TEMPORAL VARIATION IN THE VITAL RATES OF AN INSULAR POPULATION OF SPOTTED OWLS (*STRIX OCCIDENTALIS OCCIDENTALIS*): CONTRASTING EFFECTS OF WEATHER

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Abstract.—We studied the demography of an insular California Spotted Owl (*Strix occidentalis occidentalis*) population in southern California for 12 years. We used model selection based on information theory to examine the relationship between weather and reproduction and survival. Mean annual fecundity was 0.139 (SE = 0.050) for subadult females and 0.345 (SE = 0.028) for adult females. Adult females had higher fecundity than subadult females during all years, and fecundity in both age classes was higher when a wet year preceded a dry spring (i.e. breeding season). A model incorporating these factors explained 100% of the estimated temporal process variation in fecundity. Mean apparent survival was 0.796 (SE = 0.012), 0.880 (SE = 0.041), 0.692 (SE = 0.062), and 0.368 (SE = 0.038) for adult, second-year subadult, first-year subadult, and juvenile (first-year) owls, respectively. We found no temporal process variation in survival. Using a Leslie projection matrix, we estimated the finite rate of population change to be 0.906 (SE = 0.018) over the entire period of study (1987–1998), which indicated that the population declined ~9% per year during the study. That rate of decline was higher than a rate ($\hat{\lambda}_{1991–1998}$ = 0.921, SE = 0.020) we estimated for a shorter period (1991–1998) that matched the time interval used in a recent meta-analysis of Spotted Owl population dynamics. We believe that both the present estimates and those of the meta-analysis are valid, given their respective goals. The study population was characterized by relatively high, constant survival of territorial birds, low and variable annual reproduction, and relatively low juvenile survival. Because weather was strongly correlated with reproduction, fecundity rates for the species may decline during short-term droughts and when storms occur during the breeding season. Weather extremes may not, however, be sufficient to affect temporal variation in survival of Spotted Owls in this part of their range. *Received 25 July 2003, accepted 24 June 2004.*

Resumen.—Estudiamos la demografía de una población insular de *Strix occidentalis occidentalis* en el sur de California durante 12 años. La selección de los modelos se basó en la teoría de la información para examinar la relación entre clima, y reproducción y supervivencia. La fecundidad anual media fue 0.139 (EE = 0.050) para las hembras subadultas y 0.345 (EE = 0.028) para las hembras adultas. Las hembras adultas presentaron una fecundidad más alta que las hembras subadultas durante todos los años, y la fecundidad para ambas clases de edad fue mayor cuando un año húmedo precedió una primavera seca (i.e. la estación reproductiva). Un modelo que incorporó estos factores explicó el 100% de la variación en el proceso temporal estimado de fecundidad. La supervivencia media aparente fue 0.796 (EE = 0.012), 0.880 (EE = 0.041), 0.692 (EE = 0.062) y 0.368 (EE = 0.038) para las lechuzas adultas, los subadultos del segundo año, los subadultos del primer año y los juveniles (primer año), respectivamente. No encontramos variación en el proceso temporal de supervivencia. Usando la matriz de proyección de Leslie estimamos que la tasa finita de cambio poblacional fue 0.906 (EE = 0.018) a lo largo de todo el período de estudio (1987–1998), lo que indicó que la población disminuyó en un ~9% por año durante el estudio. Esta tasa de disminución fue mayor que una tasa ($\hat{\lambda}_{1991–1998}$ = 0.921, EE = 0.020) que estimamos para un período más corto (1991–1998) que coincidió con el intervalo de tiempo usado recientemente en un meta-análisis de la dinámica poblacional de *S. o. occidentalis*. Creemos que tanto la estimación presente como la del meta-análisis son válidas en relación con sus objetivos respectivos. La población de estudio se caracterizó por una supervivencia constante relativamente alta de las aves territoriales, por una reproducción anual baja y variable, y por una supervivencia relativamente baja de los juveniles. Debido a que el clima se correlacionó fuertemente con la reproducción, las tasas de fecundidad para la especie

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pueden disminuir durante períodos de sequía breves y cuando se registran tormentas durante la época reproductiva. Los extremos climáticos, sin embargo, pueden no ser suficientes como para afectar la variación temporal en la supervivencia de *S. o. occidentalis* en esta parte de su rango de distribución.

WEATHER CAN INFLUENCE survival and reproduction of birds (Grant and Grant 1996, Li and Brown 1999, Nott et al. 2002). Concern over changes in global climate has placed new emphasis on how weather affects bird populations (Li and Brown 1999). For example, it is important to understand how weather influences populations near the edge of a species' range (Root and Schneider 2002), because those populations are often small (Brown 1995) and thought to be limited by suboptimal climate, rather than regulated by density dependence (Randall 1982). In addition, small isolated populations may be at greater conservation risk if they are strongly affected by weather.

The California Spotted Owl (*Strix occidentalis occidentalis*) is distributed as one large population in the Sierra Nevada and a series of small, insular populations from central coastal California south to northern Baja California, Mexico, at the southern edge of its range (Gutiérrez et al. 1995). Reproductive and survival rates of Northern Spotted Owls (*S. o. caurina*) and reproductive rates of Mexican Spotted Owls (*S. o. lucida*) have been correlated with weather parameters (Franklin et al. 2000, Seamans et al. 2002, respectively). However, the mechanism by which weather affects those vital rates is unknown. In the case of reproduction, weather could have indirect effects (e.g. high precipitation fostering plant growth, which results in more food resources for the owl's primary prey) and direct effects (e.g. long periods of inclement weather could reduce foraging efficiency; see Franklin et al. 2000) on owl productivity. In a recent meta-analysis of the California Spotted Owl's population dynamics, the authors hypothesized that California Spotted Owl reproduction, like that of the other two subspecies, may fluctuate in response to weather conditions (Franklin et al. 2004). In contrast, annual survival rates of California Spotted Owls fluctuate less than their rates of reproduction, which suggests that weather may have less of an effect on survival than on reproduction (Franklin et al. 2004). However, weather data needed to evaluate that hypothesis were not available at the time of the meta-analysis. Here, we assess the relationship between weather and fitness components (reproduction and survival) of an insular population of California Spotted Owls in the San Bernardino Mountains. Specifically, we evaluate the general ecological theory (Randall 1982) and explicit hypothesis expressed in the California Spotted Owl meta-analysis—that weather influences the owl's vital rates. Given that southern California has a milder climate than most of the remaining range of the California Spotted Owl, our study could provide a useful comparison for other studies investigating influence of weather on Spotted Owl vital rates. In addition, because there have been studies of weather effects on demography of both Northern and Mexican spotted owls, there is a foundation of *a priori* models on which to build our analysis. We present our specific *a priori* models (hypotheses) below.

METHODS

Study area.—The study was located ~140 km east of Los Angeles, California. It encompassed all habitats potentially available to Spotted Owls in the San Bernardino Mountains and covered an area of ~2,140 km². Most Spotted Owls in this range occupied mixed evergreen and montane forests between 1,000 and 2,600 m elevation (Gutiérrez et al. 1992, LaHaye et al. 1997). The forests were dominated by canyon live oak (*Quercus chrysolepis*), big-cone Douglas fir (*Pseudotsuga macrocarpa*), white fir (*Abies concolor*), incense-cedar (*Calocedrus decurrens*), Jeffrey pine (*Pinus jeffreyi*), and ponderosa pine (*P. ponderosa*). Other forests that occasionally harbored Spotted Owls included pinyon pine (*P. monophylla*)–juniper (*Juniperus occidentalis*), and lodgepole pine (*P. contorta*) forests. Forest vegetation within our study area was isolated from adjacent mountain ranges by extensive areas of chaparral (dominated by *Adenostoma fasciculatum*), desert, and urban environments, which were all unsuitable to Spotted Owls (LaHaye et al. 1994). Annual precipitation averaged 500–1,000 mm, depending on aspect, elevation, and topography (Minnich 1988). The climate was Mediterranean, with most precipitation occurring in winter as rain or snow (Minnich 1986).

Field techniques.—Annually, we systematically surveyed all previously occupied Spotted Owl sites as well as all previously unoccupied forested stands within the study area, using standard survey methods for this species (Franklin et al. 1996). Our initial study area was 550 km² (1987–1988), which we expanded in 1989 to include the entire mountain range (i.e. the boundaries of the population). We conducted surveys at night by imitating Spotted Owl vocalizations for ≥15 min at each call point or by calling continuously while walking designated survey routes. Once owls were located, we estimated their social status (single or paired) and reproductive output (number of young produced) using techniques outlined by Franklin et al. (1996). For purposes of analysis, we converted reproductive output to an estimate of fecundity (i.e. we assumed a 50:50 sex ratio among owlets and divided reproductive output by 2). We classified owls into juvenile, one-year-old (first-year subadult; S1), two-year-old (second-year subadult; S2), or adult age classes on the basis of plumage characteristics (Franklin et al. 1996). We attempted to capture all owls in the mountain range. We placed a locking, aluminum federal band on one leg and a unique combination of color band and tab on the other. Owls were

subsequently identified by resighting color band and tab combinations or by physically recapturing owls whose color bands had become unreadable. Our capture efficiency was high; and even though we did not band every juvenile detected each year, the proportion of unbanded birds entering the territorial population in the later years of the study was <5% (LaHaye et al. 2001), which suggested that immigration–emigration rates were extremely low. Thus, we feel that our analysis was based on an extremely high sampling proportion (*sensu* Nichols 1992) of the Spotted Owls in the San Bernardino Mountains.

A priori *hypothesis (model) development.*—We assessed the relationship between weather, reproduction, and survival by ranking a set of hypotheses we developed *a priori* to data analysis using model selection in an information-theoretic framework (see below, and Burnham and Anderson 1998). Adults and nestlings may be negatively affected by inclement weather during one or more critical periods within a year (Franklin et al. 2000, North et al. 2000). Therefore, we divided the weather year (1 December–30 November) into winter (1 December–14 February), prelaying (15 February–31 March), and nesting (1 April–31 May) periods (Verner et al. 1992, Gutiérrez

TABLE 1. *A priori* hypotheses and statistical models for modeling fecundity of California Spotted Owls in the San Bernardino Mountains, California, 1987–1998.

Model number	Hypothesis	Model variables and predictions [a]
1	Effect of precipitation on owls	$\pm pw \pm ppl \pm pnp$
2	Wet winter followed by a warm spring [b]	$+ pw + tpl + tnp$
3	Effect of wet winter followed by a warm wet prelaying and nesting period	$\pm pw + tpl \pm ppl + tpl * ppl + tnp \pm pnp + tnp * pnp$
4	Effect of long-term drought	$+ pnp + ppl + pw + (pt\text{-}1) + (pt\text{-}2) + (pt\text{-}3)$
5	Effects of precipitation in previous year [c]	$+ (pt\text{-}1)$
6	Effect of winter temperatures one and two years prior to current year and precipitation two and three years prior to current year	$+ (tw\text{-}1) - (tw\text{-}2) + (pt\text{-}2) + (pt\text{-}3)$
7	Effect of low prey and cold wet winter	$+ (tw\text{-}1) - (tw\text{-}2) + (pt\text{-}1) + (pt\text{-}2) + (pt\text{-}3) + tw - pw$
8	Effect of low prey and interaction between winter precipitation and temperature	$+ (tw\text{-}1) - (tw\text{-}2) + (pt\text{-}2) + (pt\text{-}3) + (pt\text{-}1) + tw - pw + tw * pw$
9	Effect of temperature on owls	$+ tw + tpl + tnp$
10	Effects of cold wet winter [b]	$+ tw - pw$
11	Effect of cold wet winter	$+ tw - pw + tw * pw$
12	Effects of cold wet prelaying period [b]	$+ tpl - ppl$
13	Effects of cold wet nesting period [b]	$+ tnp - pnp$
14	Effects of cold wet prelaying and nesting periods [b]	$+ tpl - ppl + tnp - pnp$
15	Effects of cold wet winter and prelaying periods [b]	$+ tw - pw + tpl - ppl$
16	Effects of cold wet winter and nesting periods	$+ tw - pw + tnp - pnp$
17	Effects of cold wet winter, prelaying, and nesting periods	$+ tw - pw + tpl - ppl + tnp - pnp$
18	Effect of cold wet winter and prelaying period	$+ tw \pm pw + tw * pw + tpl \pm ppl + tpl * ppl$
19	Effect of heat stress	$- heat$

[a] + = positive correlation, – = negative correlation, ± = potential strong effect, but correlation may be positive or negative.
[b] Model taken from Franklin et al. (2000).
[c] Model taken from Seamans et al. (2002).

TABLE 2. *A priori* hypotheses and statistical models for modeling apparent survival of California Spotted Owls in the San Bernardino Mountains, California, 1987–1998.

Model number	Hypothesis	Model variables and predictions [a]
1	Effect of winter precipitation	$+ age \pm pw$
2	Effect of wet winter and spring	$+ age + pw + ppl + pnp$
3	Effect of wet year during *t-1* [b]	$+ age + (pt\text{-}1)$
4	Effects of long-term drought	$+ age + pw + ppl + pnp + (pt\text{-}1) + (pt\text{-}2) + (pt\text{-}3)$
5	Effect of low prey and cold wet winter	$+ age + (tw\text{-}1) + (tw\text{-}2) + (pt\text{-}1) + (pt\text{-}2) + (pt\text{-}3) + tw - pw$
6	Effect of winter temperature	$+ age - tw$
7	Effect of winter precipitation and temperature	$+ age - tw + pw + tw * pw$
8	Effect of cold wet winter and prelaying period [c]	$+ age - tw - pw - tpl - ppl$
9	Effect of cold wet spring	$+ age - tpl - ppl - tnp - pnp$
10	Effect of cold wet winter and spring	$+ age - tw - pw - tpl - ppl - tnp - pnp$
11	Effect of cold wet winter and spring.	$+ age + tw - pw + tpl - ppl + tnp - pnp + tw * pw + tpl * ppl + tnp * pnp$
12	Effect of heat stress [c]	$+ age - heat$
13	Age effects with constant survival	$+ age$

[a] + = positive correlation, – = negative correlation, ± = potential strong effect, but correlation may be positive or negative.
[b] Model taken from Seamans et al. (2002).
[c] Model taken from Franklin et al. (2000).

et al. 1995) based on an annual cycle that we defined for our study population. We used some previously developed hypotheses about effects of weather in our analyses (Franklin et al. 2000, Seamans et al. 2002) and assessed other hypotheses that we believed were relevant to our study area (Tables 1 and 2). We derived our hypotheses according to the following logic about possible relationships between weather and the owl's vital rates.

We hypothesized that temperature and precipitation were the weather variables most likely to influence Spotted Owl reproduction and survival on the study area. Those meteorological conditions could affect owls indirectly by influencing the survival or activity of their prey, or directly by influencing their physical condition or ability to hunt (rain reduces detection rates of prey) (Franklin et al. 2000). Spotted Owls in the San Bernardino Mountains prey mainly on dusky-footed woodrats (*Neotoma fuscipes*; Smith et al. 1999). Because we did not collect information on woodrat abundance and availability, we used precipitation and temperature as surrogate variables for environmental conditions that might favor prey reproduction and hence prey abundance. Specifically, annual precipitation directly correlates with soil moisture, which affects plant growth and, consequently, the food of woodrats (Williams et al. 1992). Cold temperatures during late winter and early spring may reduce mast production from oaks (Sork et al. 1993), an important food of woodrats (Atsatt and Ingram 1983).

Spevak (1983) reported that most small mammal species in southern California declined during drought, but that declines of dusky-footed woodrat

were particularly large. Because high precipitation during the winter and spring should ultimately increase woodrat forage through an increase in net primary production, we predicted that short-term (Models 1–3, Table 1; Models 1–2, Table 2) or long-term (Models 4–5, Table 1; Models 3–4, Table 2) drought prior to breeding season would reduce reproduction and survival in the San Bernardino Mountain Spotted Owl population by reducing the food available to prey. Similarly, cold temperatures during the spring may reduce flower survival in oaks (Sork et al. 1993), which would reduce mast used by woodrats. If woodrats declined, we would expect subsequent declines (i.e. multi-year lag effects) in Spotted Owl fecundity and survival (Models 6–8, Table 1; Model 5, Table 2).

Because Spotted Owls are adapted to cold climates (Barrows 1981), we hypothesized that models representing cold temperatures with no other variables (Model 9, Table 1; Model 6, Table 2) would not be correlated with fecundity or survival and would not be supported by the data. However, cold and wet winters may reduce energetic reserves of females prior to the breeding season, which would reduce overall reproductive and survival rates for the population (Models 10–11, Table 1; Model 7, Table 2). In contrast, wet and warm winters may increase the prey base, which would increase Spotted Owl reproductive and survival rates. Precipitation during the breeding season (prelaying and nesting periods) may negatively influence reproduction and survival by reducing an owl's ability to hear and detect prey (Hirons 1982) and by decreasing prey activity (Linsdale and Tevis 1951, Vickery and Bider 1981). In addition, cold temperatures reduce the activity of some prey species

(Vickery and Bider 1981), which, combined with high precipitation, may increase energetic demands on adult owls. We predicted that those negative influences of precipitation were more costly to owls during the breeding season than before it, because of the increased energetic demands of reproduction. During the nesting period, females spend most of their time on the nest, while males provide females with food (Forsman et al. 1984). Thus, the breeding season is energetically costly for both members of the pair, because only one owl forages for two individuals. For example, some female Tawny Owls (*Strix aluco*) abandoned nests if their mate did not provide adequate food during incubation (Southern 1970). Also, nestlings have not attained adult plumage during this period and are vulnerable to inclement weather (Howell 1964). Therefore, Spotted Owl fecundity may decline when there is cold and wet weather during the prelaying and nesting periods (Models 12–14, Table 1; Franklin et al. 2000). Poor spring weather following a cold and wet winter could have a particularly strong influence on Spotted Owl fecundity (Models 15–18, Table 1). Because Spotted Owls appear to follow a bet-hedging life-history strategy (Franklin et al. 2000) and would likely forgo reproduction to maximize their own survival when conditions deteriorate, we hypothesized that spring weather would not strongly influence Spotted Owl survival. Therefore, we hypothesized that cold and wet weather would affect Spotted Owl survival only if it occurred for long periods (Models 8–11, Table 2).

Weathers et al. (2001) demonstrated that the upper thermal neutral zone for California Spotted Owls (35.2°C) was lower than expected for birds of their size. Therefore, heat stress might reduce survival and reproductive rates of Spotted Owls. Daytime temperatures commonly exceeded that level during the summer in portions of the mountain range occupied by owls, which could lead to energetic stress and subsequent reduction in owl reproduction (Model 19, Table 1) and survival (Model 12, Table 2) the following year. We hypothesized a "null" model—based on previous work (Franklin et al. 2004)—that survival may be constant through time, which was an intercept-only model for apparent survival in our *a priori* model set (Model 13, Table 2). We did not include a constant time model for fecundity because reproductive rates of California Spotted Owls fluctuate temporally (Franklin et al. 2004). We conducted no *a posteriori* modeling in our analysis.

We obtained daily maximum temperature, minimum temperature, and precipitation data from the Lake Arrowhead, Beaumont, and Big Bear Lake, California, National Oceanographic and Atmospheric Administration cooperative weather stations. Data were highly correlated among weather stations (all $R >$ 0.92). In addition, precipitation was correlated among all southern California mountain ranges occupied by Spotted Owls (LaHaye et al. 1994). Therefore, we used data from the Big Bear Lake station only because it was centrally located and had the most complete records. We calculated average daily precipitation for the entire weather year prior to the current breeding season (*t-1*), as well as total precipitation for weather years *t-2* and *t-3*. We also calculated average daily precipitation for the winter, prelaying, and nesting periods of the current weather year. We averaged daily minimum temperature for the winter of years *t-2*, *t-1*, *t*, and the prelaying and nesting periods of year *t*. Finally, we calculated the number of heat-stress days (i.e. maximum temperature >30°C when Spotted Owls show behavioral signs of heat stress; Weathers et al. 2001) during each summer for years *t* and *t-1*, because Spotted Owls appear to be relatively heat-intolerant (Ting 1998, Weathers et al. 2001). Before conducting analyses, to avoid multicollinearity, we calculated Pearson product-moment correlations between all of the weather variables to assess their correlation. Temperature during the winter two years prior to the current weather year and temperature during the winter prior to the current weather year (correlation coefficient = 0.77) were the only weather variables that appeared to be strongly correlated.

Data analysis.—We used model selection based on information theory (Burnham and Anderson 1998) to rank hypotheses about fecundity and apparent survival rates. The increase in study-area size in 1989 could have induced heterogeneity in capture probabilities and introduced a bias into estimates of apparent survival. However, that bias is relatively small for survival estimators (Williams et al. 2002) and does not apply to fecundity estimates, so we used data from the entire study period to estimate survival and fecundity. In addition, because study-area size was increased to encompass the entire population, we felt that a potential positive bias in survival was acceptable, given the controversy surrounding survival estimates of California Spotted Owls (Franklin et al. 2004). We defined fecundity as number of female offspring per female (Caughley and Birch 1971). We first converted the *a priori* hypotheses for fecundity (Table 1) and apparent survival (Table 2) into statistical models, which incorporated age, time, and weather covariates (see Appendix for acronyms). We ranked statistical models by how well they fit the data using Akaike's Information Criterion adjusted for small sample sizes (AIC$_c$; Hurvich and Tsai 1989) and then evaluated performance of the best-ranked models using components-of-variance analysis (Franklin et al. 2001). Finally, we estimated the finite rate of population change (λ) with a Leslie projection matrix, using the best estimates of fecundity and apparent survival (Caswell 2001). We used global models to evaluate statistical assumptions of the fecundity and survival analyses, because they contained all potential effects and relationships (Burnham and Anderson 1998).

Thus, we considered candidate statistical models as submodels of the global models.

Reproductive output (i.e. number of young fledged per female) and apparent survival increased with age class in other Spotted Owl populations (Franklin et al. 2000, Seamans et al. 2002). Therefore, we assessed whether age should be included in all models of fecundity and apparent survival using AIC_c and model selection (Burnham and Anderson 1998). If a global model including a categorical variable for age was ranked higher (i.e. lower AIC_c; Hurvich and Tsai 1989) than one without age, we included age in all models. Similarly, we assessed the number of age-class categories that should be included in apparent-survival analyses by comparing AIC_c values of models with two age classes (juvenile, nonjuvenile), three age classes (juvenile, subadult [S1 + S2], adult), and four age classes (juveniles, S1, S2, adult).

We used mixed modeling (PROC MIXED; SAS Institute 1997) with a repeated-measures design to estimate fecundity on the basis of weather covariates. We assumed an equal sex ratio of offspring at fledging (Franklin et al. 1996). We considered territory and year as random effects, weather covariates as fixed effects, and year as the experimental unit because years received the treatment (i.e. weather). Territory was considered to be a blocking factor, and individual territories were assumed to be independent units within years. We used a repeated-measures design to analyze the mixed models because territories were not independent samples among years (i.e. we attempted to estimate fecundity for each territorial female each year).

The assumptions of mixed modeling are that error terms are distributed normally with constant variance (Littell et al. 1996). However, analysis of variance methods, such as our mixed modeling analysis, are robust to departures from normality (White and Bennetts 1996). Because dependence among repeated samples and nonconstant variances could have posed a problem, we modeled the variance–covariance structure (Littell et al. 1996). Once the most parsimonious variance–covariance structure was identified, we used standard maximum-likelihood estimation (Littell et al. 1996) and AIC_c to rank candidate models.

We estimated apparent survival from individual capture histories using MARK (White and Burnham 1999). We assessed goodness-of-fit of the global model and estimated the quasi-likelihood adjustment for overdispersion ($\hat{c}$) using tests in RELEASE (Burnham et al. 1987). We modeled recapture first, and then modeled apparent survival using the most parsimonious recapture structure. We produced model-averaged estimates of apparent survival with their associated unconditional standard errors (Burnham and Anderson 1998).

We used components-of-variance analysis to evaluate the absolute performance of the best model (Franklin et al. 2001). First, we partitioned the total variance in a general time model into sampling and process variation. Then, we estimated the residual process variation remaining in the AIC_c-selected model (Burnham et al. 1987). Therefore, we used three criteria to evaluate our models and their covariates; model selection (AIC_c rank), 95% confidence intervals of slope parameter estimates (i.e. slope parameter estimates with confidence intervals that included zero were not strongly correlated with response variables), and variance components.

We estimated λ as the dominant eigenvalue of a stage-classified projection matrix (Caswell 2001) to describe the population trend over the study period. Use of projection matrices to estimate λ for Spotted Owl populations has been controversial, because of potential bias associated with undetected emigration, particularly of juveniles (U.S. Department of the Interior 2003, Franklin et al. 2004). However, because our population was essentially demographically closed and because we attempted to band and monitor the entire population, we felt that the analysis was appropriate (see also Franklin et al. 2004). Elements within the matrix consisted of mean estimates of stage-specific fecundity and apparent survival of female owls. Because we used four age classes (i.e. stages) of owls, the projection matrix was 4 × 4, and we assumed a postbreeding census. Standard errors for the weighted mean values of survival, fecundity, and estimate of λ were calculated using the delta method (Seber 1982).

Comparison of fecundity, survival, and finite rate of population change with the California Spotted Owl meta-analysis.—We used several more years of data than were used in a recent meta-analysis, which included San Bernardino owl population data (Franklin et al. 2004). Thus, our analysis using all years of the study was not directly comparable to Franklin et al. (2004). Therefore, to facilitate comparison between Franklin et al.'s (2004) results and our study, we also estimated the rate of population change for the population using the same period as that used in the meta-analysis (1991–1998). Because we were interested only in comparing population trends, we did not explore temporal trends in survival and fecundity. We selected the appropriate age structure using model selection as described for previous analyses, and then calculated mean estimates of vital rates. We briefly report only the most salient results.

RESULTS

Population data.—We detected Spotted Owls at 143 new and historical (i.e. previously known) territories between 1987 and 1998. We banded 285 adult (129 female and 156 male), 63 subadult (31 female and 32 male), and 478 juvenile (62 female, 67 male, and 409 unknown sex) owls over the 12-year study. We estimated the reproductive
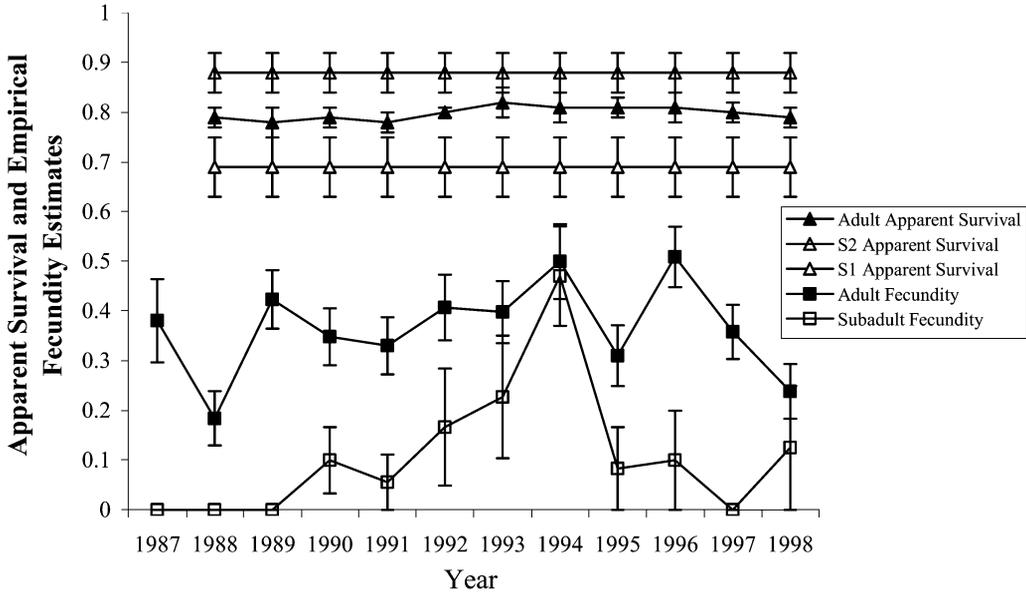
Fig. 1. Annual estimates of apparent survival and empirical estimates of adult and subadult fecundity for a Spotted Owl population in the San Bernardino Mountains, California, from 1987 to 1998. Error bars represent ±1 SD.

activity of 786 pairs (some of the 222 individually banded territorial females nested more than once) from 1987 to 1998 (range: 30–85 pairs annually). Females were S1 or S2 in 97 of the 786 pairs for which fecundity was estimated.

Estimation of fecundity.—A log-linear variance–covariance structure fit the reproductive data best, indicating that sampling variance increased with increasing mean annual fecundity. Empirical estimates of fecundity varied from 0.184 to 0.509 for adults and 0.000 to 0.471 for subadults (Fig. 1). In contrast to the empirical estimates, our fecundity data did not support the interactive nature of age and time depicted in empirical estimates. Our best model (i.e. lowest AIC_c value) included an additive effect of age with weather covariates (Model 4; Table 3). The model included long-term precipitation variables and precipitation during the nesting season. The model had a high AIC_c weight with no closely competing models. Its structure was

$$\hat{F} = 0.068 + 0.223 * (age) - 0.027 * (pnp) - 0.003 * (ppl) + 0.002 * (pw) + 0.032 * (pt\text{-}1) - 0.018 * (pt\text{-}2) + 0.009 * (pt\text{-}3)$$

where $\hat{F}$ = estimated annual fecundity; $age = 1$ for adult females and 0 for subadult females;

and *pnp*, *ppl*, *pw*, (*pt-1*), (*pt-2*), and (*pt-3*) were continuous variables for those weather attributes (see Appendix). Fecundity was greater for adult females (i.e. *age* covariate > 0; 95% CI = 0.161 to 0.302) than for subadults. As we predicted, fecundity was lower during wet springs (i.e. "precipitation during nesting period" covariate < 0; 95% CI = –0.045 to –0.012) and increased with increasing precipitation during the previous year (i.e. "precipitation during previous weather year" covariate > 0; 95% CI = 0.018 to 0.047). Contrary to our *a priori* predictions, precipitation two years earlier (95% CI = –0.035 to –0.005) showed a negative relationship with fecundity. The confidence intervals of the remaining variables included zero. Estimates of variance components indicated that ~62% of the total variation [$\text{var}(\hat{F}_t)$ = 0.0081] was process variation ($\hat{\sigma}^2_{temporal}$ = 0.0050, 95% CI = 0.0019 to 0.0314) and the best weather model accounted for 100% of that temporal process variation in fecundity.

Estimation of apparent survival.—Goodness-of-fit tests in RELEASE indicated some lack of fit to the survival data ($\hat{c}$ = 1.210). Therefore, the variance–covariance matrix and model selection were adjusted using $\hat{c}$. Adults had the highest recapture probabilities ($\bar{\hat{p}}$ = 0.825, SE = 0.006), whereas S1 had the lowest ($\bar{\hat{p}}$ = 0.375, SE = 0.050).

TABLE 3. Results of model selection for predicting fecundity of Spotted Owls in the San Bernardino Mountains, California, 1987–1998. Only models within 10 AIC_c units are listed below.

Model number	Model structure	AIC_c	ΔAIC_c	AIC_c weight
4	$+ age - pnp - ppl + pw + (pt\text{-}1) - (pt\text{-}2) + (pt\text{-}3)$	814.66	0.00	0.66
5	$+ age + (pt\text{-}1)$	816.96	2.30	0.21
14	$+ age + tpl + ppl + tnp + pnp$	820.50	5.84	0.04
17	$+ age - tw - pw + tpl + ppl + tnp + pnp$	820.72	6.06	0.03
19	$+ age - heat$	821.56	6.90	0.02
13	$+ age + tnp - pnp$	822.86	8.20	0.01
12	$+ age + tpl + ppl$	823.16	8.50	0.01

However, probability of recapturing adults slightly declined as mean annual fledging-success increased.

Using the best recapture structure ($p(S1, S2, a(fledge))$), we modeled apparent survival using capture histories of 160 females and 188 males initially captured as adults or subadults and 478 owls initially banded as juveniles. The survival model that was most strongly supported by the mark–recapture data included indicator variables representing age and a continuous variable representing precipitation during the previous year (Table 4) and had the following structure:

$$Logit\ (\hat{\phi}) = -0.540 + 0.599 * (pt\text{-}1) + 1.586 * (adult) + 2.528 * (S2) + 1.349 * (S1)$$

where $\hat{\phi}$ = estimated apparent survival, *adult* =

1 for adult owls and 0 for subadult and juvenile owls, *S2* = 1 for second-year subadult owls, and 0 for other age classes, *S1* = 1 for first-year sub-adult owls and 0 for other age classes, and (*pt-1*) was a continuous variable representing amount of precipitation during the previous weather year. Several models were nearly as likely as the best-fit model (Table 4). All parameter estimates for weather variables in the best model and in competing models had 95% confidence intervals that included zero. In contrast, the parameter estimates for *adult*, *S2*, and *S1* covariates did not include zero for any of the models except for the second-ranked model, where the confidence interval for *adult* overlapped zero. Model averaged estimates indicated that apparent survival was higher for S2 owls ($\hat{\bar{\phi}}$ = 0.880, SE = 0.041) than for adults ($\hat{\bar{\phi}}$ = 0.796, SE = 0.012) and that

TABLE 4. Results of modeling apparent survival of Spotted Owls in the San Bernardino Mountains, California, 1987–1998. The structure for recapture was identical for each model[a].

Model number	Model structure and correlation	$QAIC_c$	$\Delta QAIC_c$	$QAIC_c$ weight	Number of parameters
3	$age^{b} + (pt\text{-}1)$	2871.80	0.00	0.22	9
6	$age + tw$	2872.15	0.35	0.19	9
1	$age + pw$	2872.16	0.36	0.19	9
13	age	2872.29	0.49	0.17	8
12	$age - heat$	2874.25	2.45	0.07	9
7	$age - tw + pw + tw * pw$	2874.41	2.61	0.06	11
2	$age + pw - ppl - pnp$	2875.23	3.43	0.04	11
8	$age + tw + pw - tpl - ppl$	2876.02	4.22	0.03	12
9	$age + tpl + ppl + tnp + pnp$	2877.46	5.66	0.01	12
10	$age + tw + pw - tpl - ppl + tnp - pnp$	2878.00	6.20	0.01	14
4	$age + pw - ppl - pnp + (pt\text{-}1) + (pt\text{-}2) + (pt\text{-}3)$	2879.27	7.47	0.01	14
5	$age + (tw\text{-}1) - (tw\text{-}2) + (pt\text{-}1) + (pt\text{-}2) + (pt\text{-}3) + tw - pw$	2880.65	8.84	0.00	15
11	$age + tw + pw - tpl - ppl - tnp - pnp - tw * pw + tpl * ppl - tnp * pnp$	2882.34	10.53	0.00	17

[a] Age structure for recapture was $p(S1, S2, adult(fledge))$.
[b] Age structure for apparent survival in the age model is (*juvenile, S1, S2, adult*).

adults had higher apparent survival than S1 ($\hat{\bar{\phi}}$ = 0.692, SE = 0.062) and juvenile owls ($\hat{\bar{\phi}}$ = 0.368, SE = 0.038). However, the components-of-variance analysis indicated that no temporal process variation existed for apparent survival ($\hat{\sigma}^2_{temporal}$ = 0.0000, 95% CI = 0.0000 to 0.0001). Because there was no temporal process variation in apparent survival, weather did not affect temporal variability in that demographic parameter during the years of the present study.

Estimation of finite rate of population change.—Assessment of fecundity indicated that reproduction was temporally variable, and greater for adults than for subadults. Therefore, we used a weighted mean estimate of fecundity for adults (b_a = 0.345, SE = 0.028) and subadults (b_s = 0.139, SE = 0.050) as elements in the Leslie matrix. We used model-averaged estimates of apparent survival to represent age-specific survival elements in the Leslie matrix (see above). The Leslie matrix based on those vital rates indicated that the San Bernardino Spotted Owl population declined during the study period ($\hat{\lambda}$ = 0.906, SE = 0.018, 95% CI = 0.871 to 0.942).

Comparison of fecundity, survival, and finite rate of population change with California Spotted Owl meta-analysis.—Our modeling indicated that the data set equivalent to a recent meta-analysis (1991–1998, Franklin et al. 2004) supported the same age classes for fecundity (adults, subadults) and apparent survival (adults, S2, S1, juveniles) as our entire data set (1987–1998). Estimates of mean fecundity (adult $\hat{F}_{1991–1998}$ = 0.377, SE = 0.036; subadult $\hat{F}_{1991–1998}$ = 0.184, SE = 0.058) and apparent survival (adult $\hat{\phi}_{1991–1998}$ = 0.811, SE = 0.014; S2 $\hat{\phi}_{1991–1998}$ = 0.884, SE = 0.039; S1 $\hat{\phi}_{1991–1998}$ = 0.702, SE = 0.063; juvenile $\hat{\phi}_{1991–1998}$ = 0.377, SE = 0.039) using the truncated data set were greater than estimates derived using the entire data set (1987–1998). However, because we were interested only in estimating finite rate of population change with those data, we did not assess whether the differences were biologically meaningful. The estimate of λ using those vital rates was slightly higher than the estimate using all years ($\hat{\lambda}_{1991–1998}$ = 0.921, 95% CI = 0.881 to 0.960) but still indicated a declining population.

DISCUSSION

It has been hypothesized that weather influences avian populations through its effects on reproduction and survival (Lack 1966).

Precipitation can cause large annual differences in avian reproductive success and population density (e.g. see Kostrzewa and Kostrzewa 1990, Gargett et al. 1995, Newton 1998, Krüger et al. 2002). The relationship between precipitation and reproductive success in birds appears to be particularly strong in arid environments, where it is most difficult to balance water demands (Coe and Rotenberry 2003). We also found that precipitation strongly correlated with reproduction in the study population of Spotted Owls. Specifically, we found that fecundity was highest during dry springs preceded by a wet year, which we predicted. Similar relationships have been observed in other raptor populations (Newton 1998). Negative effects of wet weather on reproduction during the nesting season have also been observed in Northern (Franklin et al. 2000) and California (North et al. 2000) Spotted Owl populations. However, we did not find a correlate related to long-term drought (i.e. our best model indicated that the amount of precipitation two years preceding the current reproductive season was negatively correlated with fecundity). That result either was a spurious correlation or reflected an unknown feedback process that would negatively affect owls after a delay of two years. Although we did not know the mechanism by which weather affected fecundity, we infer that the influence was strong, because our weather models explained all of the process variation in fecundity.

We propose two potential hypotheses that could represent the mechanisms behind the correlation between weather and fecundity in our Spotted Owl population. First, Smith et al. (1999) noted that whereas non-nesting and unsuccessfully nesting owls had similar diets, successful nesters had a higher proportion of dusky-footed woodrats in their diet. Because woodrat numbers decline during droughts in southern California (Spevak 1983), there may be an indirect link between lower-than-average precipitation during the previous year and poor reproduction in the study population of Spotted Owls. Therefore, this mechanism represents negative effects of a "short-term" drought during the preceding year, rather than "long-term" drought as we initially predicted.

Second, fecundity was lowest during years with above-average precipitation during the breeding season. Extended periods of precipitation during spring could reduce survival of

nestlings through energy loss (Wijnandts 1984, Franklin et al. 2000, North et al. 2000) and could reduce adult hunting success by limiting prey activity (Linsdale and Tevis 1951, Gentry et al. 1966) or prey detectability (Rijnsdorp et al. 1981, Hirons 1982). These hypotheses represent both indirect and direct effects of weather on reproductive performance during the current breeding season. In addition, our results support the hypothesis, noted in a meta-analysis of five California Spotted Owl populations, that the temporal variation in reproductive output may be attributable to the influence of weather (Franklin et al. 2004).

Our estimates of adult apparent survival differed from estimates for other Spotted Owl populations in three ways. First, our estimate of adult survival was lower than estimates for other populations (Noon et al. 1992, Forsman et al. 1996, Seamans et al. 1999); however, we do not know if that difference was biologically meaningful. Second, our estimate of second-year subadult survival was higher than that of adult survival; whereas estimates from other studies showed that subadult survival was lower than adult survival (Franklin et al. 1999, 2000; Seamans et al. 1999, 2002; Blakesley et al. 2001). Again, we do not know if this is biologically meaningful or an artifact of sample size. Third, and most important, in contrast to previous studies (Franklin et al. 1999, Seamans et al. 1999, Franklin et al. 2000, Blakesley et al. 2001, Seamans et al. 2002), we found no temporal variation in apparent survival. Although birds can usually ameliorate the immediate direct effects of extreme weather conditions (Newton 1998), it appears that weather can influence survival in other Spotted Owl populations (Franklin et al. 2000, Seamans et al. 2002). Therefore, we conclude that either (1) variation in weather extremes in southern California may not exceed the tolerance limits for survival of this owl or (2) we did not observe extremes large enough to cause an effect.

Estimation of population trends has been fundamental to conservation of the California Spotted Owl (Noon and Franklin 2002, U.S. Department of the Interior 2003, Franklin et al. 2004). In a recent meta-analysis, Franklin et al. (2004) suggested that matrix projection methods for estimation of λ were not appropriate for Spotted Owls in particular, and open populations in general, because of

unknown bias associated with permanent or temporary emigration of juveniles from study areas. However, they indicated that the San Bernardino population was probably an exception because it functioned as an essentially closed population. Nevertheless, Franklin et al. (2004) used a reparameterized Jolly-Seber estimator to assess population change of the San Bernardino owl population to maintain consistency among the meta-analysis study populations. To satisfy the assumption of constant study-area size required by a reparameterized Jolly-Seber estimator, they truncated the length of time for the San Bernardino owl study from 12 to 8 years. Their analysis estimated that the San Bernardino population was statistically stable from 1992 to 1998. In contrast, our analysis based on the Leslie projection matrix showed that our population declined from 1987 to 1998, as well as from 1992 to 1998. As noted above, estimates of λ from projection matrices can be biased if either juvenile or adult survival is biased. However, we have strong evidence that the San Bernardino population was essentially closed (i.e. no evidence of immigration to or emigration from the mountain range; LaHaye et al. 1994, 2001). The San Bernardino Mountains are surrounded by unsuitable habitat, which would reduce the potential for emigration or immigration. Therefore, we felt that our estimates of juvenile survival were not strongly biased by emigration (e.g. proportion of unbanded birds entering the territorial population was 3.7% in 1997 and 4.6% in 1998; LaHaye et al. 2001). Our estimates indicated that the two approaches, at least for the study population, yielded different inferences about the population's trend (Franklin et al. 2004). Although there may be an unknown bias in estimating λ with our demography data (e.g. not enough years of study for juveniles to become territorial so that their survival estimates could be appropriately estimated), we do not believe that a bias in juvenile survival is a cause for the difference, because of the high proportion of juveniles banded and because the low proportion of unbanded owls entering the population has been consistent for several years prior to the end of the study (LaHaye et al. 2001). Despite the differences between the meta-analysis and our current study, we believe that both analyses are valid, given their respective goals.

Although our 12-year study was relatively long as compared with many studies, it was only slightly longer than the average life-span of a territorial owl and did not include a series of years with above-average precipitation (Core 2002) followed by mild springs, which might have allowed improved survival, reproduction, and recruitment (i.e. conditions correlated with improved fecundity in the study population). Poor short-term environmental conditions can reduce demographic rates (Van Horne et al. 1997). Thus, we feel that studies spanning two to three decades may be required to observe the full range of climatic variability and illustrate how that variation affects the vital rates of the population. However, the present results clearly indicate that weather exerts a strong influence on fecundity (i.e. weather explained all temporal process variation in fecundity) despite the relatively mild weather in southern California as compared with other areas of the Spotted Owl's west-coast range. Moreover, it appears that drier-than-average years (i.e. short-term drought within the year prior to a given breeding season) preceding wetter-than-average springs is related to a reduction in Spotted Owl reproduction in the southern portion of the subspecies' range. The contrasting effects of precipitation on reproduction, but not on survival, may reflect different life-history requirements during the annual cycle of this Spotted Owl population.

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APPENDIX. Acronyms and descriptions of covariates used in modeling of fecundity and apparent survival of Spotted Owls in the San Bernardino Mountains, California, 1987–1998.

Acronym	Description
tw	Winter temperature
pw	Winter precipitation
tpl	Temperature in prelaying period
ppl	Precipitation in prelaying period
tnp	Temperature in nesting period
pnp	Precipitation in nesting period
hs_{t-1}	Number of heat-stress days during previous summer
$tw * pw$	Interaction between winter temperature and precipitation
$tpl * ppl$	Interaction between temperature and precipitation during prelaying period
$tnp * pnp$	Interaction between temperature and precipitation during nesting period
$tw\text{-}1$	Minimum winter temperature during previous year
$tw\text{-}2$	Minimum winter temperature two years prior to current year
$pt\text{-}1$	Precipitation one year prior to current year
$pt\text{-}2$	Precipitation two years prior to the current year
$pt\text{-}3$	Precipitation three years prior to the current year
$S1$	First-year subadult
$S2$	Second-year subadult
a	Adult
$fledge$	Estimate of fecundity
sex	Separate estimates for males and females
t	Time (t = current year, $t\text{-}1$ = previous year, etc.)
$heat$	Number of heat stress days during the current summer
$\hat{\sigma}^2_{temporal}$	Estimate of temporal process variation
$\text{var}(\hat{F}_t)$	Total variation in temporal estimates of fecundity
$\hat{F}$	Estimate of fecundity
$\hat{\phi}$	Estimate of apparent survival
$\hat{\lambda}$	Estimate of finite rate of population change from Leslie matrix
$\hat{p}$	Estimate of recapture probability