

MEXICAN SPOTTED OWL (*STRIX OCCIDENTALIS*) POPULATION DYNAMICS: INFLUENCE OF CLIMATIC VARIATION ON SURVIVAL AND REPRODUCTION

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ABSTRACT.—Understanding the mechanisms causing temporal variability in demographic parameters is essential to understanding fluctuations in populations. As part of a long-term demographic study, we evaluated influence of climate on Mexican Spotted Owl (*Strix occidentalis lucida*) annual survival and reproduction in two study areas, one in Arizona and one in New Mexico. Spotted Owl survival in New Mexico and reproductive output in both study areas were positively related to total amounts of precipitation from the previous year, previous winter, or monsoon season. For both study areas, temporal process variation in reproductive output ($CV[R] = 51.2$ and 75.2% for Arizona and New Mexico, respectively) was greater than that for survival ($CV[\phi] = 12.9$ and 7.1% for Arizona and New Mexico, respectively). Precipitation from the previous year explained 73% of $\hat{\sigma}^2_{\text{temporal}}$ reproductive output for Arizona owls and precipitation from the previous monsoon explained 42% of $\hat{\sigma}^2_{\text{temporal}}$ in reproductive output for New Mexico owls. Precipitation from the previous monsoon season explained 53% of $\hat{\sigma}^2_{\text{temporal}}$ in Arizona owl survival and precipitation from the previous winter explained 56% of $\hat{\sigma}^2_{\text{temporal}}$ in New Mexico owl survival. The two populations of Spotted Owls we studied appeared to have the same life-history strategy hypothesized for a population of Northern Spotted Owls (*S. o. caurina*), although the Mexican subspecies apparently responded quite differently to climatic variation. Received 6 February 2001, accepted 29 October 2001.

RESUMEN.—Entender los mecanismos que causan variabilidad temporal en los parámetros demográficos es esencial para entender las fluctuaciones poblacionales. Como parte de un estudio demográfico a largo plazo, evaluamos la influencia del clima en la supervivencia y reproducción anual de *Strix occidentalis lucida* en dos áreas de estudio, una en Arizona y otra en New Mexico. La supervivencia de *S. o. lucida* en New Mexico y el rendimiento reproductivo en ambas áreas de estudio estuvieron positivamente relacionados con la precipitación total del año anterior, del invierno anterior, o de la estación monsonica. Para ambas áreas de estudio, la variación temporal en el rendimiento reproductivo ($CV[R] = 51.2$ y 75.2% para Arizona y New Mexico, respectivamente) fue mayor que la variación en la supervivencia ($CV[\phi] = 12.9$ y 7.1% para Arizona y New Mexico, respectivamente). La precipitación del año anterior explicó el 73% de la $\hat{\sigma}^2_{\text{temporal}}$ en el rendimiento reproductivo de las lechuzas de Arizona, y la precipitación de la estación monsonica previa explicó el 42% de la $\hat{\sigma}^2_{\text{temporal}}$ en el rendimiento reproductivo de las lechuzas de New Mexico. La precipitación de la estación monsonica previa explicó el 53% de la $\hat{\sigma}^2_{\text{temporal}}$ en la supervivencia de las lechuzas de Arizona y la precipitación del invierno previo explicó el 56% de la $\hat{\sigma}^2_{\text{temporal}}$ en la supervivencia de las lechuzas de New Mexico. Las dos poblaciones de *S. o. lucida* que estudiamos parecen presentar la misma estrategia de historia de vida hipotetizada para una población de *S. o. caurina*, aunque la subespecie mexicana aparentemente respondió de modo bastante distinto a la variación climática.

AN UNDERSTANDING of limiting factors that cause population fluctuations is important to the study of any species' ecology and manage-

ment and for estimating population viability (Sinclair 1991, White 2000). Environmental stochasticity, viewed over any period of time, can be a major influence to which organisms must adapt. Climate is one aspect of environmental variation that can influence animal numbers.

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For example, long-term drought may reduce forage that ultimately leads to individual starvation. Such long-term perturbations can also play a role in extinction, especially for species that occur in low abundance or have low potential for population growth (Dennis et al. 1991). Thus, the limiting effects of climate are important to the understanding of population dynamics and persistence. In addition, the study of climatic influences on survival and reproduction over space and time is useful because survival and reproduction are two key demographic rates that influence population size.

The Mexican Spotted Owl (*Strix occidentalis lucida*) is a forest and canyon dwelling owl of the southwestern United States and northern Mexico (Gutiérrez et al. 1995), and has been listed as a threatened species (U.S. Department of the Interior 1993). The owl uses a range of habitats but reaches its greatest known numbers in the conifer forests of the mountainous Upper Gila Recovery Unit (U.S. Department of the Interior 1995). In a previous article, we estimated that two populations within this recovery unit were declining at ~10% per year, but causes behind those declines were unknown (Seamans et al. 1999).

To understand mechanisms behind those declines, we examined temporal variation in Mexican Spotted Owl reproduction and survival attributable to climate. We used an information-theoretic approach (Burnham and Anderson 1998) to rank plausibility of climate-related hypotheses regarding Mexican Spotted Owl survival and reproductive output. We used climate covariates in a model selection framework to explain temporal variation in Mexican Spotted Owl survival and reproduction. After an appropriate model was chosen, we conducted a components of variance analysis (Box et al. 1978) to determine relative magnitude of temporal process variation ($\hat{\sigma}_{\text{temporal}}^2$; natural variation in a given parameter over time), and sampling variation ($\text{var}[\hat{\theta}|\theta]$; variation due to estimating a parameter). To assess the influence of climate, we examined what portion of $\hat{\sigma}_{\text{temporal}}^2$ could be explained by our best climate models.

METHODS

STUDY AREAS

We conducted our study from 1991 to 1998 in Arizona and New Mexico (Seamans et al. 1999). The Ar-

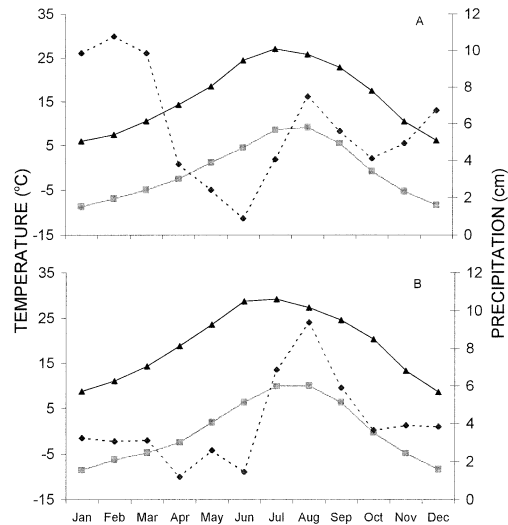


FIG. 1. Mean monthly maximum and minimum temperature (solid lines) and monthly precipitation (dashed line) from 1990–1998, central Arizona (A) and west-central New Mexico (B). Data are means from two U.S. Weather Service weather stations in Arizona and three in New Mexico.

izona study area was 585 km² located in central Arizona on the Coconino Plateau (May 2000). Elevation ranged from 1,800 to 2,660 m. The New Mexico study area was 323 km² located in west-central New Mexico in the Tularosa Mountains (Peery et al. 1999). Elevation ranged from 1,900 to 2,900 m. Both areas were characterized by warm summers and cold winters with two distinct periods of precipitation: winter snow and summer monsoon thundershowers (Fig. 1). Average annual precipitation from 1990 through 1998 was 73 and 51 cm for the Arizona and New Mexico study sites, respectively.

SURVEYS

Spotted Owls were surveyed from April through August each year. Field methods used to locate, capture, and band owls, and assess reproductive output followed those described by Franklin et al. (1996) and Seamans et al. (1999). Owls were sexed on the basis of pitch of their calls, males having a lower pitched call than females (Forsman et al. 1984). We identified four age-classes on the basis of plumage characteristics (Forsman 1981, Moen et al. 1991): young of the year (juvenile); one year-old (first-year subadult); two year-old (second-year subadult); and ≥ 3 years old (adult).

MODELING APPROACH

Valid inferences about relationships occurring in biological systems are largely dependent on appro-

appropriate analysis of data. The typical approach of using null hypothesis testing is often of little use in model or variable selection because of arbitrary significance levels, null hypotheses that are almost always initially false, and comparison of multiple hypotheses often results in inflated stated error rates (Anderson et al. 2000). An alternative analytical method is the information theoretic approach (Akaike 1973), which uses likelihood theory and focuses on relationships of variables, estimates of effect size, and estimates of precision. Under the likelihood framework, plausibility of competing models can be ranked by using the likelihood of any model, given the data.

Central to making valid inferences using model selection is a good set of *a priori* hypotheses regarding the biology of the subject of interest. That set of models can be developed by searching relevant literature or from observations made by the researcher. Only *a priori* models are examined during the model selection phase, otherwise the analysis can become an exercise in data dredging. Therefore, the utility of selected models in explaining biological relationships is dependent on the insight of the researcher and how relevant is the *a priori* set of models. To explore how good selected models are, amount of variation in the data explained by the best *a priori* models can be examined using a variance components analysis (e.g. Gould and Nichols 1998). That is done by partitioning temporal variation (i.e. year to year biological variation) from sampling variation. Models that explain high amounts of variation are more plausible than models that explain little variation.

MODEL DEVELOPMENT AND ANALYSIS

Climate model development.—We developed an *a priori* set of hypotheses, expressed as candidate models (following Burnham and Anderson 1998), regarding influence of precipitation (P) and ambient temperature (T) on Spotted Owl annual survival and reproductive output (Table 1). Models were developed based on our own observations of Spotted Owls, literature on Spotted Owls and their prey, and literature on other avian species (see Franklin et al. 2000). We hypothesized that climate may directly affect Spotted Owls through thermoregulatory constraints or reduction of foraging success, or indirectly by affecting their prey. Predictive climate covariates were developed to reflect conditions within critical Spotted Owl life-history periods, and to reflect potential lag effects in primary productivity and presumed prey response.

We assumed that winter was one critical period for Spotted Owl survival (W ; November–March). Spotted Owls hunt primarily by sound (Forsman et al. 1984), therefore, rain and snow during winter may reduce owls' ability to see or hear prey by reducing auditory cues, by covering small mammal burrows or nests with snow, and by obscuring subnivean

movements. Nesting may be another critical period for survival (N ; April–May). While nesting, females are relatively sedentary and exposed to predators and inclement weather and males must increase foraging to feed both the female and young (Delaney et al. 1999). Thus, we hypothesized that cold and wet conditions during W and N may have direct negative effects on survival (Table 1; models S1–S2).

We hypothesized that indirect effects of climate on survival may occur through prey population dynamics. Primary prey in these areas were white-footed mice (*Peromyscus* spp.) and woodrats (*Neotoma* spp.; Seamans and Gutiérrez 1999). Those two small mammal genera primarily feed on forbs, grasses, and seeds (Bailey 1931, Goodwin and Hungerford 1979). Dry conditions during the previous winter (W' ; winter in year $t - 1$, model S3) may reduce spring forage, and hence prey reproduction during the following summer, which in turn may reduce prey populations for the next winter (winter in year t , when survival was estimated). Much of the annual precipitation in the southwestern United States occurs during the summer monsoon season (Fig. 1; Mitchell 1976). Dry conditions during the monsoon (M ; July–September) reduces production of late summer primary productivity, which may limit late-season reproduction by prey and reduce prey overwinter abundance (model S4). Further, an important mast tree in both study areas is the Gambel oak (*Quercus gambelii*), which may fail to produce acorns during harsh spring conditions (which coincides with the nesting period for Spotted Owls) or during monsoon drought (Neilson and Wullstein 1983, Clary and Teidmann 1992). Therefore, we hypothesized that Spotted Owl survival could be negatively affected by cold and dry conditions during the preceding April–May (N') or dry conditions during the preceding monsoon (model S5). We also hypothesized low precipitation one year (Y ; November–October) prior to the winter survival period would negatively affect survival through reduced long-term primary productivity and prey response (model S6). In addition, Spotted Owls may benefit from increased precipitation only up to a point. This threshold-type model should take the form of a loglinear effect (model S7). Alternatively, there may be an optimal amount of precipitation for Spotted Owl survival, where too little or too much precipitation during the previous year may negatively affect survival. That model should be described by a quadratic equation (e.g. $Y + Y^2$).

Most climatic patterns we hypothesized to influence Spotted Owl survival also may influence reproduction. Spotted Owls begin courtship behavior in February or early March, with clutch initiation around 1 April (Forsman et al. 1984, Delaney et al. 1999). Body condition of the female prior to laying probably determines reproductive capacity, with egg follicle development dependent on fat reserves ac-

TABLE 1. *A priori* models for effects of ambient temperature and precipitation on Mexican Spotted Owl apparent survival and reproductive output. Abbreviations are as follows: *T* = average minimum temperature, *P* = total precipitation, *N* = nesting period, *F* = courtship period, *W* = winter, *M* = monsoon period, and *Y* = previous year. A prime symbol (') indicates period from previous year.

Hypothesis	Model	Model structure	Expected result
Survival (ϕ)			
S1. Negative effects of cold and wet in <i>W</i>	$\phi(T_W + P_W)$	$\beta_0 + \beta_1(T_W) + \beta_2(P_W)$	$\beta_1 > 0, \beta_2 < 0$
S2. Negative effects of cold and wet in <i>N</i>	$\phi(T_N + P_N)$	$\beta_0 + \beta_1(T_N) + \beta_2(P_N)$	$\beta_1 > 0, \beta_2 < 0$
S3. Positive effect of precipitation in <i>W'</i>	$\phi(P_{W'})$	$\beta_0 + \beta_1(P_{W'})$	$\beta_1 > 0$
S4. Positive effect of precipitation in <i>M</i>	$\phi(P_M)$	$\beta_0 + \beta_1(P_M)$	$\beta_1 > 0$
S5. Positive effect of precipitation in <i>M</i> and <i>N'</i> and warm temp. in <i>N'</i> on Gambel oak mast	$\phi(P_M + P_{N'} + T_{N'})$	$\beta_0 + \beta_1(P_M) + \beta_2(P_{N'}) + \beta_3(T_{N'})$	$\beta_1 > 0, \beta_2 > 0, \beta_3 > 0$
S6. Positive effect of high precipitation from previous year.	$\phi(P_Y)$	$\beta_0 + \beta_1(P_Y)$	$\beta_1 > 0$
S7. Nonlinear threshold type of effect of high precipitation from previous year	$\phi(P_{mY})$	$\beta_0 + \beta_1(P_{mY})$	$\beta_1 > 0$
Reproductive output (R)			
R1. Negative effects of cold and wet in <i>W</i>	$R(T_W + P_W)$	$\beta_0 + \beta_1(T_W) + \beta_2(P_W)$	$\beta_1 > 0, \beta_2 < 0$
R2. Positive effect of precipitation in <i>M</i> and <i>N'</i> and warm temp. in <i>N'</i> on Gambel oak mast	$R(P_M + P_{N'} + T_{N'})$	$\beta_0 + \beta_1(P_M) + \beta_2(P_{N'}) + \beta_3(T_{N'})$	$\beta_1 > 0, \beta_2 > 0, \beta_3 > 0$
R3. Negative effects of cold and high precipitation during <i>F</i>	$R(T_F + P_F)$	$\beta_0 + \beta_1(T_F) + \beta_2(P_F)$	$\beta_1 > 0, \beta_2 < 0$
R4. Negative effects of cold and high precipitation during <i>N</i>	$R(T_N + P_N)$	$\beta_0 + \beta_1(T_N) + \beta_2(P_N)$	$\beta_1 > 0, \beta_2 < 0$
R5. Positive effect of high precipitation in <i>Y</i>	$R(P_Y)$	$\beta_0 + \beta_1(P_Y)$	$\beta_1 > 0$
R6. Positive effect of high precipitation in <i>M</i>	$R(P_M)$	$\beta_0 + \beta_1(P_M)$	$\beta_1 > 0$
R7. Positive effect of high precipitation in <i>W'</i>	$R(P_{W'})$	$\beta_0 + \beta_1(P_{W'})$	$\beta_1 > 0$
R8. Nonlinear threshold type of effect of high precipitation from previous year	$R(P_{mY})$	$\beta_0 + \beta_1(P_{mY})$	$\beta_1 > 0$

cumulated during the preceding months (e.g. Tawny Owl [*Strix aluco*]; Hiron 1982). Further, Newton and Marquiss (1984) found female European Kestrel (*Falco tinnunculus*) body condition was affected by environmental conditions two to three months prior to laying. Cold and wet conditions during the two

months prior to laying (*F*; February–March) may be detrimental to developing those fat reserves (model R3). For many raptor species, cold wet conditions during nesting negatively affect reproductive success (e.g. Peregrine Falcon [*Falco peregrinus*]; Mearns and Newton 1988; Buzzard [*Buteo buteo*] and North-

ern Goshawk [*Accipiter gentiles*]; Kostrzewa and Kostrzewa 1989). Cold and wet conditions during nesting (N ; April–May) may make foraging harder for males and may force females to leave the nest to forage, thus exposing eggs or newly hatched young to weather and predators (model R4). In addition, prey abundance and availability prior to nesting should also influence female body condition (Hirons 1982). Thus, we hypothesized that total precipitation in the year prior to nesting (Y), the previous monsoon (M), and the winter in year $t - 1$ (W) may influence primary productivity and, therefore, prey abundance (models R5–7). We also hypothesized the same nonlinear forms of these effects ($\ln Y$ and $Y + Y^2$) as with survival (e.g. model R8; see Franklin et al. 2000).

Estimation of climate covariates.—Average minimum temperature ($^{\circ}\text{C}$) and total precipitation (centimeters) were estimated during important life-history periods for the Spotted Owl and during other times of the year that may have been important to the owl's prey (Fig. 1). We estimated average minimum temperature and precipitation for Arizona by averaging daily measurements from two National Weather Service weather stations (Mormon Mountain and Munds Park) located in the study area. Because there were no weather stations located in the New Mexico study area, we used three local stations (Reserve, Frisco Divide, and Beaverhead) to approximate conditions. Those stations formed a rough triangle incorporating the study area and were located 13, 27, and 48 km from the study area and ranged in elevation from 1,740 to 2,460 m. Based on our observations during owl surveys in these adjacent areas, weather patterns were similar between those stations and the study area.

Survival estimation.—We used open population capture–recapture models to estimate apparent survival (ϕ) and recapture (p) probabilities for territorial Spotted Owls (Cormack 1964, Jolly 1965, Seber 1965). We estimated apparent survival because we did not have an estimate of emigration, which is needed to estimate true survival. However, on the basis of previous telemetry studies, territorial owls move off territories infrequently and emigration is probably minor (Raphael et al. 1996). Juvenile survival was not modeled because juveniles may have permanently emigrated from the study areas, which would result in an underestimate of survival (Raphael et al. 1996). Data were summarized in a capture history matrix that included the sex and age of each owl as categorical variables. Male and female survival was modeled jointly to explore possible differences between sexes. If survival rates were judged to be similar between the sexes based on model selection criteria (see below), they were combined to increase our sample sizes.

We modeled survival using program MARK (White and Burnham 1999). Program MARK esti-

mates survival and recapture probabilities using numerical maximum-likelihood techniques. Program MARK also computes a bias-corrected version of Akaike's Information Criterion (AIC_c) value for each model which permits objective selection of the best models (Akaike 1973, Burnham and Anderson 1998). Model notation used in this article followed that of Lebreton et al. (1992) and Franklin et al. (2000). We tested capture–recapture assumptions (Franklin et al. 1996) by estimating overdispersion (\hat{c}) within respective data-sets. We estimated c as deviance from a saturated model divided by the mean simulated deviance from 500 bootstrap simulations (White et al. 2002). The bootstrap procedure used the estimates of the saturated model to generate data with no overdispersion (i.e. meeting capture–recapture assumptions).

Recapture rates must be estimated appropriately or estimates of survival may be biased. Recapture rate was modeled with the effects of owl age (a ; using two age-classes; subadult and adult), sex (s), time (categorical time [t], linear time [lt], quadratic time [$t + t^2$], or loglinear time [$\ln t$]), and the interaction of those effects. We then modeled effects of survey effort, observer experience (C), presence of a project leader during the field season (PL), and owl reproductive status on recapture rates. A project leader was an experienced field biologist responsible for leading field activities. Because of funding, we did not have a project leader for two years of study in New Mexico. Survey effort was used to constrain recapture rates using walk-in hours (Ew), and the total number of survey hours (Eb ; both walk-in and night survey hours). Experience of field observers on recapture rates was modeled by using number of field seasons the observers within each year had worked with Spotted Owls. For reproductive status, we considered the annual proportion of territories fledging young (F) and the annual proportion of territories nesting (N) as constraints on recapture rates. In our experience, nesting owls may be easier to capture.

We first modeled the effects of age, sex, and time on survival. The top sex, age, and time models were then further constrained using annual climate covariates (Table 1). We modeled effect of each climatic variable on survival, then considered 10 additional models that included additive or interactive effects of multiple variables. The study areas were first modeled separately, then jointly for comparison (" g " represents study area effect). We ranked models that represented the relationship between demographic parameters and climate covariates using AIC_c corrected for small sample size (AIC_c ; Akaike 1973, Burnham and Anderson 1998). AIC_c values were corrected for overdispersion (\hat{c}) within the data sets (QAIC_c ; Burnham and Anderson 1998). Overdispersion (\hat{c}) was estimated from the bootstrap goodness-of-fit results conducted prior to survival analysis (White et al. 2002). We addressed uncertainty in se-

lecting the best model by calculating AIC weights (w_i ; Buckland et al. 1997).

Reproductive output estimation.—We used only paired owls for reproductive analyses. We used a linear mixed modeling approach (Littell et al. 1996) to construct models where reproductive output (R_i ; number of young fledged) from an individual territory within a year was the dependent variable, age of the female pair member and climate covariates were fixed effects, and territory and year were random effects. Male age was not considered because the sample size of subadult males was too small. Territory was treated as a random blocking factor because observations from the same territory among years may not have been independent. Because we were interested in the effect of climate on reproductive output for each particular year, “year” was treated as the experimental unit in a repeated measures design, where territories were considered the subsamples within years. The general form of the model was $R_i = \mathbf{X}\beta + \mathbf{Z}u + e$, where β was a vector of fixed parameters, \mathbf{X} the fixed parameter design matrix, u a vector of unknown random effect parameters, \mathbf{Z} the design matrix for the random effect parameters, and e a vector of random errors (Littell et al. 1996).

Heterogeneous variances within- and between-subjects commonly occur within all types of data, and failure to account for heterogeneity when present can result in misleading inferences (Littell et al. 1996). We dealt with possible heterogeneity by using a restricted maximum-likelihood approach to first structure the random error covariance matrix (Littell et al. 1996). Selection of the best covariance structure was based on AIC_c . Once an appropriate covariance structure was found, we used full maximum-likelihood estimation to model reproductive output in response to climate covariates. One mixed model analysis was conducted for each hypothesized model. Models then were ranked on the basis of AIC_c . Initially, we modeled reproductive output for each study area separately to assess local climate correlates. We then modeled the study areas jointly for comparison. Models were ranked that represented the relationship between demographic parameters and climate covariates using AIC_c . We addressed uncertainty in selection of the best models by calculating AIC weights (w_i).

Estimation of variance components.—Temporal process variation ($\hat{\sigma}^2_{\text{temporal}}$) in reproductive output was estimated using an intercept-only (mean) model from our linear mixed modeling approach, which included territory as the blocking factor and year as the experimental unit in a repeated measures design. We then used the best climate model to assess how much of $\hat{\sigma}^2_{\text{temporal}}$ remained unexplained by climate. The two models allowed us to estimate $\hat{\sigma}^2_{\text{climate}}$ (amount of $\hat{\sigma}^2_{\text{temporal}}$ explained by climate) and the unexplained process variation ($\hat{\sigma}^2_{\text{residual}}$). Thus, $\hat{\sigma}^2_{\text{temporal}} = \hat{\sigma}^2_{\text{climate}} + \hat{\sigma}^2_{\text{residual}}$. We calculated $\hat{\sigma}^2_{\text{temporal}}$ for survival following

White et al. (2002), while calculation of $\hat{\sigma}^2_{\text{climate}}$ and $\hat{\sigma}^2_{\text{residual}}$ followed the same procedure used for reproductive output. For reproductive output, log-based 95% confidence intervals were calculated for $\hat{\sigma}^2_{\text{temporal}}$ using SE ($\hat{\sigma}^2_{\text{temporal}}$) from the mixed model output (Burnham et al. 1987).

Weighted means of R or ϕ ($\hat{\theta}$) were calculated following Burnham et al. (1987). We calculated coefficients of temporal process variation as $\hat{\sigma}^2_{\text{temporal}}/\hat{\theta}$ to estimate degree to which survival and reproduction varied over time. We estimated total variability (S^2) of parameter estimates as: $S^2 = 1/n - 1 \sum_i^p (\hat{\theta}_i - \hat{\theta})^2$, where $\hat{\theta} = 1/n \sum_i^p \hat{\theta}_i$, where n was number of annual parameter estimates, $\hat{\theta}_i$ were estimated from the least squares means for R_i , and ϕ_i from the best survival model. Variability due to estimating a parameter, $\text{var}(\hat{\theta}|\theta)$, could then be estimated as $S^2 - \hat{\theta}^2_{\text{temporal}}$ (Franklin et al. 2000).

RESULTS

SURVIVAL

During the study period, we banded 52 male and 51 female territorial owls in Arizona and 47 male and 47 female territorial owls in New Mexico. There was a small amount of overdispersion (i.e. lack of independence or individual heterogeneity) for the three data sets used to model survival (Arizona, $\hat{c} = 1.234$; New Mexico, $\hat{c} = 1.205$; combined study areas, $\hat{c} = 1.220$). We judged these amounts to be slight, and not a serious violation of capture—recapture assumptions.

The best recapture rate structure for Arizona was a quadratic function of time ($t + t^2$). The best survival model for Arizona, ($\phi[t]$), indicated survival was fully time dependent, with time as a categorical variable. This model was $15\times$ more likely than the next best model (Table 2). The estimate for ϕ_2 was at the boundary of 1.0, and a realistic variance could not be estimated. We did account for this parameter when calculating QAIC_c. The best climate model for Arizona (Table 2) indicated a positive relationship between increased monsoon precipitation and survival (regression coefficient [β_{PM}] = 3.488, 95% CI = 1.042, 5.934).

The best model structure for New Mexico indicated recapture rates were positively related to presence of a project leader in the field. For New Mexico, all top survival models included some form of precipitation and higher survival by adults than subadults (Table 2). There were three models that were two to three times more

TABLE 2. Ranking of Mexican Spotted Owl apparent survival (ϕ) models with and without climate covariates in central Arizona and west-central New Mexico.

Model	K^a	QAIC _c ^b	Δ QAIC _c	w^c
Arizona apparent survival models				
$\phi(t), p(t + t^2)$	10	343.65	0.00	0.725
$\phi(P_M), p(t + t^2)$	7	349.35	5.71	0.042
$\phi(P_{In Y}), p(t + t^2)$	5	350.03	6.38	0.030
$\phi(P_V), p(t + t^2)$	5	350.71	7.06	0.021
$\phi(P_{W+WW}), p(t + t^2)$	6	350.95	7.30	0.019
New Mexico apparent survival models				
$\phi(a + P_W), p(PL)$	5	366.64	0.00	0.203
$\phi(a + P_{Y+Y^2}), p(PL)$	6	366.96	0.33	0.172
$\phi(a + P_{In W}), p(PL)$	5	367.00	0.37	0.169
$\phi(a + P_{In Y}), p(PL)$	5	368.59	1.95	0.077
$\phi(a + P_{W+WW^2}), p(PL)$	6	368.70	2.07	0.072
$\phi(a + P_V), p(PL)$	5	369.25	2.61	0.055
$\phi(a + T_N + P_N + P_M), p(PL)$	7	370.50	3.86	0.029
Apparent survival models, data from both study areas				
$\phi(t), p(Eb)$	9	719.25	0.00	0.424
$\phi(g + t), p(Eb)$	10	721.02	1.77	0.175
$\phi(g \times t), p(Eb)$	16	721.14	1.88	0.165
$\phi(a2 + t), p(Eb)$	10	721.32	2.06	0.151
$\phi(g + P_{Y+Y^2}), p(Eb)$	6	725.76	6.50	0.016
$\phi(g + P_V), p(Eb)$	5	726.61	7.35	0.011
$\phi(g + P_M), p(Eb)$	5	726.83	7.58	0.010
$\phi(P_M), p(Eb)$	4	727.08	7.82	0.008
$\phi(g + P_{In W}), p(Eb)$	5	727.49	8.24	0.007

^a Number of parameters in model.

^b Akaike's information criterion corrected for small sample size and overdispersion.

^c Akaike's information criterion weights.

likely than competing models. Model ($\phi[a + P_W]$) suggested a positive relationship between survival in winter t and precipitation during winter $t - 1$ (Fig. 2; $\beta_{PW} = 1.649$, 95% CI =

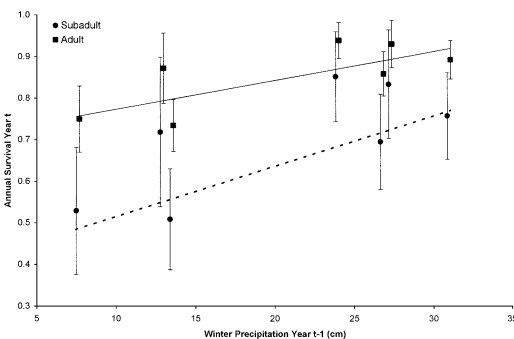


FIG. 2. Relationship between Mexican Spotted Owl annual survival and precipitation from the previous winter in west-central New Mexico. Annual survival estimates from “ $a + t$ ” model. Error bars represent ± 1 SE. Lines represent predicted values from best survival model (solid for adults, dashed for subadult).

0.346, 2.953). Model ($\phi[a + P_{InW}]$) suggested a similar relationship as model ($\phi[a + P_W]$), except that survival leveled off at higher amounts of precipitation ($\beta_{InW} = 6.197$, 95% CI = 1.264, 11.129). Model ($\phi[a + P_{Y+Y^2}]$) indicated survival was related to a quadratic form of the total yearly precipitation leading up to the winter for which survival was estimated.

When study areas were modeled jointly, the best recapture rate structure was positively related to amount of annual survey effort (sum of day and night survey hours). The four best models had a time-specific survival component (t), and accounted for $\sim 96\%$ of the QAIC_c weight. The top model indicated survival rate was time specific, with time as a categorical variable. That model was $\sim 2.5\times$ more likely than the next best model, and $26\times$ more likely than the best survival model that included a climate covariate (Table 2). The next two best models included an additive effect between study area and time, and an interaction between study area and time (Fig. 3). The addi-

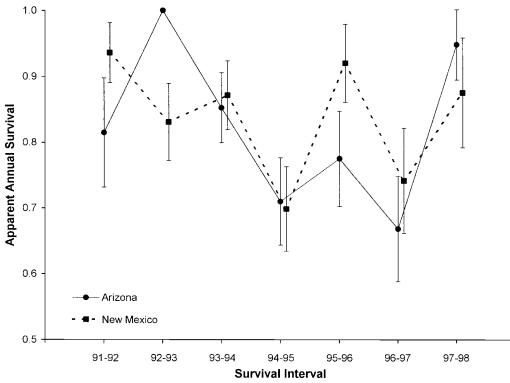


FIG. 3. Estimates of annual survival for Mexican Spotted Owls in central Arizona and west-central New Mexico, 1991–1998. Annual survival estimates from “t” model for both study areas. Error bars represent ±1 SE.

tive model, $(\phi[g + t])$ indicated New Mexico owls experienced slightly higher survival (~1%) than Arizona owls. The best two survival models for both study areas combined with climate covariates included the total precipitation from the previous year, one in a quadratic, and one in a linear form (Table 2).

REPRODUCTIVE OUTPUT

We assessed reproductive output of 44 Spotted Owl pairs on 177 occasions in Arizona and 35 Spotted Owl pairs on 164 occasions in New Mexico. Mean annual reproductive output over all years was 1.04 for Arizona (SE = 0.08; range 0.44–1.70 per year) and 0.64 for New Mexico (SE = 0.07; range 0.10–1.47 per year). The same 7 hypothesized climate models were examined for each study area, and 10 complementary models that included interactive and additive effects and nonlinear forms of climate covariates. We examined those same models for each study area in addition to considering the effect of study area.

The best linear mixed modeling covariance structure for Arizona was compound symmetric, indicating variances were similar among years. That structure was used for examining all subsequent models of reproductive output and climate for Arizona data. The top four reproductive output models for Arizona were within 2 AIC_c of each other (Table 3). The four models had positive slope values and confidence intervals that did not include zero, indi-

TABLE 3. Ranking of Mexican Spotted Owl reproductive output (R) models with and without climate covariates in central Arizona and west-central New Mexico.

Model	K^a	AIC_c^b	ΔAIC_c	w^c
Arizona reproductive output models				
$R(a + P_Y)$	7	475.51	0.00	0.230
$R(a + P_M)$	7	475.59	0.08	0.221
$R(a + P_{ln Y})$	7	475.62	0.11	0.218
$R(a + P_W)$	7	477.10	1.59	0.104
$R(a)$	6	480.26	4.74	0.093
New Mexico reproductive output models				
$R(a + P_M)$	13	371.17	0.00	0.171
$R(a + P_Y)$	13	371.43	0.26	0.150
$R(a + It)$	13	371.75	0.58	0.128
$R(a + P_{ln Y})$	13	371.85	0.68	0.121
$R(a)$	12	372.59	1.42	0.084
$R(P_W)$	13	373.64	2.47	0.050
Reproductive output models, data from both study areas				
$R(a + P_Y)$	13	842.93	0.00	0.261
$R(a + P_{ln Y})$	13	844.24	1.31	0.136
$R(a + P_W)$	13	844.49	1.56	0.120
$R(a + g + P_Y)$	14	844.95	2.02	0.095
$R(a + P_{Y + Y^2})$	14	845.07	2.14	0.089
$R(a + g + P_W)$	14	845.91	2.98	0.059
$R(a + g)$	13	852.01	9.08	0.003
$R(a)$	12	856.76	13.83	<0.001
$R(g)$	12	867.42	24.49	<0.001
$R(-)$	11	870.40	27.48	<0.001

^a Number of parameters in model.
^b Akaike's information criterion corrected for small sample size.
^c Akaike's information criterion weights.

ating a positive trend in reproductive output with increasing precipitation during the previous year, during the previous winter, or during the previous monsoon season (Fig. 4), and higher reproductive output by adult females. AIC_c weights indicated models $(R[a + P_Y])$ and $(R[a + P_M])$ were about twice as likely as model $(R[a + P_W])$. Model $(R[a + P_{ln Y}])$ was the loglinear form of model $(R[a + P_Y])$. Model $(R[a + P_Y])$ suggested a positive relationship between reproductive output and precipitation from the previous year ($\beta_{PY} = 0.016$, 95% CI = 0.007, 0.026). Model $(R[a + P_M])$ suggested a positive relationship between reproductive output and monsoon precipitation ($\beta_{PM} = 0.067$, 95% CI = 0.028, 0.106).

The best linear mixed modeling covariance structure for New Mexico was a power of the means, indicating annual variances were proportional to their means. There were five models within 2 AIC_c units of each other (Table 3). The best climate models had positive slope val-

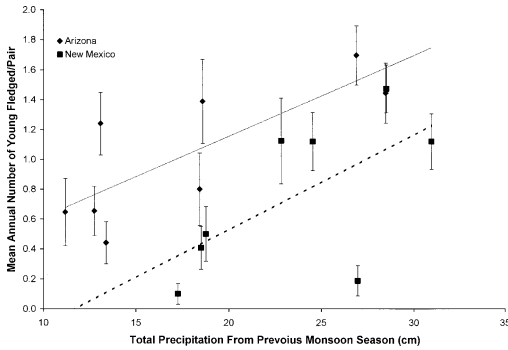


FIG. 4. Relationship between Mexican Spotted Owl annual reproductive output and precipitation from the previous monsoon season in central Arizona and west-central New Mexico, 1991–1998. Error bars represent 95% confidence intervals. Lines represent predicted values from best reproductive model (solid for Arizona, dashed for New Mexico).

ues and 95% confidence intervals that did not include zero, indicating a positive relationship between reproductive output and the amount of precipitation from the previous monsoon season (Fig. 4) or from the previous year, and higher reproductive output by adult females. Of the top five models, three included climate covariates, one was a time-dependent model (lt ; indicating a linear decline in R), and one was an age-only model. AIC_c weights indicated models $(R[a + P_M])$ and $(R[a + P_Y])$ were about as likely as each other, only slightly better than models $(R[a + lt])$ and $(R[a + P_{inY}])$, and about twice as likely as all others. Model $(R[a + P_M])$ suggested a positive relationship between re-

productive output and monsoon precipitation ($\beta_{PM} = 0.065$, 95% CI = 0.007, 0.123), and model $(R[a + P_Y])$ suggested a positive relationship between reproductive output and precipitation from the previous year ($\beta_{PY} = 0.024$, 95% CI = 0.002, 0.046).

The best linear mixed modeling covariance structure using data from both study areas was a power of the means, indicating variances within years were proportional to their means. There were three top models within 2 AIC_c units of each other (Table 3). AIC_c weights indicated model $(R[a + P_Y])$ was at least twice as likely as all other models. Model $(R[a + P_Y])$ indicated a positive linear relationship between reproductive output and total precipitation from the previous year ($\beta_{PY} = 0.013$, 95% CI = 0.007, 0.019) and higher reproductive output by adult females.

TEMPORAL VARIABILITY

Although the estimate of $\hat{\sigma}^2_{temporal}$ in survival was $\sim 3 \times$ greater for Arizona than New Mexico, the 95% confidence intervals overlapped substantially (Table 4). The best climate model for Arizona ($\phi[P_M]$) indicated precipitation from the previous monsoon season explained $\sim 53\%$ of $\hat{\sigma}^2_{temporal}$ in survival estimates. The best climate model from New Mexico ($\phi[P_W]$) indicated precipitation from the previous winter explained 56% of the $\hat{\sigma}^2_{temporal}$ in survival estimates. Sampling variation was comparable between the study areas (Table 4). Annual sur-

TABLE 4. Estimated variance components for Mexican Spotted Owl reproductive output and apparent survival in central Arizona and west-central New Mexico. Ninety-five percent confidence intervals are in parentheses.

	Arizona		New Mexico	
	Reproductive output (R)	Apparent survival (ϕ)	Reproductive output (R)	Apparent survival (ϕ)
$\hat{\theta}$	1.0348	0.8427	0.6399	0.8441
$\hat{var}(\hat{\theta})^a$	0.0066	0.0007	0.0045	0.0002
$\hat{var}(\hat{\theta} \hat{\theta})^b$	0.0455	0.0041	0.0293	0.0044
$\hat{\sigma}^2_{temporal}$	0.2806	0.0118	0.2316	0.0036
	(0.0941, 0.9214)	(0.0037, 0.0675)	(0.0813, 0.8766)	(0, 0.0339)
$CV(\hat{\theta})^c$	0.5119	0.1289	0.7521	0.0711
$\hat{\sigma}^2_{climate}$	0.2057	0.0063	0.0968	0.0020
$\hat{\sigma}^2_{residual}$	0.0749	0.0055	0.1348	0.0016

^a Mean annual variance.

^b Sampling variation.

^c Coefficient of temporal process variation estimated as $\hat{\sigma}^2_{temporal}/\hat{\theta}$.

vival estimates were not strongly correlated between the study areas ($r = 0.47$, $P = 0.29$).

Estimates of $\hat{\sigma}^2_{\text{temporal}}$ in reproductive output were similar between the study areas (Table 4). Estimates of $\hat{\sigma}^2_{\text{temporal}}$ for reproductive output were large compared to those for survival, which was reflected in the coefficients of temporal variation for parameters. For Arizona, model ($R[a + P_Y]$) accounted for 73% of $\hat{\sigma}^2_{\text{temporal}}$ in reproductive output, whereas 55% of the total variability was due to sampling error. For New Mexico, model ($R[a + P_M]$) accounted for just over 42% of $\hat{\sigma}^2_{\text{temporal}}$ in reproductive output, and sampling variation was again about half of the total variation (47%). Annual estimates of reproductive output ($r = 0.893$, $P = 0.003$) and precipitation ($r = 0.881$, $P = 0.002$) were highly correlated between study areas.

DISCUSSION

Precipitation appeared to play a role in influencing most Spotted Owl demographic rates during our study. With the notable exception of survival in Arizona, the most likely models included a positive relationship between annual demographic parameters and precipitation. However, because there often were competing climate models, the precise mode of climate influence was probably more complex than our models depicted. There have been few studies regarding Spotted Owl population limitation, with most examining only the effect of climate on reproductive output. Wagner et al. (1996) and Zabel et al. (1996) found negative relationships between Northern Spotted Owl fecundity and precipitation during the nesting season, or during the previous winter. LaHaye et al. (1994) found a positive relationship between California Spotted Owl reproductive output and precipitation from the previous year. Franklin et al. (2000) found that Northern Spotted Owl survival and reproductive output were both negatively correlated with precipitation and positively correlated with temperature during the nesting period. The study by Franklin et al. (2000) used the same analytical methods we did, therefore, we expect our results to be statistically comparable to theirs.

Our results indicated precipitation was probably important in providing indirect benefits for Mexican Spotted Owls. Precipitation from the previous monsoon season, previous winter,

or previous year appeared in all the top reproductive output models, and in New Mexico survival models. This was contrary to Franklin et al.'s (2000) top models for the Northern Spotted Owl, but not surprising given that the Mexican Spotted Owl inhabits a more xeric landscape with a different climatic regime. Similar results have been reported for other avian species inhabiting relatively xeric environments (Newton 1998). In fact, some species that inhabit both xeric and mesic environments can show opposite responses to high precipitation patterns (e.g. California Quail [*Callipepla californica*]; Leopold 1977).

The growing season in the higher elevations of the southwestern United States is ~7 months (April–October), but primary productivity is often limited by variable precipitation (Dick-Peddie 1993). Precipitation during winter is important for growth of spring annuals whereas precipitation from the monsoon period is important for late summer annuals as well as Gambel oak acorn crops that ripen in the fall (Neilson and Wullstein 1983, Dick-Peddie 1993). The importance of Gambel oak mast for wildlife has been documented in the mountainous southwestern United States (e.g. Reynolds and Balda 1970, Patton 1975). In addition, other studies indicate annual variation in precipitation is important to birds in the Southwest. For example, Ligon (1978) hypothesized that Piñon Jay (*Gymnorhinus cyanocephalus*) reproduction in New Mexico was dependent on vegetative growth mediated by late summer precipitation and the subsequent flush of insects. Blancher and Robertson (1987) found a positive relationship between Western Kingbird (*Tyrannus verticalis*) reproduction, insect abundance, and precipitation from the previous year in Arizona.

Although it is not always clear if behavior, food, or some other factor is limiting small mammal populations (Krebs and Delong 1965, Healy 1967, Fordham 1971), here we address only food because other limiting factors would be difficult or impossible to evaluate without more information. Woodrats and white-footed mice, the primary prey for Spotted Owls in our study areas (Seamans and Gutiérrez 1999), eat a wide variety of foods, including forbs, grasses, insects, nuts, and seeds (Bailey 1931, Finley 1958, Goodwin and Hungerford 1979). These foods should respond positively to winter pre-

precipitation. In addition, ingestion of green vegetation may influence rodent reproduction (Reichman and Van De Graff 1975). Thus, germination and sprouting of annuals during the monsoon may extend the breeding season of small mammals in the Southwest, and may increase overwinter abundance of prey.

Ward and Block (1995) found the abundance of principal prey in habitats occupied by Mexican Spotted Owls to be temporally variable, and noted that in the Sacramento Mountains of southern New Mexico, a year of high reproductive output by Spotted Owls was accompanied by an irruption of white-footed mice, upon which the owls appeared to concentrate foraging. The cause of the temporal variability in prey abundance was unknown. With the exception of Ward and Block (1995), there have been few published studies regarding demographics of small mammals in the mountainous Southwest. Many researchers have found positive trends in small mammal abundance and precipitation in grassland and desert communities of the Southwest (e.g. Beatly 1969, Reynolds and Turkowski 1972, Brown and Heske 1990). Although those communities do not necessarily share common species with the more forested regions, they are subject to similar precipitation patterns. However, interaction of varying temperature and moisture regimes at different elevations in the Southwest may affect small mammal populations differently.

Spotted Owl annual reproduction was strongly correlated between the study areas, was subject to similar climatic patterns, and appeared to be influenced by precipitation. Arizona owls experienced higher average reproductive output than those in New Mexico. Although the top model with both study areas combined did not support a study-area effect, the study-area effect model was within ~ 2 AIC_c units and, therefore, not beyond consideration. The fact that Arizona received substantially more precipitation than New Mexico may partially explain that difference in reproductive output. However, there was still a notable amount of temporal variation unexplained by our best climate models. This indicates some other factors (such as unmodeled climate effects, prey, habitat, or some interaction between those factors) were unaccounted for in our models.

Survival rates were not very different between study areas, as evidenced by model selection results, but parameter estimates from the independent study area analyses indicated they were only weakly correlated. Although climate explained a high percentage of the temporal variation in Arizona survival rates, the best climate model was far down the list of potential models based on QAIC_c. However, temporal variability in Arizona survival was slightly greater than that of New Mexico. That may have indicated that Spotted Owls in Arizona had more difficulty in dealing with environmental stochasticity. Alternatively, if poor environmental conditions can be ameliorated by habitat as suggested by Franklin et al. (2000), habitat could account for some of the observed differences between study areas. New Mexico has a higher density of owls and a higher proportion of mature mixed-conifer habitat, which is generally selected by owls if available, in both study areas (Peery et al. 1999, May 2000). In addition, the New Mexico study area experienced less habitat perturbation in the form of logging and firewood cutting in recent years than the Arizona study area.

Northern Spotted Owls are believed to follow a "bet-hedging" life-history strategy where reproduction exhibits high temporal variation whereas adult survival is high with low temporal variation (Franklin et al. 2000). Our components of variance results for both study areas support this view, with estimates of temporal variability in reproductive output much higher than those for survival. Although the hypothesized mechanism for the influence of precipitation on survival and reproductive output was different than that found by Franklin et al. (2000), it is interesting that the life-history strategies remained similar between the subspecies. It appears precipitation may have been responsible for much of the temporal variability observed in reproductive output, and to a lesser extent survival. Thus, environmental stochasticity may play a large role in population limitation and is probably responsible for part of the decline observed in those populations during the period of study (Seamans et al. 1999). However, the dynamics of those populations are undoubtedly more complex, as expressed by percentage of variation unexplained by our climate models. In addition, our results should not be interpreted as cause and effect

because our study was observational, not experimental. An experimental study on a meaningful scale would be difficult to conduct on Spotted Owl population dynamics. We feel that repetition of similar observational studies as we have done here supplies the next best avenue for valid inference. Therefore, extended research on those two populations and others in the Southwest is needed to validate our results and to elucidate the role of other potential limiting factors.

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