

SEX RATIOS OF FLEDGLING AND RECAPTURED SUBADULT SPOTTED OWLS IN THE SOUTHERN SIERRA NEVADA

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ABSTRACT: Estimates of instantaneous growth rates (λ) of spotted owl (*Strix occidentalis*) populations have been based on demographic data that uniformly assumed an equal sex ratio among fledglings. In this study, sex ratios of subadults, banded as juveniles, and fledgling California spotted owls (*S. o. occidentalis*) were observed and compared to an assumed 1:1 ratio. The sensitivity of lambda (λ) to variations in fledgling sex ratio was then examined. The sexes of 73 fledgling spotted owls from 1993 and 1994 were 42:31 (males:females) in the Sierra National Forest (SNF) and Sequoia and Kings Canyon National Parks (SNP). Sex ratios of fledglings ranged from 2.5:1 (SNF 1993) to essentially 1:1 (SNF 1994, SNP 1993 and 1994) but did not differ significantly from 1:1 in any sample. The sex ratio of 25 subadults in both study areas was significantly different from 1:1 and strongly biased towards males (19:6). This more likely results from differential dispersal differences between juvenile male and female owls, with the females likely dispersing beyond study area boundaries more often than males. Lambda was only slightly sensitive to variation in fledgling sex ratio, and was influenced more by yearly variation in fecundity than in observed vs. assumed sex ratios within years. Variations in fledgling sex ratio observed in this study are probably not biologically significant when considered at the larger scale of a regional population, as opposed to the small subpopulations under study in SNF and SNP, or over longer time scales than the two years reported here.

Key words: California spotted owl, Fecundity rate, Fledgling, Owl, Sex ratio, Spotted owl, *Strix occidentalis occidentalis*, Subadult.

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INTRODUCTION

Demographic data on the California spotted owl (*Strix occidentalis occidentalis*) is essential to understanding its population dynamics and monitoring population changes. Five life history parameters are needed to estimate rates of population change: survival rates of juvenile, subadult, and adult birds; age at first reproduction; and fecundity (Thomas et al. 1990). In recent assessments of the status of spotted owls, inferences about population growth rates (lambda) have been based, in part, on a fecundity rate that assumed an equal sex ratio (Thomas et al. 1990, Noon et al. 1992). My objectives in this study were to (1) compare the observed sex ratios for fledglings and subadults with an assumed 1:1 sex ratio; and (2) examine the sensitivity of lambda (λ) to variations in fledgling sex ratios.

I wish to thank all the people who devoted time and effort gathering data for this project, especially Thomas Munton and Kenneth Johnson for their supervision of the field crews. Thanks to Gary Eberlein for his graphics work and to William Laudenslayer for his words of encouragement and constructive comments. Finally, I would like to thank Jared Verner, Leslie Chow, Stephen A. Laymon, Marty Berbach, and an anonymous reviewer for their comments on this manuscript.

STUDY AREA AND METHODS

This study was conducted in the southern Sierra Nevada, in Sierra National Forest (SNF) and Sequoia and Kings Canyon National Parks (SNP) (Fig. 1). Study area

boundaries were delineated by major topographic features such as ridges, major drainages, and administrative boundaries. The SNF study area covered 684 km² and the SNP study area covered 342 km². Vegetation within the study areas consisted of montane hardwood (610 m - 1,220 m), montane hardwood conifer (1,221 m - 2,439 m), and Sierra mixed conifer (2,440 m - 2,743 m) (Mayer and Laudenslayer 1988).

I located, captured, and banded, fledgling spotted owls using standard methods (Forsman 1976, 1983). After banding, the brachial vein was punctured and blood was

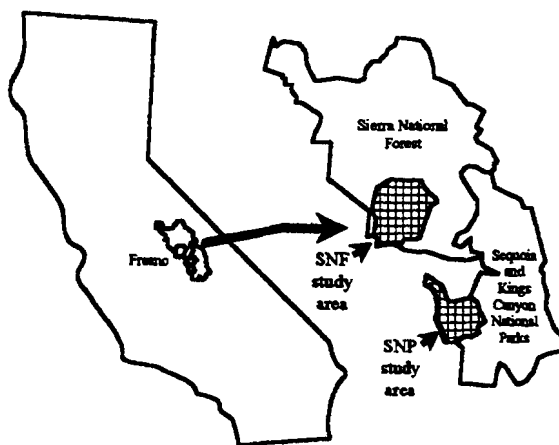


Fig. 1. Location of the study areas for California spotted owls in the southern Sierra Nevada, California.

collected in 0.01 cc capillary tubes and stored in a preservative solution. Blood from a group of adult owls, whose sexes had been determined by vocalizations, was used as a control for the analyses of the fledgling sample. Sex verification from blood samples was done by nuclear deoxyribonucleic acid (DNA) flow cytometry (Tiersch et al. 1991).

I estimated the sex ratio of subadults returning to both study areas by recapturing birds banded as fledglings from 1990 to 1993. I located returning subadults using vocal imitations of spotted owls to elicit responses. Once located, owls were sexed by vocalization and/or behavior (Forsman 1983), captured, and banded with a distinct color band to prevent recounting.

I used the exact binomial test ($P = 0.05$) to determine if sex ratios differed from 1:1 for fledglings and subadults banded as fledglings. The null hypothesis was $H_0: P = 1/2$, where P is the proportion of males.

I calculated λ using the Lefkovich stage-projection matrix model (Lefkovich 1965) with reported vital rates for SNP (Noon et al. 1992). Population trends were considered increasing if $\lambda > 1.0$, stable if $\lambda = 1.0$, and in decline if $\lambda < 1.0$. Four of the five demographic parameters used to estimate λ were held constant: juvenile survival rate (s_j) = 0.296; subadult (s_s) and adult survival rates (s_a) were combined as "nonjuvenile survival rate" = 0.895; and the age at first reproduction = 2 years old (Noon et al. 1992). I varied the fifth parameter, fecundity (b), defined as the number of female offspring produced per territorial female (Noon and Biles 1990, Thomas et al. 1990, Noon et al. 1992), by substituting either observed fecundity or assumed fecundity. Observed fecundity rates (b_1) were calculated as: $b_1 = (F_1/S)/N$, where F_1 is the observed estimate of female fledglings from the DNA analysis, S is the proportion of the fledglings sampled, and N is the number of females ≥ 2 years old checked for reproduction. Assumed fecundity rates (b) were calculated as: $b = (F/N)/2$, where F is the total number of fledglings counted. Variance in annual fecundity was based on variance among females across the years of study, divided by the appropriate sample size. I only examined the sensitivity of λ to variations in fledgling sex ratio for SNP. Published estimates of vital rates were unavailable for SNF.

An estimate of λ and its standard error allowed the tests of hypotheses: $H_0: \lambda \geq 1$, versus the alternative $H_a: \lambda < 1$. The appropriate test statistics followed a Z-distribution, given by: $Z = |(\lambda - 1)/\delta_\lambda|$. Tests were one-tailed with a specified alpha level of 0.05 and are reported as a P value.

RESULTS

I collected 75 blood samples from fledgling California spotted owls between June and September 1993-1994. Approximately 80% of the known fledglings in the study

areas were tested. I took eight additional samples from adults of known sex. In the adult control group (4 males and 4 females) results from DNA testing agreed with all sex identifications by voice and/or behavior. DNA analysis also produced similar results for five subadults sexed as fledglings that returned to the study areas in 1994. Of the 75 fledglings, 42 were male and 31 were female. Two lacked sufficient DNA to be tested. The number of female offspring produced per territorial adult female ranged from 0.21 to 0.38 (Table 1). Separated by study area and year, SNF had 15 males and six females in 1993, whereas sex ratios in all other samples were nearly equal (Fig. 2). None of these sex ratios, including SNF in 1993, differed significantly from 1:1.

The sex ratio of twenty-five subadults, banded as fledglings, (19 males and six females) differed significantly from 1:1 ($P < 0.01$). Results for both SNF (11:4) and SNP (8:2) were similar.

Statistical tests failed to reject the null hypothesis $\lambda \geq 1.0$ ($P = 0.05$). In all analyses, λ was about five times more sensitive to adult survival rate than to fecundity and first-year survival rates. Using the lowest estimate of fecundity

Table 1. Estimated fecundity rates of California spotted owls in SNF and SNP study areas using observed sex ratios and assumed 1:1 sex ratios, by study area and year

Study area Year	Adult females (≥ 2 years old)	Juvenile females	Fecundity ¹
Sierra National Forest			
1993			
Observed	31	6.6	0.21
Assumed 1:1	31	11.5	0.37
1994			
Observed	43	14.0	0.33
Assumed 1:1	43	14.0	0.34
Sequoia/Kings Canyon National Parks			
1993			
Observed	24	6.8	0.29
Assumed 1:1	24	7.5	0.31
1994			
Observed	29	11.0	0.38
Assumed 1:1	29	11.0	0.38

¹ Number of female offspring produced per territorial adult female.

derived from the observed sex ratio for SNP (0.29) resulted in a population decline of about 2 percent per year (Table 2). The highest observed fecundity (0.38) produced a stable population (Table 3). Estimates of λ assuming a 1:1 sex ratio (Table 4) were nearly identical to those of the observed sex ratios by year. Changes in yearly fecundity rates affected λ more than fledgling sex ratios in SNP.

DISCUSSION AND CONCLUSIONS

My study resulted in detecting significantly more male than female subadults returning to the study areas. I do not know whether this is due to sex differences in turnover rates, dispersal distances between natal sites and first breeding territories, or is sampling error caused by differential responses to imitated calls. In studies of bird dispersal, females moved farther from their natal sites than males in most species studied to date (Newton 1989). Any

or all of these factors could influence the observed sex ratio of returning subadults. This bias toward males suggests that sex ratios of subadults banded as fledglings may not be good estimators of fecundity rate.

I did find that observed fledgling sex ratios do not depart significantly from 1:1, although the observed sex ratio was slightly biased toward males. Male fledglings outnumbered females 2.5:1 in SNF in 1993. This sex ratio could be biologically significant if it were sustained in a closed population. However, juvenile dispersal between the SNF and SNP subpopulations has been documented (Steger et al. 1995). One season of an uneven fledgling sex ratio in a subpopulation would be unlikely to affect the sex

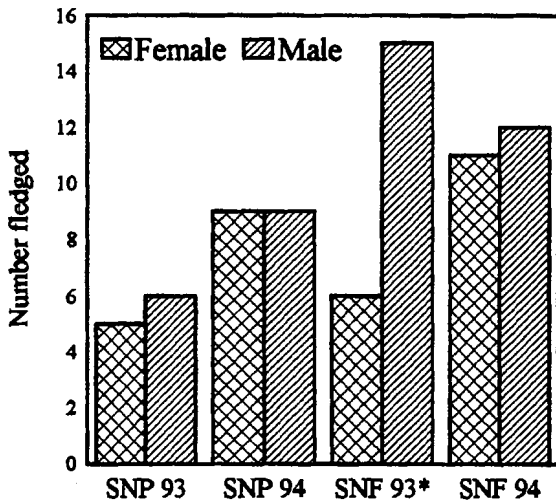


Fig. 2. Number of fledgling owls sexed by DNA analysis by year and study area. *SNF was significantly different from a 1:1 ratio at 0.08 level.

Table 3. Estimates of the annual finite rate of population change (λ) for the California spotted owl in Sequoia and Kings Canyon National Parks, with test statistics and P value for the test of the null hypothesis that $\lambda \geq 1.0$ vs. $\lambda < 1.0$.

Parameter	Estimated	Sample size	Standard error	Sensitivity	P
Juvenile survival (s_0)	0.296	130	0.055	0.310	
Nonjuvenile survival (s)	0.895	45	0.047	1.010	
Fecundity (b1)	0.380	28	0.086	0.241	
Population change (λ)	0.996		0.055		0.48

¹ Number of female young per territorial female, from 1994 (observed sex ratio).

Table 4. Estimates of the annual finite rate of population change (λ) for the California spotted owl in Sequoia and Kings Canyon National Parks, with test statistics and P value for the test of the null hypothesis that $\lambda \geq 1.0$ vs. $\lambda < 1.0$.

Year	Parameter	Estimated	Sample size	Standard error	Sensitivity	P
1993	Juvenile survival (s_0)	0.296	130	0.055	0.261	
	Nonjuvenile survival (s)	0.895	45	0.047	1.007	
	Fecundity (b) ¹	0.310	24	0.080	0.249	
	Population change (λ)	0.980		0.053		0.34
1994	Juvenile survival (s_0)	0.296	130	0.055	0.310	
	Nonjuvenile survival (s)	0.895	45	0.047	1.010	
	Fecundity (b) ¹	0.380	28	0.086	0.241	
	Population change (λ)	0.996		0.055		0.48

¹ Number of female young per territorial female, from 1993 and 1994 (1:1 sex ratio).

Table 2. Estimates of the annual finite rate of population change (λ) for the California spotted owl in Sequoia and Kings Canyon National Parks, with test statistics and P value for the test of the null hypothesis that $\lambda \geq 1.0$ vs. $\lambda < 1.0$.

Parameter	Estimated	Sample size	Standard error	Sensitivity	P
Juvenile survival (s_0)	0.296	130	0.055	0.247	
Nonjuvenile survival (s)	0.895	45	0.047	1.007	
Fecundity (b1)	0.290	24	0.075	0.252	
Population change (λ)	0.974		0.053		0.31

¹ Number of female young per territorial female, from 1993 (observed sex ratio).

ratio at a regional scale. Additional years of data will show if 1993 was an anomaly. If it is not, then investigation into the underlying causes of male biased sex ratio would be warranted.

Results of this study agree with Noon and Biles (1990) that estimates of λ are only slightly sensitive to variations in fledgling sex ratio. Lambda values were influenced to a greater extent by yearly changes in fecundity rates than by observed or assumed sex ratio within years. Wide variations in yearly fecundity rates (0.04 in 1991 to 0.89 in 1992) have been observed in SNP (Steger et al. 1995). Vital rates derived from short term studies in SNP have also varied (Noon et al. 1992, Steger et al. 1995). These fluctuations in vital rates influence λ values and ultimately management decisions. Longer term studies of fecundity and other vital rates are needed to help better understand influences such as sex ratio variation, weather conditions, and shifts in prey abundance.

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