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Sources of variability in spotted owl population growth rate: testing predictions using long-term mark–recapture data

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Abstract For long-lived iteroparous vertebrates that annually produce few young, life history theory predicts that reproductive output (R) and juvenile survival should influence temporal variation in population growth rate (λ) more than adult survival does. We examined this general prediction using 15 years of mark–recapture data from a population of California spotted owls (*Strix occidentalis occidentalis*). We found that survival of individuals ≥1 year old (φ) exhibited much less temporal variability $\left(\widehat{\mathrm{CV}} = 0.04\right)$, where CV is coefficient of variation, than R $\left(\widehat{\mathrm{CV}} = 0.83\right)$, and that R was strongly influenced by environmental stochasticity. Although λ was most sensitive ($\hat{e}$; log-transformed sensitivity) to φ ($\hat{e} = 0.77$), and much less sensitive to either R ($\hat{e} = 0.12$) or juvenile survival (survival rate of owls from fledging to 1 year old; $\hat{e} = 0.12$), we estimated that R contributed as much as φ to the observed annual variability in λ. The contribution of juvenile survival to variability in λ was proportional to its $\hat{e}$. These results are consistent with the hypothesis that natural selection may have favored the evolution of longevity in spotted owls as a strategy to increase the probability of experiencing favorable years for reproduction. Our finding that annual weather patterns that most affected R (temperature and precipitation during incubation) and φ (conditions during winter related to the Southern Oscillation Index) were equally good at explaining temporal variability in λ supports the conclusion that R and φ were equally responsible for variability in λ. Although currently accepted conservation measures for spotted owl populations attempt to enhance survival, our results indicated that conservation measures that target R may be as successful, as long as actions do not reduce φ.

Keywords Elasticity · Fitness components · Life history strategy · Spotted owl · Temporal variability

Introduction

Understanding the link between a species' population dynamics and its life history strategy is important for refining theory regarding life history strategy (Caughley 1994) and for conservation planning (Mills et al. 1999). Because survival and reproductive output (R) determine individual fitness, there is a direct link between demography and the evolution of life history strategy (Stearns 1992). This relationship allows population growth rate (λ) to be considered as a measure of fitness and survival and R to be considered as fitness components (Caswell 2001). For most iteroparous vertebrates that annually produce few young, proportional changes in the survival rate of adults are thought to have a greater effect on λ than proportional changes in all other fitness components, with this relationship apparently strengthening in species with longer generation times that produce fewer young (Gaillard et al. 2000; Sæther and Bakke 2000). It has also been estimated that fitness components that have the greatest influence on λ typically exhibit the least amount of temporal variability (Gaillard et al. 1998). This phenomenon may be caused by canalization

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(a process in which developmental mechanisms reduce phenotypic variation) and should be more pronounced in traits under strong selective pressure (Stearns and Kawecki 1994).

Natural selection in long-lived species is thought to favor mechanisms that buffer adult survival against environmental variation because survival makes such a large contribution to λ (Pfister 1998; Gaillard and Yoccoz 2003). However, the influence that environmental variability has on life history evolution is debatable (e.g., Ricklefs 2000; Orzack and Tuljapurkar 2001). One prediction is that increased temporal variability in R is a consequence of individuals not breeding in a poor-quality year in order to reduce costs that would negatively affect long-term survival. Such a tradeoff to increase fitness has been predicted for organisms in general (Cohen 1966; Schaffer 1974), and may play a role in the evolution of life history (Stearns 1992). A related hypothesis is that uncertainty in juvenile (i.e., pre-reproductive) survival should increase the benefits of iteroparity and increased longevity because an increased number of reproductive attempts increase the chances of reproducing when environmental conditions become more favorable (Murphy 1968).

The spotted owl (*Strix occidentalis*) has been the subject of many population biology investigations because its conservation is linked to the management of mature conifer forests having high economic value (Gutiérrez et al. 1995). Annual variation in spotted owl demographic parameters, such as survival and R, appears to be correlated with weather (i.e., environmental stochasticity; Franklin et al. 2000; Seamans et al. 2002; LaHaye et al. 2004; Olson et al. 2004). For the northern spotted owl (*Strix occidentalis caurina*), it has been estimated that λ is most sensitive to changes in survival of adults ($\geq$3 years old) compared to changes in other fitness components (Lande 1988; Noon and Biles 1990). In addition, the spotted owl is apparently similar to many other long-lived species because survival of individuals $\geq$1 year old (φ) exhibits the least amount of temporal variability among fitness components (Franklin et al. 2000; Seamans et al. 2002; LaHaye et al. 2004; Olson et al. 2004).

We investigated demographic rates of California spotted owls (*S. occidentalis occidentalis*) under varying weather conditions over a 15-year period in the central Sierra Nevada, California. We examined the following predictions based on life history theory:

1. Environmental variability (temporal variability in weather) has a greater effect on R than on φ.
2. λ is most sensitive to annual φ and least sensitive to R and juvenile survival.
3. φ exhibits the least amount of temporal variability among demographic parameters because of its importance to λ.
4. Juvenile survival and R play a larger role in determining annual variation in λ than expected based on the sensitivity of λ to these parameters.
5. If juvenile survival and R have the greatest influence on annual variation in λ there should be a strong relationship between these parameters, weather, and λ.

Our modeling of empirical data provides a direct approach for testing hypotheses stemming from life history theory and advances our understanding of variability in λ for animal populations.

Materials and methods

Study species

The spotted owl is a medium-sized owl that inhabits mountainous terrain in western North America (Gutiérrez et al. 1995). The spotted owl is territorial and monogamous (Gutiérrez et al. 1995), and generally does not switch sites after establishing a territory (Blakesley et al. 2006). Although floaters (non-territorial individuals of breeding age) exist in populations, only territorial owls are known to breed (Gutiérrez et al. 1995). Noon et al. (1992) hypothesized that because territorial spotted owls have a high annual survival rate (>0.80; Franklin et al. 2004), it is likely they have a long lifespan (we have observed both male and female owls as old as 17 years successfully reproducing). One-year-old spotted owls are reproductively mature although they are less likely to breed than older individuals (Gutiérrez et al. 1995). Spotted owls produce a maximum of one brood per year. A pair begins roosting together 1–2 months prior to nesting, and, on our study area, typically initiate nesting by mid-April and fledge young in June (Gutiérrez et al. 1995). Natal dispersal occurs in the fall (Forsman et al. 2002). The critical time for survival is winter (Franklin et al. 2000).

Spotted owl data collection

We surveyed spotted owls from 1 April to 28 August on a 925-km^2 study area located in the central Sierra Nevada, California (Seamans et al. 2001). Within this area we surveyed owls on a 355-km^2 Density Study

Area 1990–2004 and a 570-km^2 Regional Study Area 1997–2004. Each year we completely surveyed the entire Density Study Area for spotted owls while we surveyed only areas in and around known spotted owl territories on the Regional Study Area. We estimated R (the number young fledged per female) and captured and banded owls following Franklin et al. (1996). We identified four age-classes based on plumage characteristics (Forsman 1981; Moen et al. 1991): juvenile; 1 year old (first year subadult); 2 years old (second-year subadult); and ≥3 years old (adult).

Weather data

We used data recorded at five local weather stations to depict weather conditions on the study area: Lake Spaulding (39°19′N 120°38′W, elevation 1,572 m); Bowman Dam (39°27′N 120°39′W, elevation 1,641 m); Bald Mountain (38°54′N 120°42′W, elevation 1,341 m); Hell Hole Reservoir (39°04′N 120°25′W, elevation 1,468 m); and Blodgett Experimental Forest (38°55′N 120°40′W, elevation 1,345 m). The latter three stations were on the study area and reported hourly readings for precipitation and temperature. Stations at Lake Spaulding and Bowman Dam were approximately 10–20 km north of the study area and reported daily readings of snow depth. University of California Berkeley Blodgett Experimental Forest (Georgetown, California) supplied data for Blodgett, and other data were obtained from the Western Regional Climate Center (Reno, Nevada). In addition, we used data from the National Weather Service Climate Prediction Center (http://www.cpc.ncep.noaa.gov/; accessed January 2005) to estimate the direction (El Niño- or La Niña-like conditions), strength (magnitude of the index) and phase of the Southern Oscillation. Rather than categorize periods as El Niño or La Niña, we used monthly values for the southern oscillation index (SOI) directly. The strength of the Southern Oscillation was correlated with the magnitude of the SOI value.

Weather models

We developed a priori hypotheses to examine how weather influenced survival, R, and λ (Table 1). We developed hypotheses based on our own observations of spotted owls, as well as literature on spotted owls and other avian species (sensu Franklin et al. 2000). We formulated hypotheses based on the effects of weather during annual periods that we hypothesized were important for spotted owls or their prey: winter (November–March), fall (September–October), summer (June–August), incubation (April), and brooding (May). We constructed a statistical model for each a priori hypothesis that represented a predicted relationship between the hypothesized weather effect and a spotted owl demographic parameter (White 2001).

We hypothesized two types of weather effects on owls: direct and indirect. We predicted that weather would directly affect spotted owls by affecting their thermoregulatory requirements and the cost and benefits of foraging activities (Newton 1998; Franklin et al. 2000). Therefore, we hypothesized that survival, R, and λ would be negatively affected by cold and wet (average daily precipitation) conditions during winter (models S1 and R3; Table 1), incubation (S2, R1), and brooding of young (R2). Rather than using mean daily maximum or minimum temperature values, we used the minimum daily energy requirements for spotted owls to depict the effect of temperature. We used the metabolic equations developed by Weathers et al. (2001) for spotted owls and hourly temperature readings to calculate the average daily resting energy expenditure below the thermoneutral zone during annual periods. We also hypothesized that heat stress during the previous summer would have a negative effect on survival because spotted owls are relatively heat intolerant (Weathers et al. 2001) and thus would have to expend more energy for cooling, which might reduce body condition heading into the winter. We quantified the direct effect of hot temperatures by calculating the average daily resting energy expenditure above the thermoneutral zone (Weathers et al. 2001) using hourly temperature readings (S13). Extreme events may also directly affect birds (Newton 1998). Therefore, we hypothesized that extended periods of precipitation during the winter would interfere with hunting and would increase energy demands or reduce foraging time to the point of starvation, thus affecting demographic parameters. The length of time to reach starvation level for spotted owls was unknown; therefore, we used the estimate from Handrich et al. (1993) of 8 days for the barn owl (*Tyto alba*). We considered the number of periods with 8 consecutive days of measurable precipitation (≥0.025 cm) during winter (S7, R8), and maximum number of consecutive days of measurable precipitation during winter (S8, R9) as predictive covariates. We hypothesized that average daily snow depth (S5, R6) and the number of days of snow cover during winter (S6, R7) would negatively affect demographic parameters by reducing foraging success. Lastly, we hypothesized that El Niño- or La Niña-like conditions may adversely affect spotted owl demography (S3, S4,

Table 1 A priori models used to examine the relationship between weather and spotted owl survival, reproductive output (R), and population growth rate (λ) in the central Sierra Nevada, 1990–2004. Linear and log-linear forms of each weather covariate were examined unless otherwise noted. All survival models (no lag period) and R models (with a 1-year lag) were used to examine population growth rate. SOI Southern oscillation index

Hypothesis	Model[a]	Predicted effect
Apparent survival (φ)		
S1: Negative effects of cold temperatures and high precipitation during winter	$\beta_0 + \beta_1(T_W) + \beta_2(P_W)$	$\beta_1 < 0$, $\beta_2 < 0$
S2: Negative effects of cold temperatures and high precipitation during incubation, or negative effect of their interaction	$\beta_0 + \beta_1(T_I) + \beta_2(P_I) + \beta_3(T_I \times P_I)$	$\beta_1 < 0$, $\beta_2 < 0$, $\beta_3 < 0$
S3: Negative effect of both La Niña- and El Niño-like conditions during winter (quadratic form of SOI)	$\beta_0 + \beta_1(\mathrm{SOI}_W) + \beta_2(\mathrm{SOI}^2_W)$	$\beta_1 > 0$, $\beta_2 < 0$
S4: Negative effect of El Niño-like conditions during winter or negative effect of La Niña-like conditions during winter (linear SOI)	$\beta_0 + \beta_1(\mathrm{SOI}_W)$	$\beta_1 \neq 0$
S5: Negative effect of mean daily snow depth during winter	$\beta_0 + \beta_1(\mathrm{SNOWD}_W)$	$\beta_1 < 0$
S6: Negative effect of total number of days with snow cover during winter	$\beta_0 + \beta_1(\mathrm{SNOWD}_W)$	$\beta_1 < 0$
S7: Negative effect of multiple periods with precipitation during winter (number of 8-day periods during winter with measurable precipitation)	$\beta_0 + \beta_1(P\mathrm{8DAYS}_W)$	$\beta_1 < 0$
S8: Negative effect of an extended period of precipitation during winter (maximum number of consecutive days with measurable precipitation)	$\beta_0 + \beta_1(\mathrm{PMDAYS}_W)$	$\beta_1 < 0$
S9: Positive effect of mild temperatures during fall	$\beta_0 + \beta_1(T_F)$	$\beta_1 > 0$
S10: Positive effect of warm temperatures during April previous year	$\beta_0 + \beta_1(T_A)$	$\beta_1 > 0$
S11: Positive effect of long growing season previous year (number of consecutive days minimum temperature >0°C, based on 7-day running average)	$\beta_0 + \beta_1(\mathrm{GROW}_{Y-1})$	$\beta_1 > 0$
S12: Positive effect of high precipitation winter previous year	$\beta_0 + \beta_1(P_{W-1})$	$\beta_1 > 0$
S13: Negative effect of hot summer prior to winter survival period	$\beta_0 + \beta_1(T_S)$	$\beta_1 < 0$
Reproduction (R)		
R1: Negative effects of cold temperatures and high precipitation during incubation, or negative effect of their interaction	$\beta_0 + \beta_1(T_I) + \beta_2(P_I) + \beta_3(T_I \times P_I)$	$\beta_1 < 0$, $\beta_2 < 0$, $\beta_3 < 0$
R2:Negative effect of cold temperatures and high precipitation during brooding, or negative effect of their interaction	$\beta_0 + \beta_1(T_B) + \beta_2(P_B) + \beta_3(T_B \times P_B)$	$\beta_1 < 0$, $\beta_2 < 0$, $\beta_3 < 0$
R3: Negative effect of cold temperatures and high precipitation during winter preceding reproduction, or negative effect of interaction	$\beta_0 + \beta_1(T_W) + \beta_2(P_W) + \beta_3(T_W \times P_W)$	$\beta_1 < 0$, $\beta_2 < 0$, $\beta_3 < 0$
R4: Negative effect of both La Niña- and El Niño-like conditions during winter prior to reproduction (quadratic form of SOI)	$\beta_0 + \beta_1(\mathrm{SOI}_W) + \beta_2(\mathrm{SOI}^2_W)$	$\beta_1 > 0$, $\beta_2 < 0$
R5: Negative effect of El Niño- or La Niña-like conditions during winter prior to reproduction	$\beta_0 + \beta_1(\mathrm{SOI}_W)$	$\beta_1 \neq 0$
R6: Negative effect of mean daily snow depth winter prior to reproduction	$\beta_0 + \beta_1(\mathrm{SNOWD}_W)$	$\beta_1 < 0$
R7: Negative effect total number of days with snow cover during winter prior to reproduction	$\beta_0 + \beta_1(\mathrm{SNOWD}_W)$	$\beta_1 < 0$
R8: Negative effect of multiple periods with precipitation during winter prior to reproduction	$\beta_0 + \beta_1(\mathrm{P8DAYS}_W)$	$\beta_1 < 0$
R9: Negative effect of an extended period of precipitation during winter prior to reproduction	$\beta_0 + \beta_1(\mathrm{PMDAYS}_W)$	$\beta_1 < 0$
R10: Positive effect of mild temperatures during fall previous year	$\beta_0 + \beta_1(T_F)$	$\beta_1 > 0$
R11: Positive effect of warm temperatures during April previous year	$\beta_0 + \beta_1(T_{A-1})$	$\beta_1 > 0$
R12: Positive effect of long growing season previous year	$\beta_0 + \beta_1(\mathrm{GROW}_{Y-1})$	$\beta_1 > 0$
R13: Positive effect of high precipitation two winters prior to reproduction	$\beta_0 + \beta_1(P_{W-1})$	$\beta_1 > 0$

[a] Periods during the year where covariates apply are: current winter (*W*), incubation (*I*), brooding (*B*), fall (*F*), previous April (*A–1*), summer (*S*), previous winter (*W–1*), previous year (*Y–1*)

R4, R5). Redmond and Koch (1991) estimated that periods preceded by 4 months of negative SOI values were strongly correlated with El Niño conditions, while periods preceded by 4 months of positive SOI values were generally considered to represent La Niña conditions. Thus, to depict conditions for winter (November–March) we averaged monthly SOI values from the previous August–November. El Niño events (negative index values) in California typically result in higher than average rainfall and warmer temperatures, while La Niña events (positive index values) are typically drier and cooler than average.

Weather may indirectly affect spotted owls by affecting vegetation growth, which would affect either prey numbers or prey availability by enhancing conditions for the owl's prey. For example, warm temperatures and increased precipitation may increase vegetative growth and seed production. *Neotoma* spp., *Peromyscus* spp., and *Glaucomys sabrinus* were the primary prey for owls on our study (Gutiérrez et al. 1995). These mammals obtained their food from seeds, vegetation, and fungi (Williams et al. 1992; Pyare and Longland 2002). Therefore, we hypothesized that average daily precipitation during the previous winter (S12, R13) would have a positive effect on vegetative growth, small mammal populations, and spotted owl demographic parameters (Seamans et al. 2002; LaHaye et al. 2004). The dominant oaks in our study area (*Quercus kelloggii* and *Quercus chrysolepis*) were 2-year oaks (pollination in spring year t, with acorns dropping in the fall year $t + 1$), and temperatures during pollination may influence their mast production (Koenig et al. 1999). A similar relationship, with the same 1-year lag, has been suggested for Ponderosa pine seed production (Maguire 1956). Therefore, we hypothesized that warm temperatures (average daily temperature) during spring (S10, R11) would positively affect the acorn crop, which would affect *Peromyscus* spp. (Gashwiler 1979) and *Neotoma* spp. (Kelly 1990) survival and reproduction, and, consequently, spotted owl demographic parameters the following year. We did not know if weather limits *G. sabrinus* populations (Rosenberg et al. 2003; Ransom and Sullivan 2004). However, research on small mammals has shown that they may take advantage of favorable conditions and expand their breeding seasons (Modi 1984; Kelly 1990). Therefore, we also hypothesized that mild conditions in the fall (S9, R10; average daily temperature) or an extended growing season (S11, R12) would positively affect the owl's winter survival or next year's R. We approximated the length of the growing season by calculating the number of consecutive days with minimum temperature >0°C, based on 7-day running averages.

Estimation of demographic parameters and their variability

We considered each weather-related hypothesis (Table 1) as an a priori model representing the effect of specific environmental conditions on variation in survival and R. We modeled λ using all a priori survival and R models. For each R model used to model λ we used covariate values from the previous year. For example, precipitation and temperature during incubation in 2000 were used to estimate R in 2000 (Table 1; model R1) and λ in the interval 2000–2001. We considered all of the a priori hypotheses for each parameter to be competing models. We did not use highly correlated ($r > 0.5$) weather covariates in the same model. We used an information theoretic approach to compare models based on their relative ability to explain variation in the data (Burnham and Anderson 1998). We ranked competing models that represented the relationship between weather and demographic parameters using Akaike's information criteria (AIC) corrected for small sample size ($\mathrm{AIC_C}$). We addressed uncertainty in selecting the best models by calculating $\mathrm{AIC_C}$ weights (w_i; Burnham and Anderson 1998).

We used an open population Cormack–Jolly–Seber model in program MARK (White and Burnham 1999) to estimate annual "apparent survival" of owls ≥1 year old (φ) using the capture histories of subadult and adult females and males from 1990 to 2004. We considered our estimates of survival to be "apparent survival" because they represented the probability of a banded owl surviving and remaining within the study population. We could not model juvenile survival because too few of the banded juveniles were recaptured in subsequent years (Franklin et al. 2004). Before analysis of weather models we examined the survival dataset for overdispersion ($\hat{c}$) using a global model in program Release (Burnham et al. 1987). We found no evidence of overdispersion ($\hat{c} < 1$). When estimating φ and recapture rates, we considered age (AGE; subadult or adult), sex (SEX), and time [each interval is a categorical variable (t), linear time trend (lt), or quadratic time trend] constraints in addition to weather covariates. We combined 1- and 2-year-olds into one age-class (subadults) after modeling them separately and finding no difference in survival. We first used a global structure (AGE, SEX, and categorical time) on φ and modeled recapture rates with the following constraints: intercept only, age, sex, time, and annual survey effort (Franklin et al. 2004). Annual survey effort was the number of total hours within a year dedicated to capturing and recapturing owls and assessing reproduction. We selected the best recapture rate structure based on AIC$_C$, and then used this structure for all subsequent φ models. We next modeled φ using only sex, age, and time constraints, and their interactions. We then used the best sex and age structures when modeling weather covariates. We estimated total temporal process variation ($\hat{\sigma}^2_{\text{temporal}}$; the natural variation in annual survival rates attributable to differences among years) using an intercept-only model in the variance components module of program MARK (Burnham and White 2002). We assessed the performance of our best weather model by examining the change in $\hat{\sigma}^2_{\text{temporal}}$ between the intercept-only model and best weather model.

We estimated annual R (annual number young fledged per female) from 1990 to 2004 using PROC MIXED in program SAS (Littell et al. 1996). We used a mixed model ANOVA (Searle et al. 1992) with the number of young fledged as the dependent variable, age of female [AGE; subadult (1 and 2 year olds) or adult (≥3 years old)] and weather covariates as fixed effects, year as a random effect, and individual female as a random blocking factor. We considered year as the experimental unit in a repeated measures design (Franklin et al. 2000, 2004). We first used restricted maximum likelihood estimation to model the following block covariance structures: log-linear variance; compound symmetric; first order autoregressive; and heterogeneous autoregressive (Littell et al. 1996). We selected the best covariance structure based on AIC$_C$, and then used this structure with full maximum likelihood estimation to model fixed effects. We estimated $\hat{\sigma}^2_{\text{temporal}}$ of R using an intercept-only model within the restricted maximum likelihood approach. Temporal process variation explained by a weather model was calculated as $\hat{\sigma}^2_{\text{temporal}}$ from an intercept-only model minus $\hat{\sigma}^2_{\text{temporal}}$ from the weather model (i.e., the remaining process variation left unexplained by the weather covariates).

To examine the effect of weather on λ, we estimated the annual rate of population change in territorial owls (λ_t) directly from spotted owl capture histories using Pradel's "reverse-time" model (Pradel 1996; Nichols and Hines 2002; Franklin et al. 2004) in program MARK. We use the acronym "$\hat{\lambda}_t$" to distinguish the Pradel estimate from the estimate of λ using a projection matrix (see below). We only used the capture histories of individuals on the Density Study Area to estimate λ_t. We used the best recapture rate structure from our survival analysis and a categorical time structure on φ for all λ_t modeling. We did not include the first estimable λ in models because of a possible learning effect by observers (Franklin et al. 2004). In addition to weather covariates, we also examined categorical time (each interval is a categorical variable; t), lt, and quadratic time trend constraints on λ_t. We estimated temporal process variation $\left(\hat{\sigma}^2_{\text{temporal}}\right)$ using an intercept-only model in the variance components module of program MARK (Burnham and White 2002). We assessed the performance of our best weather model by examining the change in $\hat{\sigma}^2_{\text{temporal}}$ between the intercept-only model and best weather model.

Contributions of demographic parameters to λ and variability in λ

We used a single-sex projection matrix to estimate asymptotic λ, which allowed for estimation of the proportional contribution of each matrix element to λ using elasticity analysis (Caswell 2001). Elasticities can be used for comparison of life history strategies within and among taxa (de Kroon et al. 2000) and for assessing the relative contribution of fitness components to variation in λ (van Tienderen 1995; Horvitz et al. 1997). We used the acronym "$\hat{\lambda}_{\text{PM}}$" to identify the estimate of λ using the projection matrix. We used our estimates of R and φ as matrix elements. We divided R by 2 to estimate the number of female offspring per female. We did not have an estimate of juvenile survival so we used an estimate from a study of California spotted owls in the San Bernardino Mountains (LaHaye et al. 2004; $\varphi_{\text{juvenile}} = 0.368$). The juvenile age-class used by LaHaye et al. (2004) began at the time of fledging and ended the first spring after fledging.

We assessed the sensitivity of λ to individual fitness components by calculating the elasticity ($\hat{e}$) of model parameters (Benton and Grant 1996; Caswell 2001). The relative sensitivity of $\hat{\lambda}_{\text{PM}}$ to variation in fitness components (i.e., R, φ, and juvenile survival) depends on both the $\hat{e}$ and the temporal variation of the fitness components (Horvitz et al. 1997; Gaillard et al. 2000). For example, φ may have high elasticity but have less importance in determining annual changes in λ than components with lower elasticity yet greater temporal variability. We estimated the variance of λ [var(λ)] following Tuljapurkar and Caswell (1997):

$$\text{var}(\lambda) = \sum_{ij} \hat{e}_{ij} \times \widehat{\mathbf{CV}}^{\mathbf{2}}_{ij}$$

where e_{ij} was the elasticity of the element (θ) in row i and column j in the matrix, and CV was the element's

Table 2 Models (95% confidence set) relating spotted owl survival, *R*, and λ to weather in the central Sierra Nevada, 1990–2004. Models are ordered by Akaike's information criteria (AIC) corrected for small sample size (AIC_C), and w_i is the model weight. Acronym *in parentheses* following model ranking refers to model description in Table 1. *SEX* Sex effect, *AGE* age effect (1 and 2 year olds versus individuals ≥3 years old); for other abbreviations, see Table 1

Model	AIC_C	ΔAIC_C	w_i	Model likelihood	K[a]	Model coefficients					
						β_0	β_1	β_2	β_3	β_4	β_5
Apparent survival (φ)											
1. (**S5**) $\beta_0 + \beta_1[\mathrm{LN}(\mathrm{SNOWD_W})] + \beta_2(\mathrm{SEX})$	1,192.2	0.0	0.186	1.000	5	0.76	3.46	0.37	–	–	–
2. $\beta_0 + \beta_1(\mathrm{SEX})$	1,193.8	1.5	0.086	0.461	4	1.36	0.37	–	–	–	–
3. (**S3**) $\beta_0 + \beta_1(\mathrm{SOI_W}) + \beta_2(\mathrm{SOI^2_W}) + \beta_3(\mathrm{SEX})$	1,193.9	1.7	0.080	0.428	6	1.46	–0.16	–0.07	0.36	–	–
4. (**S9**) $\beta_0 + \beta_1(T_F) + \beta_2(\mathrm{SEX})$	1,194.7	2.5	0.053	0.284	5	–0.61	7.08	0.37	-	-	-
5. (**S2** + **S4**) $\beta_0 + \beta_1(\mathrm{SOI_W}) + \beta_2(T_I) + \beta_3(P_I) + \mathrm{B}_4(\mathrm{T_I} \times P_I) + \beta_5(\mathrm{SEX})$	1,194.9	2.6	0.050	0.267	7	2.02	–0.14	–0.01	–4.85	0.03	0.37
6. (**S6**) $\beta_0 + \beta_1(\mathrm{SNOWC_W}) + \beta_2(\mathrm{SEX})$	1,195.0	2.8	0.045	0.244	5	0.81	0.68	0.37	–	–	–
7. (**S10**) $\beta_0 + \beta_1(T_A) + \beta_2(\mathrm{SEX})$	1,195.2	2.9	0.041	0.271	5	2.37	–0.02	0.37	–	–	–
8. β_0 (intercept only)	1,196.1	3.9	0.027	0.142	3	1.52	–	–	–	–	–
(*R*)											
1. (**R1** + **R5**) $\beta_0 + \beta_1(\mathrm{SOI_W}) + \beta_2(T_I) + \beta_3(P_I) + \beta_4(T_I \times P_I) + \beta_5(\mathrm{AGE})$	968.0	0.0	0.996	1.000	23	2.89	–0.25	–0.02	–9.13	0.06	0.18
2. (**R1** + **R7**) $\beta_0 + \beta_1(\mathrm{SNOWC_W}) + \beta_2(T_I) + \beta_3(P_I) + \beta_4(T_I \times P_I) + \beta_5(\mathrm{AGE})$	982.1	14.1	0.001	0.001	23	2.26	0.01	–0.03	–7.07	0.06	0.18
3. $\beta_0 + \beta_1(\mathrm{AGE})$	986.4	18.4	0.000	0.000	19	0.59	0.18	–	–	–	–
λ											
1. $\beta_0 + \beta_1$ (linear trend)	1,881.8	0.0	0.265	1.000	19	0.12	–0.02	–	–	–	–
2. (**S3**) $\beta_0 + \beta_1(\mathrm{SOI_W}) + \beta_2(\mathrm{SOI^2_W})$	1,882.1	0.3	0.230	0.866	20	0.03	–0.07	–0.03	–	–	–
3. (**S3** + **R1**) $\beta_0 + \beta_1(\mathrm{SOI_W}) + \beta_2(\mathrm{SOI^2_W}) + \beta_3(T_I) + \beta_4(P_I)$	1,882.2	0.4	0.218	0.823	22	0.41	–0.07	–0.03	–0.69	0.53	–
4. (**S12**) $\beta_0 + \beta_1[\mathrm{LN}(P_{W\text{–}1})]$	1,884.4	2.7	0.070	0.265	19	0.16	–0.56	–	–	–	–
5. β_0 (intercept only)	1,885.8	4.1	0.028	0.107	18	0.00	–	–	–	–	–
6. (**S5**) $\beta_0 + \beta_1(\mathrm{SNOWD_W})$	1,886.4	4.7	0.026	0.097	19	–0.10	0.19	–	–	–	–
7. (**R1**) $\beta_0 + \beta_1(T_I) + \beta_2(P_I)$	1,886.5	4.7	0.025	0.095	20	0.37	–0.63	0.36	–	–	–

[a] Number of estimable parameters in model

Table 3 Estimates of temporal variance components of spotted owl demographic parameters (θ) in the central Sierra Nevada, 1990–2004. For other abbreviations, see Table 1

	Apparent survival (φ)	R	λ
$\hat{\bar{\theta}}^{a}$	0.8212	0.6392	1.0009
$\mathrm{SE}(\hat{\bar{\theta}})$	0.0129	0.0763	0.0225
$\hat{\sigma}^2_{\mathrm{temporal}}$	0.0009	0.2796	0.0031
	(0, 0.0062)^{b}	(0.1447, 0.7504)	(0, 0.0236)
$\left(\mathrm{CV}(\hat{\bar{\theta}})\right)$	0.0368	0.8272	0.0556
$\hat{\sigma}^2_{\mathrm{model}}{}^{c}$	0.0005	0.2350	0.0031
$\hat{\sigma}^2_{\mathrm{residual}}$	0.0004	0.0446	0.0000
	(0, 0.0064)^{b}	(0.0166, 0.3176)	(0, 0.0179)
%Explained^{d}	60	84	100

[a] Mean point estimate for parameter

[b] 95% confidence interval

[c] Amount of $\hat{\sigma}^2_{\mathrm{temporal}}$ explained by best weather model

[d] Percentage of $\hat{\sigma}^2_{\mathrm{temporal}}$ explained by top weather model

coefficient of variation, $\hat{\sigma}_{\mathrm{temporal}}/\theta$. We presented the contribution of each matrix element as a proportion of the total var(λ), thus, the sum of contributions equals 1.0. For juvenile survival, we estimated $\hat{\sigma}^2_{\mathrm{temporal}}$ as the variance of the minimum known proportion surviving from each cohort from the San Bernardino Mountains (CV = 0.41). We used the raw data from the LaHaye et al. (2004) study and calculated the minimum known proportion surviving for year *t* as the as the proportion of fledglings banded in year *t* that were subsequently recaptured in a later year (R. J. Gutiérrez, unpublished data). We considered this an approximation of temporal variability in juvenile survival, and, in an exploratory analysis, examined values 50% above and below this value to assess their influence on var(λ).

Table 4 Percentage of temporal variation in λ accounted for by life history characteristics (matrix elements) used in projection matrix to estimate λ of spotted owls in the central Sierra Nevada, 1990–2004. Percentages estimated using a range of values for temporal variation in juvenile survival

Matrix element	$\hat{e}^{a}$	Percentage of variability in λ accounted for when coefficient of variation for juvenile survival is:		
		0.21	0.41	0.61
Reproductive output $\left(\hat{\bar{R}}^{b}\right)$	0.12	51.8	47.5	41.7
Juvenile survival $(\hat{\bar{\varphi}}_{J})$	0.12	4.3	12.4	23.0
Survival >1 year olds $(\hat{\bar{\varphi}})$	0.77	43.9	40.2	35.3

[a] Matrix element elasticity

[b] Mean estimate of the parameter over all years

Results

Weather and survival

During the 15-year study we identified 246 individuals ≥1 year old on 924 capture occasions (does not include multiple captures of the same individual in the same year). The best recapture rate structure indicated recapture rates varied by annual survey effort. We used this structure for all subsequent φ modeling. The capture–recapture data best supported a model that included a sex effect, suggesting males had higher φ than females. Thus, we considered a sex effect on φ in subsequent modeling with weather covariates.

We examined 23 weather models that included linear and non-linear forms of weather covariates (Table 1), and 12 additional models that included weather covariates from winter plus weather covariates from the incubation period. For competing models that included the same weather covariates, one in linear and one in non-linear form, we presented only the model with the lowest AIC$_{\mathrm{C}}$ (Table 2). We estimated that there was little temporal variation in φ (Table 3). Thus, a model with sex effects only was one of three competing models (<2 AIC$_{\mathrm{C}}$ units), although a sex effect explained no temporal variation in φ. Our research question involved quantifying temporal variation in φ, so we chose to use the most competitive weather model for making further inference. However, a sex effect was supported and therefore all top weather models contained a sex effect. The best approximating weather

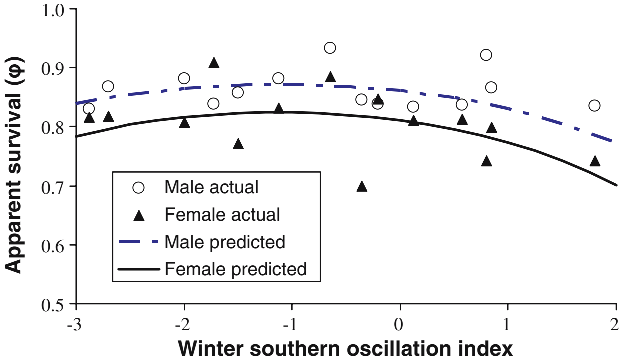

Fig. 1 Actual and predicted annual apparent survival (φ; probability of surviving and remaining within the study population) of male and female spotted owls (*Strix occidentalis*) ≥1-year-old, based on capture–recapture data for spotted owls from the central Sierra Nevada, 1990–2004. Actual values (*open circles* male, *filled triangles* female) are mean estimates for each year from a random effects means model. Predicted values (*dotted lines* male, *solid lines* female) are from a weather model containing the quadratic form of the southern oscillation index (SOI) for winter

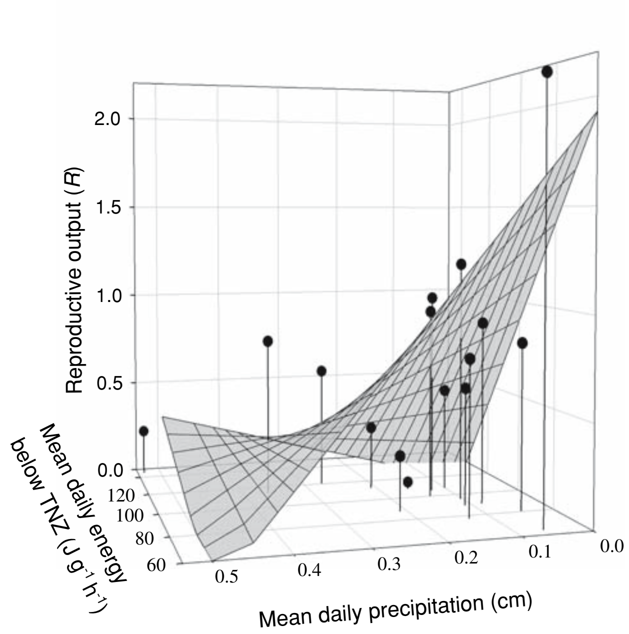

Fig. 2 Actual (*filled circles*) and predicted (*mesh*) annual reproductive output (*R*) for spotted owls (*S. occidentalis*) ≥1 year old based on *R* data for spotted owls from the central Sierra Nevada, 1990–2004. Actual values are mean estimates for each year from a random effects means model. Predicted values are from a weather model with mean daily precipitation and mean daily energy required for thermoregulation for temperatures below the thermoneutral zone (*TNZ*) during the incubation period

model indicated that φ varied by the log of snow depth (Table 2). However, the regression coefficient (β) for snow depth indicated a positive relationship between snow depth and survival, which was opposite of what we hypothesized, and had confidence intervals (CIs) that included zero [$\beta(\mathrm{SNOWD_W}) = 3.46$, CI = –0.27 to 7.20]. The next best weather model (Table 2) suggested a quadratic relationship between φ and the SOI just prior to winter, with owls experiencing higher survival when conditions were neutral; neither El Niño nor La Niña. For this model, the CI of the regression coefficient for the quadratic terms barely included zero [$\beta(\mathrm{SOI_W}) = -0.16$, CI = –0.32 to 0.00; $\beta(\mathrm{SOI_W^2}) = -0.07$, CI = –0.16 to 0.02]. Because the relationship between snow depth and φ was opposite of our prediction, we used a model with the quadratic form of the SOI for inference regarding explanation of temporal variance in φ by weather. The SOI just prior to winter explained 60% of the estimated temporal process variation in φ (Fig. 1, Table 3).

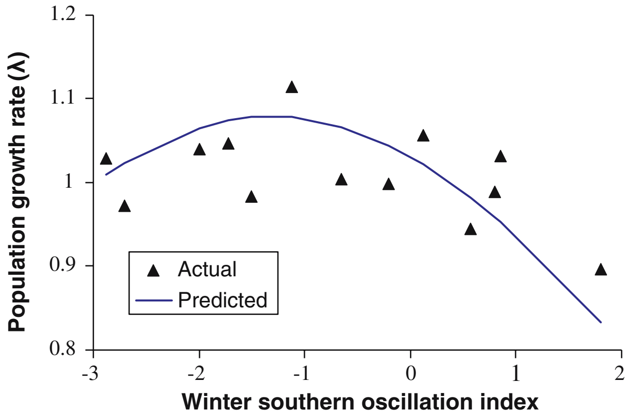

Fig. 3 Actual (*filled triangles*) and predicted (*solid lines*) annual population growth rate (λ) for spotted owls (*S. occidentalis*) ≥1 year old based on capture–recapture data for spotted owls from the central Sierra Nevada, 1990–2004. Actual values are mean estimates for each year from a random effects means model. Predicted values are from a weather model containing the quadratic form of the SOI for winter

Weather and *R*

We made 425 independent annual assessments of reproduction of 125 female spotted owls from 1990 through 2004. The best covariance structure for the repeated measures was heterogeneous-autoregressive. Mean annual *R* ranged from 0.030 to 2.129. We first compared a means model with an age- (subadult vs. adult) structured model. This comparison suggested *R* varied by age of female [a model with female age (AGE) was 4.7 $\mathrm{AIC_C}$ units lower than an intercept-only model; $\beta(\mathrm{AGE}) = 0.18$, $\widehat{\mathrm{SE}} = 0.07$], thus we included female age in all subsequent models. The best weather model (Table 2) suggested that *R* was related to environmental conditions during incubation, and was negatively correlated to the SOI associated with the winter just prior to nesting [$\beta(\mathrm{SOI_W}) = -0.26$, CI = –0.33 to –0.18]. The main effects of the best model suggested *R* declined with decreasing temperature (T; i.e., increasing mean daily minimum energy expenditure) and increasing mean daily precipitation (P) during incubation [$\beta(T_\mathrm{I}) = -0.020$, CI = –0.030 to –0.010; $\beta(P_\mathrm{I}) = -9.132$, CI = –14.30 to –3.96]. The interaction term [$\beta(T_\mathrm{I} \times P_\mathrm{I}) = 0.058$, CI = 0.021 to 0.095] suggested *R* was greatest when conditions during incubation were mild (i.e., low precipitation and minimum energy requirement), and also when conditions were severe (i.e., high precipitation and maximum energy requirement). This was the opposite of our predictions. Examination of predicted values from the best model indicated that increases in *R* during severe conditions were very slight compared to increases during mild conditions (Fig. 2). Most competing *R* models included the main effects of, and interaction between, precipitation and the minimum energy requirement during incubation. In addition, models with these two covariates accounted for nearly all $\mathrm{AIC_C}$ weight. The best top ranked weather model explained 84% of the estimated temporal process variation in R (Table 3).

Weather and λ

The top model indicated a negative linear trend in λ_t [Table 2; $\beta(\mathrm{lt}) = -0.016$, CI = –0.028 to –0.004]. The best approximating weather model, which was identical to the best survival model, indicated that λ_t varied with the quadratic form of the SOI just prior to winter [Table 2; $\beta(\mathrm{SOI_W}) = -0.070$, CI = –0.119 to –0.022; $\beta(\mathrm{SOI_W^2}) = -0.027$, CI = –0.055 to 0.000]. This model suggested λ_t was greatest when conditions were neutral; neither El Niño nor La Niña (Fig. 3). The third ranked model also included the SOI just prior to winter and, similar to the top R model, covariates depicting conditions during the prior year incubation period (Table 2). However, while the relationship between λ and temperature during incubation agreed with our prediction [$\beta(T_\mathrm{I}) = -0.692$, CI = –1.376 to –0.008], the covariate depicting mean daily precipitation did not [$\beta(P_\mathrm{I}) = 0.526$, CI = –0.268 to 1.321]. The only other competing model suggested λ_t was negatively related to the log of winter precipitation from the prior interval (i.e., a 1-year lag effect) but the CI for the coefficient included zero [$\beta(P_{\mathrm{W}-1}) = -0.561$, CI = –1.132 to 0.010]. The SOI just prior to winter explained 100% of the estimated temporal process variation in λ_t (Table 3).

Life history strategy

Use of the San Bernardino juvenile survival estimate ($\varphi = 0.368$, SE = 0.038; LaHaye et al. 2004) in the matrix projection resulted in $\hat{\lambda}_\mathrm{PM}$ equal to 0.950 (SE = 0.025). This growth rate was slightly lower than that estimated using the temporal symmetry capture–recapture methods (Table 3). Although the two methods for estimating population rate of change differ in their interpretation (Franklin et al. 2004; λ_t estimates if territorial individuals are being replaced while λ_PM estimates if territorial individuals are replacing themselves) it was not clear why they should differ. However, we felt that our use of the matrix approach was reasonable because we were interested in life history strategy and were not drawing an inference about rate of population change. We used matrix elements that depicted only two age classes (juveniles and owls ≥1 year old) because there was an insufficient number of individuals ≥1 year old and <3 years old to estimate $\hat{\sigma}^2_\mathrm{temporal}$ in R and φ separately for this age-class.

The dynamics of our study population indicated that φ had high elasticity and relatively low temporal variability, R had low elasticity and relatively high temporal variability, and juvenile survival had both low elasticity and low temporal variability (Tables 3, 4). In particular, R had a large influence on the temporal variation in $\hat{\lambda}_\mathrm{PM}$ (Table 4) relative to its elasticity. Assuming variability in juvenile survival was similar between California spotted owl populations, the contribution of juvenile survival to variability in $\hat{\lambda}_\mathrm{PM}$ was proportional to its elasticity (Table 4).

Discussion

Demographic analysis is an effective tool for understanding the relative contribution of different life stages to population growth, and for measuring the strength of selective pressure on different fitness components (Stearns 1992; Caswell 2001). It is also useful, in conjunction with an understanding of the range of natural variation in parameters, for conservation planning (Mills et al. 1999; Wisdom et al. 2000). Although comprehensive predictions from life history theory are difficult to formulate because there are always some organisms that serve as exceptions, there are some strong patterns emerging that fit within the theory, such as the relationship between the temporal variation in individual parameters and their relative importance to population growth.

Relationship between weather and variability in parameter estimates

We found that φ was relatively high (>0.80), which was consistent with other spotted owl studies (Seamans et al. 2002; Franklin et al. 2004; Anthony et al. 2006). Our point estimate of R, $\hat{R} = 0.64$ (range 0–2.12 young/female per year), was also within the range reported for spotted owls (Seamans et al. 2002; Franklin et al. 2004; Anthony et al. 2006). Our results supported the prediction that R was affected more by environmental stochasticity than was survival. Further, we found that our weather models explained a large portion of the temporal variability in R whereas they explained less variability in φ. In general, we found that the SOI was a good predictor of spotted owl φ and R, and that conditions during incubation also had an effect on R. We used the same analytical techniques as Franklin et al. (2000) and Olson et al. (2004) who found that wet conditions during the nesting period (number of days with measurable precipitation) had a negative effect on R and φ for northern spotted owls. Franklin et al. (2000) also found support for a model that indicated increased precipitation and temperature during winter had a negative effect on φ. We considered this latter model as depicting conditions that were similar to those depicted by our SOI covariate. Thus, in terms of the demographic rates R and φ, it appeared that owls in our study responded similarly to weather conditions as northern spotted owls. We are not aware of another spotted owl paper that presented modeling of λ with weather. Our model selection results indicated that weather covariates that were good predictors of φ and R (the SOI just prior to winter and conditions during incubation from the previous year) were also good predictors of λ. This general agreement between weather models for λ and those of φ and R was predicted because λ was a function of these parameters. Yet, the covariate depicting precipitation during incubation, which appeared to be a good predictor of current year R, did not agree with our predictions for λ. This may indicate that precipitation during incubation had unpredicted effects on demographic parameters other than R. Alternatively the relationship between R and variability in λ may depend on R from years other than the prior year.

Contributions of demographic parameters to population growth and its variance

Similar to previous studies of spotted owls (Lande 1988; Noon and Biles 1990; Franklin et al. 2000) we found that λ was most sensitive to φ, that φ exhibited very low temporal variability relative to R, and that R appeared to be more strongly influenced by stochastic variability than φ. This was consistent with the prediction for long-lived species where natural selection favors the evolution of high adult survival with low annual variability as a response to environmental stochasticity, whereas reproductive parameters would not provide such a response (Benton and Grant 1996; Gaillard et al. 2000). One shortcoming of our approach was our inability to estimate juvenile survival with data from our study area, which was a consequence of dispersal by juveniles beyond our study area boundary. In addition, we assumed that survival, as used in the projection matrix to estimate $\hat{\lambda}_{\mathrm{PM}}$, represented true survival, whereas survival within the Pradel model we used to estimate $\hat{\lambda}_t$ represented the probability of surviving and remaining within the study area. Although our intent was to use the projection matrix to examine spotted owl life history and not to estimate λ, accurate estimates of vital rates were important for proper interpretation. However, the probability that φ was underestimated, and thus elasticity for φ was likely greater than we calculated, only strengthens the inference that λ was most sensitive to φ.

In general, our estimates of elasticity for φ and R placed spotted owls within the range of elasticities for the parameters reported by Sæther and Bakke (2000) for other long-lived avian species. Using methods similar to ours, Doherty et al. (2004) also found a similar pattern of parameter elasticities for red-tailed tropicbirds (*Phaethon rubricauda*), a long-lived seabird. We also found that there appeared to be a tradeoff between variance and elasticity; traits with higher elasticity had lower variation, suggesting that φ was canalized in spotted owls. Thus, it appeared that natural selection may have reduced variation in φ (Gaillard and Yoccoz 2003), which was consistent with predictions from life history theory (e.g., Gaillard et al. 1998, 2000; Pfister 1998). However, Doherty et al. (2004) found an equivocal relationship between parameter variances and sensitivities for the red-tailed tropicbird after re-scaling sensitivities to account for bounded parameters (i.e., parameters that were the result of probabilities that could only take on values between 0 and 1). We examined this possibility post hoc by scaling survival sensitivities using an arcsine transformation (Link and Doherty 2002), and we found no difference in the rankings or relative differences among sensitivities of parameters.

Although φ provided a baseline for the magnitude of λ (Franklin et al. 2000), we found that juvenile survival, and especially R, contributed more than previously estimated to annual variation in λ. Franklin et al. (2000) hypothesized such a relationship for the northern spotted owl but they did not test this prediction. The pattern where a demographic parameter's increasing contribution to variability in λ was associated with decreasing elasticity was consistent with what Gaillard et al. (2000) found for ungulates. In addition, the results from our modeling of λ with weather covariates also supported this pattern; the best weather model for λ suggested that weather patterns that affected both φ (the SOI) and R (conditions during the incubation period) were responsible for variability in λ. This result agrees with our conclusion that φ and R contributed approximately 40 and 47%, respectively, to variability in λ (Table 4).

It has been hypothesized that animals may use cues to assess quality of the year for breeding before breeding begins (Cohen 1967). Related to this, Gutiérrez et al. (1995) noted that there appears to be considerable variability in the number of spotted owl pairs that attempt to nest each year. For our study population, we estimated that 0–100% of pairs attempted to nest each year (unpublished data). Thus, a possible explanation for the variability in R that we observed was that spotted owls were tracking resources and only reproducing when conditions were favorable. In addition, because we found similar responses of R and φ to weather covariates, this suggested R and φ might have shared a common response to environmental stochasticity (i.e., if conditions were poor for survival they were exceptionally poor for reproduction). However, because φ exhibited such low temporal variability, we hypothesize that relatively extreme weather patterns such as those caused by a strong Southern Oscillation or those of longer duration provided sufficient selective pressure on these owls that longevity was the consequence. Thus, spotted owls in the central Sierra Nevada, and probably other spotted owl subspecies, may have undergone selection for longevity in order to increase the probability of encountering more favorable years for reproduction.

Conclusions

The spotted owl is an excellent species for testing life history theory because of the many long-term, well-designed demographic studies being conducted on this bird (Franklin et al. 2004; Anthony et al. 2006). Most of these studies employ mark–recapture methodology, thus estimation of many population parameters tends to be precise and unbiased. In addition, field methods are relatively consistent across studies allowing for pooling of data which increases sample sizes. The approach we have taken here could be applied to other spotted owl studies, which would allow a rare comparison of life history strategy within a single species.

Matrix projection and direct estimation methods of λ can benefit species conservation planning by identifying specific life stages that are most likely to increase λ (Wisdom et al. 2000; Nichols and Hines 2002). Our results suggest that either φ or R could be targeted for improvement within the context of a conservation strategy, but not one at the expense of the other. However, habitat change may play a larger role in long-term population viability for spotted owls (Akçakaya and Raphael 1998). In particular, natural disturbances or management actions that increase the temporal variability in φ will likely have negative consequences for long-term population viability (Lande 1993). For management decisions affecting spotted owls in the Sierra Nevada, we suggest that nothing be done that reduces φ, and that habitat manipulation be directed toward increasing R. We believe more information is needed on juvenile survival and dispersal characteristics to understand their dynamics and to clarify the relationship between habitat and λ.

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