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Population Ecology

Demography of Mexican Spotted Owls in the Sacramento Mountains, New Mexico

JOSEPH L. GANEY,[1] *U.S. Forest Service, Rocky Mountain Research Station, 2500 S. Pine Knoll, Flagstaff, AZ, USA*
GARY C. WHITE, *Department of Fish, Wildlife, and Conservation Biology, Colorado State University, Fort Collins, CO, USA*
JAMES P. WARD JR.,[2] *U.S. Forest Service, Rocky Mountain Research Station, 2500 S. Pine Knoll, Flagstaff, AZ, USA*
SEAN C. KYLE,[3] *U.S. Forest Service, Rocky Mountain Research Station, 2500 S. Pine Knoll, Flagstaff, AZ, USA*
DARRELL L. APPRILL,[4] *U.S. Forest Service, Rocky Mountain Research Station, 2500 S. Pine Knoll, Flagstaff, AZ, USA*
TODD A. RAWLINSON,[5] *U.S. Forest Service, Rocky Mountain Research Station, 2500 S. Pine Knoll, Flagstaff, AZ, USA*
RYAN S. JONNES,[4] *U.S. Forest Service, Rocky Mountain Research Station, 2500 S. Pine Knoll, Flagstaff, AZ, USA*

ABSTRACT Information on population dynamics is key to gauging the status of threatened or endangered species. We monitored demography of a population of threatened Mexican spotted owls (*Strix occidentalis lucida*) in the Sacramento Mountains, New Mexico from 2003 to 2011. We estimated reproductive output for territorial pairs of owls; used mark-recapture methodology and Pradel's reparameterized Jolly-Seber models to estimate annual apparent survival rates, recapture rates, recruitment rates, and annual rate of population change (λ_{RJS}) for 2005–2009; and used estimates of λ_{RJS} to assess short-term population viability. Reproductive output was highly variable for 2004–2011, whereas annual apparent survival and recapture rates were less variable among years. Annual rates of population change exceeded 1.0 for both sexes from 2005 to 2009, and empirical observations of numbers of territorial owls supported the model-based trend estimate. Abundance of territorial owls was strongly related to reproduction within the study area, suggesting that population change was driven largely by internal processes. Population viability analyses suggested that population growth was likely to continue in the short term if current conditions persist. The positive growth rates observed in our study populations are encouraging, and may indicate that current recommendations for recovering this owl are succeeding. However, our estimates of λ_{RJS} covered a very short time period, given both the potential lifespan of Mexican spotted owls and the extent of temporal variability in weather typical of the southwestern United States. Longer studies of owl demography than we present will be required to understand long-term population trends, and such studies should extend across the range of the subspecies. Published 2013. This article is a U.S. Government work and is in the public domain in the USA.

KEY WORDS demography, fecundity, Mexican spotted owl, population trend, population viability, Pradel model, recruitment, reparameterized Jolly-Seber model, survival, vital rates.

The Mexican spotted owl (*Strix occidentalis lucida*), 1 of 3 recognized subspecies of spotted owls (American Ornithologists Union 1957), inhabits canyonlands and montane forests throughout the southwestern United States and Mexico (Gutiérrez et al. 1995, Ward et al. 1995). This subspecies frequently occupies forests featuring large trees and late seral characteristics (Ganey and Dick 1995, U.S. Department of the Interior Fish and Wildlife Service [USDI FWS] 2012), and was listed as threatened in 1993, primarily because of concerns over loss of older, uneven-aged forest habitat to even-aged timber harvest (USDI FWS 1993).

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[1]*E-mail: jganey@fs.fed.us*
[2]*Present address: U.S. Fish and Wildlife Service, National Wildlife Refuge System, Inventory and Monitoring Branch, Fort Collins, CO, USA*
[3]*Present address: Texas Parks and Wildlife Department, Lubbock, TX, USA*
[4]*Present address: U.S. Forest Service, Lincoln National Forest, Cloudcroft, NM, USA*
[5]*Present address: U. S. Forest Service, Lincoln National Forest, Ruidoso, NM, USA*

Annual rates of population change are of interest in conserving any threatened species. Information on whether numbers are increasing, decreasing, or remaining stable for these species can inform managers as to whether current management practices appear sufficient, or whether additional efforts or modifications to management recommendations are required. Despite this, no current data are available on trends in populations of Mexican spotted owls (USDI FWS 2012). Studies conducted from 1991 to 2000 indicated that populations of Mexican spotted owls in 8 separate study areas all were declining at rates ranging from 4% to 30% (Seamans et al. 1999, Stacey and Peery 2002, see also Ganey et al. 2005, Stacey 2010), but current trends in these and other areas are unknown. We studied demography of Mexican spotted owls from 2004 to 2011 in the Sacramento Mountains, New Mexico. We estimated annual apparent survival, recapture probabilities, reproductive

output, and annual rates of population change (λ) for the study population. We also used the resulting estimates of λ to simulate short-term population viability of the study population. Our study provides information for evaluating population dynamics in a geographically isolated mountain range containing Mexican spotted owls, as well as the only recent information on population trend within the range of this subspecies.

STUDY AREA

Our study area included approximately 50,000 ha in the Sacramento Mountains, a montane island surrounded by a matrix of desert and semi-desert habitat in south-central New Mexico. The study area encompassed much of the central portion of the Sacramento Ranger District, Lincoln National Forest, including the village of Cloudcroft, New Mexico. The terrain consisted of heavily forested montane slopes and minor tributaries, with interspersed meadows in the larger valley bottoms. Elevation ranged from 2,000 m to 2,800 m. The predominant forest type was mixed-conifer, singularly or co-dominated by white fir (*Abies concolor*) and Douglas-fir (*Pseudotsuga menziesii*). Other common tree species included southwestern white pine (*Pinus strobiformis*), ponderosa pine (*P. ponderosa*), and quaking aspen (*Populus tremuloides*) (Kaufmann et al. 1998, Ward 2001). Precipitation averaged 65 cm/year at Cloudcroft, New Mexico (elevation 2,652 m) with summer thunderstorms providing more than 60% of annual precipitation and most of the remainder occurring as winter snowfall (Kaufmann et al. 1998).

METHODS

Data Collection

We used conventional protocols for studying spotted owl demography (Franklin et al. 1996, see also Forsman 1983). The approach entailed locating owls with call-surveys, documenting the number of young produced each year, marking or resighting individuals, and recording sex and age. We collected all data during the owl's breeding season, 1 March through 30 August, from 2003 to 2011. We used nocturnal calling surveys at 1,206 fixed call stations distributed throughout the study area to detect and document general locations of owls (Forsman 1983). Once we located general areas occupied by an individual or pair of owls, we used daytime surveys to find them at a roost or nest site.

We assessed reproductive status of located owls by feeding them live mice and observing their behavior (Forsman 1983). Breeding owls typically carried mice to the nest or to fledged young near the nest, whereas nonbreeding owls typically ate, cached, or ignored mice. We visited nesting owls between early June and mid-July to locate and count fledged young using the same mouse-baiting technique. Non-nesting or zero young fledged was inferred for individuals that ate or cached 4 mice on a single occasion without taking one to a nest or young during a daytime visit after 15 May (Seamans et al. 1999). We visited all owls located at least twice during each year to either confirm non-nesting status or determine the number of young fledged, with the second visit coming after 15 June.

We captured territorial adult and subadult owls using snare poles, baited mist nests, or by hand (Forsman 1983). We equipped all owls captured with a numbered United States Fish and Wildlife Service (USFWS) 7B aluminum lock-on band on 1 leg, and a plastic color band on the opposite leg (Forsman et al. 1996). Most bands used were solid color with a vinyl tab of a second color glued and riveted to the band. In the later years of the study, we added some bi-colored bands with easily-recognized patterns to increase the number of unique band combinations available. Rates of loss of color bands were demonstrated to be nearly 0 in extensive studies of northern spotted owls (*S. o. caurina*; Franklin et al. 1996), and we had no cases of band loss during the current study. We also marked some owls with backpack radio transmitters in 2004 and 2005.

We resighted marked owls during territory visits in subsequent years. Observers did not examine records of extant color band combinations until after visiting a site and recording their observations of band color. If field observations did not coincide with bands previously present at a site, multiple observers revisited the site to verify band colors. In the few cases in which we were unable to verify band colors in the field, we recaptured owls, identified individuals based on the USFWS band number, and re-banded them with a new color band.

We determined sexes of spotted owls based on calls and behavior (Franklin et al. 1996). Calls of males are lower in pitch than those of females, and males do not incubate or brood the young (Forsman et al. 1984, Ganey 1990). We assigned owls to 2 age classes based on plumage characteristics. Retrices of subadult (<26 months old) owls had triangular white tips, whereas the retrices of adult owls (≥26 months old) had mottled and rounded tips (Forsman 1981, Moen et al. 1991). We captured some owls while they were molting the tail feathers used to assign owls to age class. We recorded age as unknown for these owls, but treated them as adults in demographic analyses. Spotted owls typically completely molt the tail feathers every other year beginning at age 26 months (Forsman 1981), suggesting that birds captured with missing tail feathers likely were either adults undergoing their biannual molt or subadults molting into adult plumage.

Estimating Demographic Rates

We recorded reproductive output for each territory monitored as number of young fledged (0–3; Franklin et al. 1996), and summarized annual fecundity as mean number of female young fledged/territory monitored, assuming equal sex ratios among juvenile owls. We estimated apparent survival (φ), recapture probability (p; in this study, recapture probability equates to the probability of resighting banded birds), seniority probability (γ, the probability that an owl present just before time i was already present just after time $i-1$; Pradel 1996), and annual rate of population change (λ) jointly using the capture histories of color-banded owls and

the reparameterized Jolly-Seber model introduced by Pradel (1996) and implemented in program MARK (White and Burnham 1999). Hereafter, we refer to the annual rate of population change as λ_{RJS} to indicate that it was estimated using the reparameterized Jolly-Seber model. This model includes all components of population change, including death, emigration from the study area, and immigration into the study area as well as recruitment from within the study area. Consequently, it produces realized estimates of λ rather than the theoretical λ of Leslie matrix models used in many earlier analyses of spotted owl demography (Franklin et al. 2004, Anthony et al. 2006, Forsman et al. 2011). The model assumes that owls are not gained or lost because of changes in study area size. This assumption was met for the years for which we estimated λ_{RJS} and the unique owl territories included in analyses (see Results).

We first ran a balanced set of 192 models estimating φ, p, and γ using individual covariates, including owl sex for φ and p, age for φ, whether an owl was radio-marked for φ, an estimate of overall annual reproduction (to index overall reproductive effort, after Forsman et al. 2011) for φ, and time-specific effects for φ, p, and γ. We used the estimate of overall annual reproduction rather than territory-specific data because at least a few territories had missing reproduction data in all years.

We ranked models using Akaike's Information Criterion corrected for small sample size (AIC_c; Hurvich and Tsai 1989, Burnham and Anderson 2002), and estimated variable weights for all covariates using the full model set. Variable weights are informative in this context (Doherty et al. 2012) because the balanced model set results in all covariates being included in the same number of models. Variable weights suggested strong effects of age, sex, radio, and time effects on φ, p, and γ, and a weak effect of reproduction on φ (see Results).

To estimate λ_{RJS} as a derived parameter, we ran a set of 126 models using 2 groups (males and females) with all combinations of fully time-specific and additive time models for φ, p, and γ. We modeled males and females separately because of the strong evidence for sex-specific survival rates in our earlier analysis (see Results). We did not include any of the other earlier individual covariates because λ_{RJS} is a population-level parameter, and therefore is not estimable for models that incorporate individual covariates. We again ranked models based on AIC_c. We estimated λ_t (annual rate of population change over each year t) only for 2005–2009, because the first 2 estimates in the time series generally are biased high (Forsman et al. 2011) and the first and last estimates are not estimable in a time-specific model for p.

We used both model averaging (Burnham and Anderson 2002) and the full time-specific model to estimate time-specific φ and λ_{RJS} separately for female and male owls. Model averaging has the advantage of incorporating uncertainty when multiple models are competing (Burnham and Anderson 2002) and produces a more stable set of parameter estimates (Doherty et al. 2012). The full time-specific model accounts for all time and sex effects in each of the parameters estimated; therefore, this model may produce less biased estimates of process variance than model averaging (White et al. 2001). Consequently, we generated estimates using both approaches for comparative purposes. We used the methods described in Burnham and White (2002) and directly input the model-averaged estimates and variance-covariance matrix to obtain estimates of process variance, using the variance components routine in MARK.

The Pradel model allows for the decomposition of annual estimates of λ_{RJS} (λ_t) into 2 components representing annual survival (φ_t) and annual recruitment (f_t, Pradel 1996):

$$\lambda_t = \varphi_t + f_t$$

Consequently, we estimated annual recruitment as:

$$f_t = \lambda_t - \varphi_t$$

Recruitment refers to the number of new animals in the study population at time t relative to the number of animals present at time $t-1$. Recruitment includes both individuals produced in the study area who survived to enter the territorial population and immigration of owls from outside the study area.

As a check on model-based trend estimates, we summarized observed data on number of territorial owls observed (N_{owls}) and number of occupied territories across years. We used linear regression to evaluate the relationship between these parameters and year, estimated the observed rate of population change (r) as the slope of the line resulting from regressing $\log_e$ of N_{owls} against year, and estimated λ as $1+r$ (with the SE approximated by the SE of r; after Seamans et al. 1999).

Because our estimate of recruitment did not distinguish between owls produced within our study population and new owls immigrating into the population, we used linear regression to explore potential relationships between annual estimates of abundance of territorial owls and estimates of young produced within the study area in the previous year or 2 (after Seamans et al. 1999). Strong relationships provide evidence that much of the observed recruitment came from owls produced within the study area. We used total abundance of territorial owls and total young fledged in these analyses rather than female owls and fecundity (e.g., Seamans et al. 1999) because we were interested in the entire territorial population, and because this did not require us to make any assumptions about sex ratios of young fledged.

Estimating Population Viability

We estimated population viability for up to 10 years using results from the models used to estimate λ_{RJS} and the simulation approach of White et al. (2002). We used the process variance of $\log(\lambda_{RJS})$ and the sums of $\log(\lambda_{RJS})$ in the simulations rather than process variance of λ_{RJS} and products of λ_{RJS} because 1) estimates of $\log(\lambda_{RJS})$ are approximately normally distributed, and 2) given the more symmetrical distribution of $\log(\lambda_{RJS})$ relative to λ_{RJS}, the estimated process variance derived using this parameter likely is more stable than estimates derived using λ_{RJS}.

We parameterized distributions for each sex based on the log of the sex-specific mean λ_{RJS} and associated process

standard deviation from both model-averaged estimates and from the full time model. We then conducted 1,000 simulations of 10-year duration for each sex, drawing a random value each year from a normal distribution with the appropriate sex-specific mean and standard deviation. For each simulation, we summed the $\log(\lambda_{RJS})$ values for 5- and 10-year periods, back-converted these sums to λ_{RJS}, and computed the sex-specific mean annual rate of change and associated standard deviation for 5- and 10-year periods across the 1,000 simulations. We also used the results of the 1,000 simulations to estimate the probability that the population would change less than a specific value over the 5- and 10-year periods. We restricted these analyses to short time periods because they required the assumption that ecological conditions relevant to owl vital rates remain unchanged over the modeled time periods relative to conditions during the study. This assumption is unrealistic even for short time periods and becomes increasingly harder to defend over longer time periods. Thus, although the results should provide a useful heuristic view of short-term viability, we were unwilling to extend the analyses to longer time periods.

RESULTS

We captured and marked 222 territorial owls representing 78 unique owl territories. Some captured owls occupied territories that were not consistently surveyed over all years or that were located outside the primary study area. Because the Pradel model assumes that animals are not added because of changes in survey area, we restricted demographic analyses to 204 owls representing 69 unique territories that were within the area surveyed consistently during the study. Owls included in analyses included 99 females and 105 males, and 122 adults, 74 subadults, and 8 unknown aged owls as classified when captured.

Initial exploration of the effects of 8 individual covariates indicated that several affected survival and recapture rates. Variable weights demonstrated time effects on all model parameters (weights for φ and $p \geq 0.99$), sex effects on both φ (weight = 0.68) and p (weight = 0.51), and radio (weight = 1.00) and age effects (weight = 0.98) on φ (Table 1). Radios had a negative effect on apparent survival (minimum AIC_c model, $\hat{\beta} = -1.423 \pm 0.246$ [SE], odds ratio = 0.241, 95% CI 0.149–0.390). Age also was an influential predictor of apparent survival ($\hat{\beta}_{subadult} = -1.258 \pm 0.402$, odds ratio = 0.284, 95% CI = 0.129–0.625). Apparent survival was higher for females than for males, and recapture probabilities were lower for females (Table 2). The index of annual reproduction was not a strong predictor of apparent survival (Table 1).

Table 1. Variable weights computed from a balanced set of 192 models estimating apparent survival probability (φ), resight probability (p), and seniority probability (γ) of male and female Mexican spotted owls in the Sacramento Mountains, New Mexico, 2004–2009. Because φ (reproduction) is a submodel of the time-specific model $\varphi(t)$, these 2 variables cannot be included in the same model.

Variable	Weight
$\varphi(t)$	0.99
φ(radio)	1.00
φ(age)	0.98
φ(sex)	0.68
φ(reproduction)	0.01
$p(t)$	0.93
p(sex)	0.51
$\gamma(t)$	0.96

Model-averaged estimates of mean λ_{RJS}, mean $\log(\lambda_{RJS})$, and process standard deviations for both sexes were very similar to estimates from the full time-specific model {φ (sex × t) p(sex × t) γ(sex × t)}. Therefore, we report only the model-averaged estimates here. Estimated values for λ_{RJS} indicated that populations were increasing from 2005 to 2009 for both sexes (Table 3). The population viability analysis (Table 4) demonstrated that, given estimates derived from 2005 to 2009, both populations likely would continue to grow over the short term. For the 1,000 simulations summarized over 5- and 10-year periods, only males showed any probability of declining, and that probability was small and restricted to the 5-year simulation.

Annual recruitment rates for females and males were highly correlated (Pearson's $r = 0.995$, $P < 0.001$, $n = 5$) and highly variable during 2005–2009 (Table 5). Fecundity for 2004–2011 also was variable among years (Fig. 1).

Empirical observations of N_{owls} within the consistently surveyed study area supported the positive model-based population trend (Fig. 2), with estimated λ_{Nowls} (1.066 ± 0.014 [SE]) similar to the model-based estimates ($\lambda = 1.088$ and 1.073 for female and male owls, respectively; Table 3). Observations of N_{owls} ranged from a low of 89 in 2006 to a high of 128 in 2010. The observed change in owl abundance was driven by re-colonization of vacant territories ($n = 8$ historical territories re-colonized during the study), colonization of new territories ($n = 7$ new territories colonized during the study), and recruitment of mates by single owls (the proportion of occupied territories containing mated pairs increased from a low of 77.4% in 2006 to a high of 94.6% in 2010). The number of occupied territories also increased during the study, ranging from a low of 48 in 2006 to a high of 65 in 2010 and 2011.

Abundance of territorial owls was significantly related to the number of young fledged/territory in recent years. The strongest relationship was with total young fledged/territory over the previous 2 years (Fig. 3). Young fledged/territory during the previous year also explained a significant amount of the annual variation in abundance, however ($\hat{\beta} = 49.8$, SE = 10.7, $P = 0.010$, $r^2 = 0.844$, $n = 6$ years included).

DISCUSSION

Seamans et al. (1999:750) described Mexican spotted owls as having a life history strategy "characterized by high adult survival rates with low annual variation, coupled with low fecundity rates that exhibit high annual variation." Our results largely corroborate that description. Annual survival rates for both males and females were relatively high and varied little among years, whereas fecundity varied considerably among years (Fig. 1). Both our study and Seamans et al. (1999) found that abundance of territorial owls was

Table 2. Model-averaged estimates of apparent annual survival and annual recapture probability, with associated standard errors and 95% confidence limits based on a logit transformation, for male and female Mexican spotted owls in the Sacramento Mountains, New Mexico, 2004–2009. Each year (t) represents an approximate annual period from mid-May$_t$ to mid-May$_{t+1}$.

		Apparent survival			Recapture probability		
Sex	Year$_t$	Estimate	SE	95% CI	Estimate	SE	95% CI
Female	2004	0.736	0.057	0.610–0.833	0.801	0.089	0.575–0.923
	2005	0.897	0.040	0.789–0.953	0.895	0.047	0.762–0.958
	2006	0.821	0.048	0.708–0.897	0.894	0.042	0.780–0.952
	2007	0.979	0.020	0.874–0.997	0.886	0.043	0.772–0.947
	2008	0.922	0.031	0.834–0.965	0.938	0.031	0.841–0.977
	2009	0.882	0.034	0.797–0.934	0.940	0.030	0.847–0.978
Male	2004	0.699	0.059	0.573–0.801	0.828	0.088	0.591–0.941
	2005	0.877	0.045	0.758–0.942	0.912	0.040	0.796–0.965
	2006	0.791	0.053	0.669–0.876	0.910	0.040	0.795–0.963
	2007	0.977	0.022	0.863–0.997	0.904	0.039	0.795–0.958
	2008	0.906	0.036	0.808–0.957	0.948	0.026	0.864–0.982
	2009	0.863	0.039	0.769–0.922	0.950	0.026	0.867–0.982

significantly related to reproductive output over the previous 2 years, despite the fact that abundance was increasing in our study and decreasing in Seamans et al. (1999). This suggests that populations of Mexican spotted owls can either increase or decrease quickly, in response to changes in reproduction.

Populations of both female and male owls in our study area were increasing during the period covered by our estimates (2005–2009), as evidenced both by model-based results and empirical observations. The strong relationship with reproduction (discussed above) suggests that much of the observed increase in abundance in this study was due to owls produced within the study area, rather than immigration of owls from outside the study area.

Population viability analyses indicated that populations of either male or female owls would not likely decline over the next 5–10 years within our study area, assuming that environmental conditions remained similar to conditions experienced during the study. These population viability analyses likely were biased high, however, because they did not incorporate density dependence. In reality, a growing population should saturate the available habitat at some point, putting an upper limit on population growth. Thus, we view the positive population trends observed during the study period as robust, but caution that the viability analysis may be overly optimistic. We also view the assumption of unchanging environmental conditions as unrealistic.

Our results contrast sharply with studies of Mexican spotted owls conducted during the 1990s, all of which showed declining populations. Annual rates of decline in 2 demography studies ranged from almost 20%/year in a study that included 4 mountain ranges (Black Range and Magdalena, San Mateo, and Zuni Mountains) in New Mexico (Stacey and Peery 2002, Stacey 2010), to approximately 14% on the Coconino Plateau, north-central Arizona, and slightly >10%/year in the Tularosa Mountains, New Mexico (Seamans et al. 1999). Similarly, Ganey et al. (2005) estimated λ for 2 small study areas in the Sacramento Mountains from 1992 through 1994, using data from radio-marked owls and the methods of Pulliam (1988). Estimates of λ indicated an annual decline of 30% in one study area (referred to as xeric) and 4% in the second (mesic, this area was entirely contained within our current study area).

Reasons for the differences among studies are unknown. Analytical techniques have improved since earlier studies were conducted, and the reparameterized Jolly-Seber model used in this study is highly preferred over the stage-projection matrix models used in previous demography

Table 3. Model-averaged parameter estimates for population rate of change based on Pradel's reparameterized Jolly-Seber models (λ_{RJS}) of male and female Mexican spotted owls in the Sacramento Mountains, New Mexico, 2005–2009.

		Owl sex	
Parameter	Estimate	Female	Male
λ_{RJS}	$\overline{\lambda}_{RJS}$	1.088	1.073
	SE	0.037	0.040
	Process SD	0.056	0.065
	LCB[a] process SD	0.000	0.000
	UCB[a] process SD	0.247	0.272
$\log(\lambda_{RJS})$	$\log(\overline{\lambda}RJS)$	0.085	0.072
	SE	0.033	0.037
	Process SD	0.051	0.060
	LCB[a] process SD	0.000	0.000
	UCB[a] process SD	0.230	0.258

[a] LCB and UCB are lower and upper bounds of the 95% confidence interval, respectively.

Table 4. Estimates of population change (λ) and probability of specified magnitude of population change, Pr(λ), for male and female Mexican spotted owls in the Sacramento Mountains, New Mexico, over 5- and 10-year periods. We conducted 1,000 simulations per sex, with annual values randomly selected from a normal distribution parameterized with the model-averaged mean $\log(\lambda_{RJS})$ and associated process standard deviation.

	Female owls		Male owls	
Estimate	5 years	10 years	5 years	10 years
Mean change	1.548	2.401	1.437	2.073
SD	0.181	0.389	0.194	0.398
$Pr(\lambda < 1.0)$	0.000	0.000	0.003	0.000
$Pr(\lambda < 1.1)$	0.002	0.000	0.025	0.001
$Pr(\lambda < 1.2)$	0.015	0.000	0.104	0.003
$Pr(\lambda < 1.3)$	0.073	0.000	0.246	0.008
$Pr(\lambda < 1.4)$	0.217	0.000	0.445	0.028
$Pr(\lambda < 1.5)$	0.409	0.000	0.652	0.056
$Pr(\lambda < 1.6)$	0.641	0.005	0.799	0.109

Table 5. Mean (and SE) estimates of annual recruitment of male and female Mexican spotted owls in the Sacramento Mountains, New Mexico, 2005–2009. We estimated recruitment based on model-averaged estimates of annual population rate of change and apparent survival from the Pradel (1996) model.

	Recruitment[a]			
	Females		Males	
Year	Estimate	SE	Estimate	SE
2005	0.265	0.075	0.282	0.081
2006	0.086	0.086	0.076	0.093
2007	0.307	0.059	0.340	0.062
2008	0.195	0.078	0.185	0.083
2009	0.233	0.079	0.232	0.085

[a] Recruitment is the number of new animals in the population at time t relative to animals in the population at time $t-1$.

studies (Franklin et al. 2004, Boyce et al. 2005, Anthony et al. 2006, Forsman et al. 2011), or the relatively crude method used by Ganey et al. (2005). The use of different modeling techniques is not sufficient to explain differences in trend estimates between the demography studies, however, because empirical data supported model-based trends in all studies. For example, Seamans et al. (1999; Fig. 4) documented declines in abundance of territorial owls, and Stacey and Peery (2002) and Stacey (2010) documented declines in numbers of territories occupied and owl abundance, as well as extirpation of owls from 2 of their study areas. Thus, empirical data from both of these studies supported the declining model-based population trend, just as empirical data in our study supported the positive model-based trend.

The comparative results thus suggest that differences in trend among studies were due to other factors, such as differences in habitat composition and quality, management history, or environmental conditions such as weather patterns or prey density (e.g., Seamans et al. 2002, Peery et al. 2011) between the previous studies and our study.

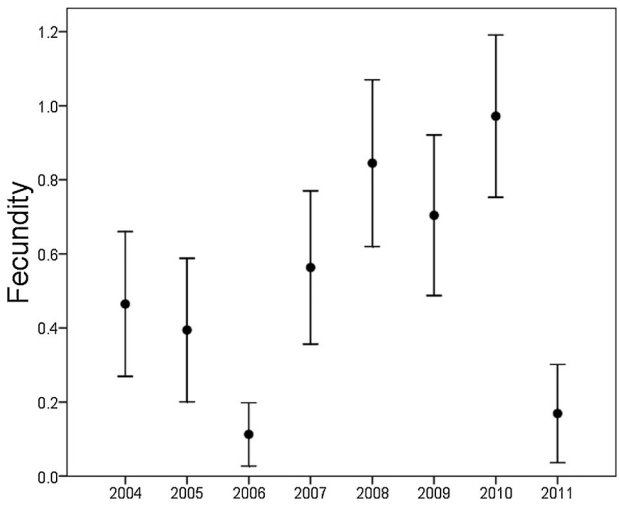

Figure 1. Fecundity (number of female young fledged per Mexican spotted owl territory monitored, mean ± 95% CI) in the Sacramento Mountains, New Mexico, 2004–2011. We estimated fecundity from counts of young assuming equal sex ratios for juvenile owls.

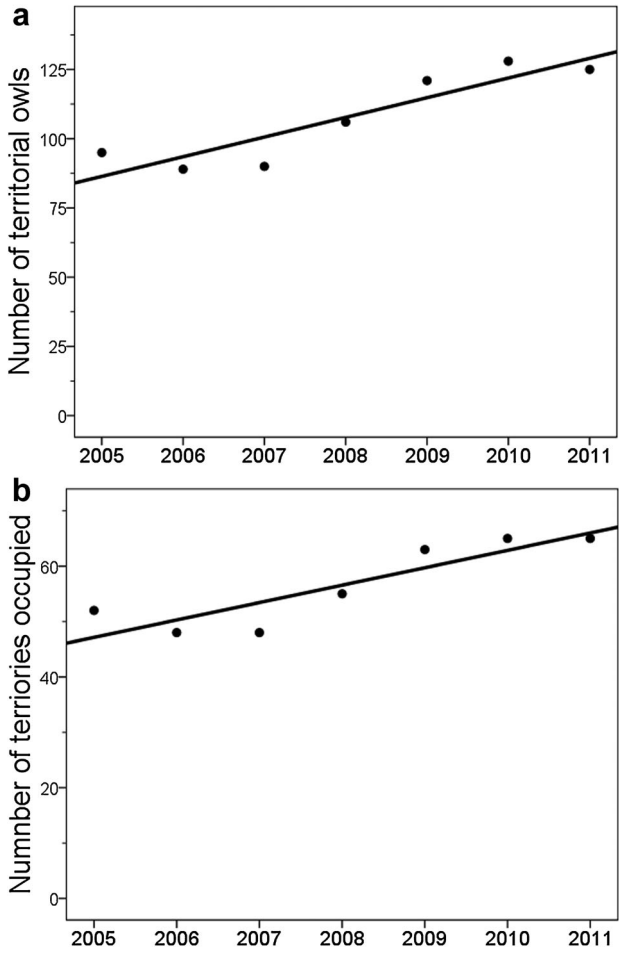

Figure 2. Number of territorial Mexican spotted owls observed (top) and occupied territories (bottom) within a consistently surveyed demography study area in the Sacramento Mountains, New Mexico, 2005–2011. We also show least-squares fit lines (number of territorial owls: $\hat{\beta} = 7.1 \pm 1.5$ [SE], $r^2 = 0.824$, $P = 0.005$; number of occupied territories: $\hat{\beta} = 3.1 \pm 0.7$ [SE], $r^2 = 0.782$, $P = 0.008$).

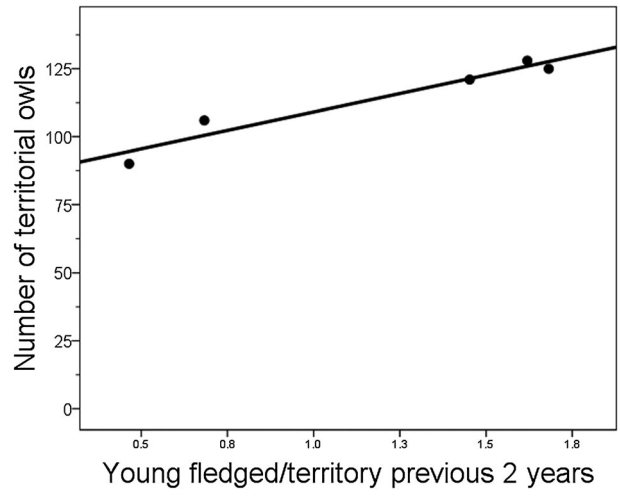

Figure 3. Relationship between annual abundance of territorial Mexican spotted owls and total young fledged/territory during the previous 2 years in the Sacramento Mountains, New Mexico ($\hat{\beta} = 27.2 \pm 4.0$ [SE], $r^2 = 0.938$, $P = 0.007$). Abundance estimates cover the years from 2007 through 2011, whereas estimates of young fledged cover the years from 2005 to 2010.

Although speculating on potential reasons for the observed differences is tempting, in fact we do not know what drove these differences. The fact that populations in widely distributed study areas all appeared to be declining during the 1990s indicates the influence of regional phenomena such as broad-scale weather patterns (Seamans et al. 1999, 2002, Peery et al. 2011).

We also do not know how meaningful the differences in population trend among studies are, because they simply may reflect variable populations studied in different phases of their population cycle. That is, we do not know whether the declines observed in earlier studies in other areas persisted into the years covered by our study, and we have no estimate of population trend within our study area during the period covered by other studies, with the exception of the period from 1992 through 1994. Our study population was not likely growing at the current rate for very long because that would require that the population was very small in earlier years. Our study period likely corresponded to a period of favorable environmental conditions for Mexican spotted owls, and longer studies probably would reveal periods of both positive and negative population growth in this population.

The Mexican spotted owl is a long-lived species living in a highly variable environment. All studies to date of Mexican spotted owl demography have focused on relatively short time periods in a few study areas of limited size. The time periods covered by these studies are inadequate to fully understand the extent of temporal variability in populations of this owl (Seamans et al. 1999, 2002), and the limited study areas do not adequately sample the pronounced spatial variation present within the range of the owl (e.g., Ganey et al. 2004, USDI FWS 2012).

Our study was of short duration relative to both owl lifespans and the temporal scale at which forest systems respond to environmental variation. Temporal variation in environmental conditions is large in southwestern forests, and future conditions are unlikely to mirror those experienced during our study. Climate in the southwestern United States is predicted to change rapidly in the future, with most climate models predicting that this area will become both warmer and drier (Seager et al. 2007). These changes may negatively influence owl vital rates (Seamans et al. 2002) and increase the probability of extinction in these populations (Peery et al. 2011). Consequently, although we view our results as cause for cautious optimism, we also recognize that it may not predict future trends in our study area, or current or future trends in other portions of the range of the Mexican spotted owl.

MANAGEMENT IMPLICATIONS

Studies of Mexican spotted owl demography have produced valuable data informing managers on owl vital rates, life history strategy, and the influence of environmental factors on vital rates (Seamans et al. 1999, 2002; Stacey and Peery 2002; Stacey 2010; this study). These studies are essentially snapshots in time and space, however, and are inadequate to understand long-term population status or trend because of their limited duration and spatial scope. More geographically widespread studies, over longer time periods, throughout the range of the subspecies will be required to better understand population dynamics of Mexican spotted owls and how those dynamics are influenced by environmental variation. Range-wide population monitoring will be required to estimate population trend and determine whether or not this subspecies is recovering. In the meantime, the positive population growth rates suggest that current management within the study area, guided by recommendations in USDI FWS (2012, see also USDI FWS 1995), may be benign with respect to Mexican spotted owls, and that implementation of those recommendations should continue.

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