, permanent emigration, and senescence. These issues are addressed using the first set of populations described. I then estimate the combined effect of the sources of bias using the second set of populations described.

*Performance of the model when parameter estimates were unbiased*

The standard projection equation assumes that all members of a given age class have the same birth and death rates and ‘‘projects’’ what the trend would be once the age distribution has stabilized. It does not generally give the trend for a real population during a specified interval, during which age distribution may be unstable due to random events (births and deaths) within years or to year-specific variation in birth or death rates.

These potential problems caused little bias in the trend estimate in these simulations (Table 3). The trend estimate was essentially unbiased even with implausibly high variation in birth rates. I did not simulate variation in survival rates between years because the USDI (1990, 1992) extensively investigated this issue and found that annual variation in survival rates was

TABLE 3. Results of simulations when the traditional definitions of terms were used in the projection equation and all estimates were unbiased.

Population*	Survival rates				Population trend		
	Age = 1		Age > 1		Ave. actual	Est. birth rates†	
	Actual	Ave. est.†	Actual	Ave. est.†		Constant	Variable‡
1	0.40	0.41	0.86	0.86	0.97	0.976	0.982
2	0.40	0.41	0.89	0.89	1.00	1.002	1.014
3	0.40	0.41	0.92	0.92	1.00	1.002	1.003

\* See Tables 1 and 2.  
 † Each estimate was based on 100 simulations.  
 ‡ Birth rates were doubled in half the years and set to zero in the remaining years. Even with this (implausibly) high variation in birth rates, the trend estimate was essentially unbiased.

TABLE 4. Results of simulations (sim.) when birth rate was defined as per territorial female and temporary emigration (caused by young birds entering the floater population) occurred at realistic rates. Because there was no permanent emigration by adults, adult survivorship estimates were unbiased.

Popu- lation*	$\bar{X}$ annual birth rate, fledglings/female		$\bar{X}$ Annual survival rate				Population trend (1.00 = stable)		
			Age = 1 yr		Age > 1 yr		$\bar{X}$ actual	$\bar{X}$ sim.†	Difference
	All ♀♀	Terr. ♀♀	Actual	$\bar{X}$ sim.†	Actual	$\bar{X}$ sim.†			
2	0.25	0.28	0.40	0.32	0.89	0.89	1.00	0.985	-0.015
3	0.25	0.32	0.40	0.14	0.92	0.92	1.00	1.002	-0.002

\* See Tables 1 and 2.

† Based on 100 simulations.

extremely small (i.e., undetectable with the models they used). Thus, for the Northern Spotted Owl, trend estimates appear to be quite reliable if unbiased estimates of the average rates are used in the projection equation.

#### *Effect of floaters on the estimators*

The USDI studies differed from my simulations in two respects. They used the birth rate for territorial females, not the average for all females, and they used a term in place of 1st-yr survivorship that is approximately the probability of surviving the 1st year and gaining a territory. They did not discuss these points in detail but both differences from my simulations result from my inclusion of floaters. Field data provide estimates of the birth rate per territorial female; these estimates were used, without any correction to account for floaters, in the projection equation. The difference between the average birth rate for territorial females and for all females (Table 4) was 0.03 fledglings per female for population 2 ( $\approx 13\%$  floaters) and 0.07 fledglings per female for population 3 ( $\approx 38\%$  floaters). Young marked at the nest were only resightable 1 yr later if they were on territories. Birds marked as young were sometimes resighted > 1 yr later when they did become territorial, and it is not entirely clear what effect such resightings had on the USDI estimates. The quantity they used as 1st-yr survivorship, however, was substantially lower than actual 1st-yr survivorship, particularly in population 3 which had more floaters (Table 4). Neither of these issues arose in the simulation of population 1 because it had no floaters.

Using higher values for birth rates tended to increase

the estimate of trend, whereas using a lower figure for 1st-yr survivorship tended to decrease it. The net effect was slight negative bias in populations 2 and 3 (Table 4). In Table 4, adult survivorship was estimated without bias, as would be expected in these simulations, because there was no adult emigration.

#### *Effects of permanent emigration on the trend estimate*

The simulation study of dispersal showed that  $\approx 40\%$  of the birds that dispersed left the study area and  $\approx 30\text{--}50\%$  of the birds beginning dispersal in the density area landed in the regional study area (Table 5). As noted (in *Methods*), 20–80% (depending on the year) of these regional area sites were monitored but the rest were not. Birds landing at non-monitored sites had resighting rates of 0%, and thus acted like emigrants. Adding permanent emigration to the simulation substantially increased the bias. Adult survival rates were underestimated by about 0.03 and the trend estimate was underestimated by about 0.10 (Table 6).

#### *Effects of senescence*

Moderate senescence (Fig. 3, Tables 1 and 2) caused a small positive bias of 0–0.02 in the trend estimates of three populations (1s, 2s, and 3s) when no other sources of bias were present.

#### *Upper and lower bounds for the true trend in population size*

The most important sources of bias in the trend estimate were: (1) the proportion of sites monitored in the regional study area (which affected emigration

TABLE 5. Owl movement probabilities obtained from the simulations of dispersal at five field study areas\* as reported by the USDI (1990, 1992).

Sex	Dispersal from density area to:			Dispersal from regional area to:		
	Within study area		Outside study area	Within study area		Outside study area
	Density area	Regional area		Density area	Regional area	
Males	0.47	0.27	0.26	0.07	0.66	0.27
Females	0.15	0.31	0.54	0.07	0.41	0.52
Both	0.31	0.29	0.40	0.07	0.54	0.39

\* Separate simulations were conducted for each of the five study areas. Values reported in this table are averages.

TABLE 6. Results of simulations when birth rate was defined as the birth rate per territorial female and temporary and permanent emigration occurred at realistic rates.

Popu- lation*	$\bar{X}$ annual birth rate, fledglings/female		$\bar{X}$ annual survival rate				Population trend (1.00 = stable)		
			Age = 1 yr		Age > 1 yr		$\bar{X}$ Actual	$\bar{X}$ sim.†	Difference
	All ♀♀	Terr. ♀♀	Actual	$\bar{X}$ sim.†	Actual	$\bar{X}$ sim.†			
1	0.31	0.31	0.40	0.12	0.86	0.84	0.97	0.87	-0.10
2	0.26	0.29	0.40	0.13	0.89	0.86	1.00	0.89	-0.11
3	0.21	0.32	0.40	0.32	0.92	0.90	1.00	0.91	-0.09

\* See Tables 1 and 2.

† Based on 100 simulations.

rates), (2) the frequency and extent of movements (which also affected emigration rates), and (3) the degree of senescence. The bias was small when high proportions of sites in the regional area were monitored and when dispersal distances were short. Accordingly, the proportion of sites visited in the regional area in the 1st yr of the study was set at 0.4 for the smallest bias simulation and 0.2 for the largest bias simulation (Table 7). The smallest bias simulation used dispersal data from males (which disperse shorter distances than females); the largest bias simulation used female dispersal. Older birds did not move in the smallest bias simulation; in the largest bias simulation, 10% of the 1st-yr females moved after breeding and 4% of the older females moved after breeding. Few birds bred as 1 yr olds, so the rate of movement by 1 yr olds had little effect on bias. The smallest bias simulation used the "extreme" degree of senescence in survivorship and productivity (Fig. 3). These senescence functions produced positive bias in the trend estimate when no other biases were present, and thus tended to offset the largely negative bias produced by other factors. The largest bias simulation assumed no senescence.

Results of these analyses showed that magnitude of the bias was the same in populations with true population trends of 0.93, 0.96, and 0.99 (Table 8). In each population, the smallest likely bias was  $\approx -0.03$  and the largest likely bias was  $\approx -0.13$ . Thus the estimated

population trends were low by  $\approx 3$  to 13%. For example, when the true annual rate of change was 0.99, estimates of this value varied from 0.86 to 0.95, depending on which sources of bias were present in the simulation.

### DISCUSSION

Thomas et al. (1990) provided a detailed discussion of habitat use, habitat preference (based on use vs. availability studies), density and demographic rates in different habitats, and long-term population trends in Spotted Owls. They concluded that habitat loss was the primary reason for declining owl populations and that, over periods of many years and over large areas, populations were declining at approximately the same rate as habitat was declining.

The USDI (1992) study suggested that Spotted Owl populations might be declining much faster than reported in Thomas et al. (1990). The evaluation reported here, however, indicates that the USDI (1992) estimates of annual rates of change in population size are too low (sampling error aside) by 3 to 13%. Their point estimate for population trend (all populations combined) was 0.90; adding the bias term would give a range of 0.93 to 1.03 for the annual rate of population change. This range is broader than the range we can establish based on other evidence. Assuming a stable or increasing trend would certainly not be reasonable given the continuing habitat loss the population is experiencing. Thus the trend must be less than 1.0. Fur-

TABLE 7. Parameters in simulations used to estimate the smallest and largest likely bias in trend estimates.

Factor	Smallest likely bias	Largest likely bias
Proportion of sites in regional area monitored in year one of the study	0.4	0.2
Values used for rates of movement	Males*	Females*
Frequency of movements by adults	None	10%/4%†
Senescence	Extreme‡	None

\* As defined in Table 5.

† 10% of the 1-yr-old territorial females, and 4% of the older territorial females, moved after each breeding season.

‡ See "extreme" curve in Fig. 3. The curve was shifted vertically to produce actual trends of 0.93, 0.96, and 0.99.

TABLE 8. Smallest and largest likely bias in estimates of population trends calculated using capture-recapture and population projection methods.

True population trend	Smallest likely bias		Largest likely bias	
	Average estimate of trend	Bias*	Average estimate of trend	Bias*
0.93	0.90	-0.03	0.80	-0.13
0.96	0.92	-0.04	0.85	-0.11
0.99	0.95	-0.04	0.86	-0.13

\*  $(r_i - r_t)/100$ , where  $r_i$  = true trend in simulation  $i$ ,  $i$  = simulation number 1, 2, 3, . . . , 100,  $r_t$  = estimated trend in simulation  $i$ .

thermore, the trend must be greater than 0.93 for reasons which will be discussed.

*An alternate approach for estimating population trends*

If the number of territorial birds remains constant when population size changes, then a simple relationship exists between the change in proportion of birds that are floaters and change in population size. Let

$N_1, N_2$  = the population sizes at times 1 (earlier)

and 2 (later), and

$p_1, p_2$  = the proportion of birds that are floaters

at times 1 and 2.

Under the assumption that the number of territorial birds remains constant,  $(1 - p_1)N_1 = (1 - p_2)N_2$ , and thus

$$\frac{N_2}{N_1} = \frac{1 - p_1}{1 - p_2}$$

The population trend (annual rate of change),  $r$ , that would produce the change  $N_2/N_1$ , satisfies  $r^t = N_2/N_1$ , where  $t$  is the number of years between times 1 and 2. Thus we may write:

$$r = \left( \frac{1 - p_1}{1 - p_2} \right)^{1/t}$$

Consider a population that declines from  $N_1$  to  $N_2$  during  $t$  years. The minimum value of  $r$  occurs when  $(1 - p_1)/(1 - p_2)$  is small or when  $1/t$  is large. These conditions, in turn, occur when  $p_2$  is much smaller than  $p_1$  or when  $t$  is small. Thus, finding the minimum value for  $t$ , the maximum value for  $p_1$ , and the minimum value for  $p_2$  establishes a minimum value for the trend,  $r$ . This approach is followed.

Habitat on federal land has been disappearing at a fairly constant rate since 1960 (Bart and Forsman 1992), and it thus seems likely that Spotted Owl populations have been declining for at least the past 20 yr and probably the past 30 yr. The floater population is largest when the population has maximum rates of survival and productivity. I used the population simulator to determine this upper limit on size of the floater population. Birth rates for females of ages 1, 2, and  $\geq 3$  yr were set at 0.15, 0.25, and 0.40 fledglings per female, respectively, and survival rates for 1st-yr and older birds were set at 0.50 and 0.91. These values are substantially higher than those reported from field studies and seem to represent reasonable upper bounds on the vital rates. With these rates, the proportion of birds that were floaters stabilized at  $\approx 60\%$ ; this value was therefore taken as a reasonable upper limit on the proportion of floaters. Estimation of the size of the floater population at present is more complex, as follows.

*Estimating the floater population.*—In this section I use the phrase “proportion of first-time breeders that

were subadults.” For a given year, this phrase means: (number of subadult, territorial females that have not previously held a territory)/(number of adult and subadult territorial females that have not previously held a territory). This proportion was between 0.25 and 0.40 in the Spotted Owl populations and showed no evidence of temporal trends during the periods of study (USDI 1992).

The basis for estimating the current size of the floater population was that a relationship must exist between the proportion of first-time breeders that are subadults and the proportion of floaters in the population. For example, if the population in an area (large enough that immigration and emigration could be ignored) contained no floaters, then all first-time breeders would be subadults. If a large proportion of the birds were floaters, then few first-time breeders would be subadults (unless adults had a strong competitive disadvantage in filling vacancies in the territorial population).

A series of analyses with the population simulator (but not involving estimation of survival rates or trends) was undertaken to investigate the proportion of first-time breeders that were subadults. This proportion varied between runs due to the stochastic nature of the program. Input parameters were adjusted so that the proportion was often stable and between 0.25 and 0.40 during the last 5 yr of the simulation, and thus mimicked the field data. The simulations were quite sensitive to adult survival rates. When these rates were below 0.90, the floaters quickly disappeared, causing the proportion of floaters that were subadults to climb rapidly above 0.40. With adult survival rates above 0.91, the number of floaters remained high or increased quickly if the initial proportion had few floaters; thus the proportion of first-time breeders that were subadults was always  $< 0.25$ . The proportion was also affected by whether or not adults had a competitive advantage over subadults in filling vacant sites. This factor was therefore varied in the simulations. Birth rates and 1st-yr survival rates were set at the same values as in other runs (Table 2A).

After choosing a suitable set of input parameters, I prepared a scatter plot showing proportion of first-time breeders that were subadults plotted against proportion of birds that were floaters. The scatter plot was then used to judge the range in proportion of floaters when the proportion of subadult first-time breeders was 0.25 vs. 0.40. These analyses showed that the proportion of floaters varied from  $\approx 0.20$  to 0.40 (Table 9). The proportion was slightly higher with higher survival rates, when fewer first-time breeders were subadults, and when adults did not have a competitive advantage over subadults in occupying vacant sites. The simulation thus indicates that floaters probably comprised  $\geq 20\%$  of the birds in the field populations.

The relevant values for calculating the population trend using the method described here are thus that the decline has been occurring for  $\geq 20$  years and that dur-

TABLE 9. Simulated relationship between proportion of first-time breeders that were subadults and proportion of birds that were floaters.

Proportion of subadult first-time breeders	Annual adult survival rate	Proportion of birds that were floaters, by ability to fill vacancies:	
		Adults and subadults had equal ability	Adults had an advantage over subadults
0.25	0.90	...*	0.27-0.35
0.25	0.91	0.33-0.43	0.27-0.40
0.40	0.90	0.20-0.35	0.20-0.32
0.40	0.91	0.23-0.38	0.20-0.37

\* Under these conditions, floaters disappeared from the population.

ing this time the proportion of floaters has decreased, at most, from  $\approx 60\%$  to  $\approx 20\%$ .

*Estimation of rate of annual change in population size.*—Returning to the estimation of rates of change, the minimum value for  $t$ , the time interval, is probably  $\geq 20$  yr;  $p_1$ , the initial proportion of floaters, is probably  $\leq 0.6$ ; and  $p_2$ , the recent proportion of floaters, is probably  $\geq 0.2$ . With  $t = 20$ ,  $p_1 = 0.6$ , and  $p_2 = 0.2$ , the total twenty-yr decline in population size is 50% and the annual rate of change is 0.966 (i.e., a decline in population size of 3.4%/yr). The true decline could certainly be smaller. For example, if floaters declined from 0.60 to 0.35 of the population and the decline began in 1960, then the population declined in size by 38%, equivalent to an average annual decline of about 1.6%. Constructing a scenario under which the population has been declining much faster than  $\approx 3\%/yr$  is difficult. For example, even if all the floaters were gone at present (which clearly is not true), the annual decline would be 4.5% if the decline began 20 years ago and 3% if it began 30 years ago.

#### *Use of demographic methods to estimate population trends*

Future work in this area should use capture-recapture and demographic models that acknowledge the existence of the floater population and the facts that floaters do not produce offspring and are seldom resighted. Temporary emigration (i.e., to the floater population) causes difficult technical problems in capture-recapture analyses (Balser 1981, Pollock et al. 1990, Lebreton et al. 1992), but a considerable amount of helpful work has been done recently or is in progress (J. Nichols, *personal communication*, K. Pollock, *personal communication*). The demographic model must recognize that the probabilities of entering and leaving the floater class change as population size changes (i.e., that population size is limited by space).

Permanent emigration also causes significant prob-

lems for both the capture-recapture and demographic analyses. Permanent emigration might be avoided by greatly increasing the size of the regional study areas. Cost would not necessarily increase, as the region could be stratified and sampling intensity could vary, and generally be lower than in the studies reported in USDI (1992). New sites would have to be sampled each year, however. If permanent emigration occurs, then its magnitude must be estimated, perhaps by telemetry studies, or immigration rates must be estimated and incorporated into the demographic analysis. As shown by my simulation analysis, exploiting the relationship between the abundance of floaters and the proportion of first-time breeders that are young birds may also be useful.

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