

BREEDING DISPERSAL OF MEXICAN SPOTTED OWLS IN THE SACRAMENTO MOUNTAINS, NEW MEXICO

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ABSTRACT.—Dispersal is a key process influencing population dynamics and gene flow in species. Despite this, little is known about breeding dispersal in threatened Mexican Spotted Owls (*Strix occidentalis lucida*), here defined as movement of a non-juvenile owl between territories where it had the opportunity to breed. We observed 28 cases of breeding dispersal during a study of color-banded Mexican Spotted Owls in the Sacramento Mountains, New Mexico, 2003–2011. This represented 4.9% of total opportunities to disperse ($n = 575$ observed occasions, range = 0–9.0% of owls dispersing per yr). Breeding dispersal probability was greater for single owls and paired owls whose mate disappeared or moved than for paired owls whose mate remained in the original territory, greater for subadult than for adult owls, and greater for owls that failed to reproduce the year prior to dispersing than for owls that reproduced successfully. There was some evidence that dispersal probability was greater for female owls and that females dispersed greater distances than males, but dispersal distances generally were small for both sexes of owls (mean distance = 5.1 and 3.6 km for females and males, respectively). All dispersing owls were paired the first year they were observed in their new territory. Breeding dispersal appeared to occur regularly but at relatively low levels in this population, and dispersal probability appeared to be associated with owl social status, reproductive status, and age prior to dispersal. Because most dispersing owls either were unpaired or lost their mate, and because most failed to reproduce the year prior to dispersal, these owls generally were able to improve their social status and reproductive success by dispersing. Received 9 January 2014. Accepted 5 April 2014.

Key words: banding, dispersal distance, dispersal probability, mate fidelity, Mexican Spotted Owl, population dynamics.

Dispersal is a key process influencing population dynamics and gene flow in species (Baker 1978, Greenwood 1980, Greenwood and Harvey 1982). Two forms of dispersal have been observed in Spotted Owls (*Strix occidentalis*). Natal dispersal involves the movement of individuals from their birth site to a location where they reproduce or would have reproduced if they survived (Howard 1960). Breeding dispersal involves the movement of non-juvenile owls between territories where they had an opportunity to breed, regardless of whether or not they actually reproduced there (Daniels and Walters 2000). Breeding dispersal thus follows natal dispersal chronologically, and can occur multiple times during the life of an individual.

Both forms of dispersal have been studied in the northern (*S. o. caurina*) and California (*S. o. occidentalis*) subspecies of the Spotted Owl (Gutiérrez et al. 1985, 2011; Miller 1989; LaHaye et al. 2001; Forsman et al. 2002; Blakesley et al. 2006; Seamans and Gutiérrez 2007), and limited information is available on natal dispersal in the Mexican subspecies (*S. o. lucida*; Duncan and Speich 1995, Arsenault et al. 1997, Ganey et al. 1998, Willey and van Riper 2000). In contrast, almost nothing is known regarding breeding dispersal in Mexican Spotted Owls (Ganey and Jenness 2013).

Mexican Spotted Owls are widely but patchily distributed throughout the southwestern United States and Mexico (Gutiérrez et al. 1995, Ward et al. 1995, U.S. Fish and Wildlife Service 2012). They are found primarily in rocky canyonlands or mountains and canyon systems featuring mixed-conifer or pine-oak (*Pinus* spp. – *Quercus* spp.) forest, and their fragmented distribution reflects the availability of such areas (Ganey and Dick 1995, Ward et al. 1995, U.S. Fish and Wildlife Service 2012). This subspecies was listed as a threatened species in 1993 (U.S. Fish and Wildlife Service 1993), leading to increased interest in population ecology of Mexican Spotted Owls.

Here, we describe breeding dispersal that we observed among a color-banded population of

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Mexican Spotted Owls in the Sacramento Mountains, New Mexico. Our primary objectives were to (1) identify factors associated with the probability of breeding dispersal by Mexican Spotted Owls, (2) identify factors associated with breeding dispersal distance in Mexican Spotted Owls, and (3) briefly summarize characteristics of observed breeding dispersal events. Based on previous work in other subspecies of Spotted Owls (LaHaye et al. 2001, Forsman et al. 2002, Blakesley et al. 2006, Seamans and Gutiérrez 2007, Gutiérrez et al. 2011), we hypothesized that the probability of breeding dispersal would be greater for single owls, paired owls that lost their mate, young owls, female owls, and owls that did not reproduce the year prior to dispersing. Based on general patterns in dispersal among birds, we hypothesized that females would disperse farther than males (Greenwood 1980, Greenwood and Harvey 1982, Marti 1999).

METHODS

Study Area.—We monitored owl movements within a study area of ~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, NM. Importantly, our study area did not encompass the entire mountain range or local population of Mexican Spotted Owls. Thus, we considered our population to be open in the sense that owls could disperse both into and out of our study population without leaving the Sacramento Mountains or traveling long distances.

Terrain within the study area consisted of heavily-forested mountain slopes and minor drainages, with interspersed meadows in the larger valley bottoms. Elevation ranged from 2,000–2,800 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 (*Pinus ponderosa*), and quaking aspen (*Populus tremuloides*) (Kaufmann et al. 1998). Precipitation averaged 65 cm/year at Cloudcroft, NM (elevation 2,652 m) with summer thunderstorms providing >60% of annual precipitation and most of the remainder

occurring as winter snowfall (Kaufmann et al. 1998).

Data Collection.—We used conventional protocols for studying demography of Spotted Owls (Franklin et al. 1996, see also Forsman 1983). This process entailed using calling surveys to locate owls, documenting the number of young produced each year, marking or resighting individuals, and recording sex and age. All data were collected during the owls' breeding season, 1 March through 30 August, from 2003–2011.

We captured territorial adult and subadult owls using snare poles, baited mist nests, or by hand (Forsman et al. 1983). All captured owls received a numbered U.S. Fish and Wildlife Service 7B aluminum lock-on band on one leg and were uniquely marked with a plastic color band on the opposite leg (Forsman et al. 1996). Marked owls then were resighted during territory visits in subsequent years. We recorded sex of captured owls based on calls and behavior (Forsman et al. 1984, Ganey 1990, Franklin et al. 1996). Owls were assigned to two age classes (subadult or adult) based on plumage characteristics (Moen et al. 1991).

Modeling Breeding Dispersal Probability and Distance.—We defined breeding dispersal as having occurred when a non-juvenile owl moved between territories where it had the opportunity to breed, regardless of whether or not we documented breeding on these territories (Daniels and Walters 2000, Forsman et al. 2002). Under this definition, opportunities for breeding dispersal occurred whenever a marked, territorial owl was observed in year t and resighted in year $t + i$, where i represents the number of years between observations. For each such interval, we recorded whether the owl remained in its original territory or dispersed to a new territory, as well as the following predictor variables: age class (adult vs. subadult) in year t , social status in year t , sex, and reproductive status in year t . Social status was recorded as: single owl, owl was paired but its mate was not present in the territory in year $t + 1$, or owl was paired and its mate remained in the original territory in year $t + 1$. Reproductive status in year t was recorded as reproduced (i.e., fledged ≥ 1 young) or failed to reproduce (0 young fledged). For all dispersal events, we estimated approximate distance moved (km) from the geographic center of the territory occupied in year t to the center of the new territory occupied in year $t + i$. We used the nest location from year t

TABLE 1. Model results for generalized linear models of breeding dispersal probability evaluated for Mexican Spotted Owls in the Sacramento Mountains, New Mexico, 2003–2011. Models are sorted by ΔAIC_c^a .

Model ^b	ΔAIC_c	w_i^c
Age + Social status + Reproductive status	0.000	0.652
Age + Social status + Reproductive status + Sex	1.670	0.283
Age + Social status	5.598	0.040
Age + Sex + Social status	6.991	0.020
Social status	10.085	0.004
Sex + Social status	11.627	0.002
Global	18.878	<0.001
Age + Reproductive status	21.034	<0.001
Sex + Reproductive status	22.061	<0.001
Reproductive status	31.197	<0.001
Age + Sex	33.147	<0.001
Age	32.477	<0.001
Null	36.780	<0.001
Sex	37.627	<0.001

^a Change in AIC_c (Akaike's Information Criterion corrected for small sample size, Burnham and Anderson 2002) from the model with the lowest AIC_c value.

^b Variables and levels included in models were: Age (adult, subadult); Social status (single owl, mated owl whose mate disappeared or moved after year t , mated owl whose mate remained on territory in year $t + 1$); Reproductive status (0 young fledged, ≥ 1 young fledged); and Sex (female, male). The null model included no covariates, and the global model included all covariates.

^c Akaike model weights (Burnham and Anderson 2002).

+ i to estimate the location of the territory center where available. Where nest locations were not available, we used the geographic center of the primary roosting area used during the nesting season (Apr–Jun) in year $t + i$ to estimate the location of the territory center.

We separately modeled the probability of breeding dispersal and dispersal distance as a function of these predictors using generalized linear models. We modeled dispersal probability using a binomial distribution and a logit link function, and dispersal distance using a linear model. We log-transformed distance for the models of dispersal distance. Based on existing literature on breeding dispersal in Spotted Owls (Forsman et al. 2002, Blakesley et al. 2006, Seamans and Gutiérrez 2007, Gutiérrez et al. 2011), we developed a suite of 14 *a priori* models using combinations of these predictor variables (Table 1). We ran these models separately for dispersal probability and dispersal distance, and evaluated models in a model selection framework using Akaike's Information Criterion corrected for small sample size (AIC_c ; Burnham and Anderson 2002). We considered any models within 2 AIC units of the top model to be competing models, and calculated Akaike model weights (w_i) to estimate the relative support for each model (Burnham and Anderson 2002). For models of dispersal probability, we used the Hosmer and Lemeshow (2000) goodness of fit

test to assess model fit. All models were run in PASW Statistics 17.0 (IBM SPSS software 2009). We report results for all models evaluated but report parameter estimates only from the best models of dispersal probability and dispersal distance.

Characteristics of Breeding Dispersal Events.—We summarized several descriptive characteristics of dispersal events, including the number of years intervening between the last observation on the original territory and the first observation on the new territory, changes in social status from year t to $t + i$, the number of observed dispersal events per owl, and differences in reproductive success before and after dispersal. We estimated difference in reproductive success pre- and post-dispersal as (number of young fledged in year $t + i$) – (number of young fledged in year t). We used a Mann-Whitney U -test to evaluate the hypothesis that this difference did not vary significantly between adults and subadults, and we used an exact version of a one-tailed Wilcoxon signed-ranks test to determine whether the difference in reproductive success was >0 (Conover 1999). Only owls whose reproductive output was known for both years t and $t + i$ were included in this analysis.

RESULTS

We observed 575 intervals between successive observations of banded owls (potential dispersal

TABLE 2. Parameter estimates (with standard errors and 95% confidence intervals) from the top-ranked generalized linear model of breeding dispersal probability for Mexican Spotted Owls in the Sacramento Mountains, New Mexico, 2003–2011.

Model/parameter	Estimate ^a	SE	95% CI ^b
Intercept	−4.174	0.711	−5.248–−3.219
Age = Adult	−0.936	0.519	−1.682–−0.156
Social status = Single	3.082	0.947	1.591–4.455
Social status = Paired, lost mate	2.218	0.479	1.549–2.934
Reproductive status = 0 young	1.525	0.523	0.791–2.342

^a Estimates are relative to reference categories, which were: Age = Subadult, Social status = Paired, did not lose mate, Reproductive status = Fledged ≥ 1 young in year t .

^b Profile likelihood confidence intervals.

occasions) involving 169 uniquely marked individuals representing 78 owl territories. Number of potential dispersal occasions averaged 3.4 ± 0.2 ($\pm$ SE, range = 1–8) occasions/owl. We documented 28 cases of breeding dispersal (4.9% of potential events), with the percentage of owls dispersing ranging from 0–9.0% per year. Among marked females ($n = 85$), 15.3% dispersed once during the study and 2.4% dispersed twice. Among males ($n = 84$), 8.3% dispersed once and 2.4% dispersed twice.

Observed dispersal events involved 32 owl territories (41% of territories) well distributed throughout the study area. Owls dispersed from 20 territories and to 20 territories, with eight territories experiencing dispersal events in both directions. Number of dispersal events ranged from 0–4 per territory. Net dispersal among these territories (computed as number of events in which owls dispersed to a territory minus number of events in which owls dispersed from that territory) ranged from −3–3 (mean = 0.0, 95% CI = −0.5–0.5).

Breeding Dispersal Probability.—There were two competing models for breeding dispersal probability, which collectively contributed 93.5% of overall model weight (Table 1). The best model included age class, social status, and reproductive status in year t (Table 1). This model fit the data well (Hosmer and Lemeshow test, $P = 0.932$) and was 2.3 times more likely than the next best model, based on model weights. This next best model included sex as well as the variables included in the top model (Table 1).

Parameter estimates for the best model indicated that adults were less likely to disperse than subadults, single owls or paired owls who lost their mate were more likely to disperse than paired owls that did not lose their mate, and owls

were more likely to disperse following years when they failed to reproduce than following years when they reproduced successfully (Table 2). Profile confidence intervals did not overlap zero for any variables in the top model. The next best model indicated that females were more likely to disperse than males, but the confidence interval around the parameter estimate for sex overlapped zero, suggesting a relatively weak effect ($\beta = 0.328$, 95% CI = −0.334–1.012, $P = 0.485$).

Observed dispersal rates were extremely low for adult owls, as well as for owls that were paired in year t and did not lose a mate (Table 3). We observed only seven cases in which an owl dispersed while its mate remained on territory; in five of these cases it was the female that dispersed. Dispersal rates also were low for owls that reproduced successfully in year t (Table 3).

Breeding Dispersal Distance.—There were two competing models for breeding dispersal distance, which collectively contributed 66.2% of overall model weight (Table 4). The best model included only sex, and the competing model was a null model containing no covariates. The top model contributed 41% of overall model weight, and was 1.6 times more likely than the null model based on model weights (Table 4). Parameter estimates for the top model indicated that females dispersed farther than males (Table 5). The confidence interval around that estimate overlapped zero only slightly, and the associated P -value (0.052) also suggested that owl sex influenced breeding dispersal distance. In addition, sex appeared in four of the six highest-ranked models of dispersal distance, and those five models collectively carried 61.5% of overall model weight (Table 4). Thus, the only variable evaluated that showed any predictive power for dispersal distance was owl sex.

TABLE 3. Percentage of territorial Mexican Spotted Owls dispersing in the Sacramento Mountains, New Mexico, 2003–2011, between year t and $t + i$, as a function of social status, age class, reproductive status in year t , and sex.

Parameter/category	N^a	% Dispersing
Social status = Single	7	42.9
Social status = Paired, mate not present year $t + 1$	111	14.4
Social status = Paired, mate present year $t + 1$	448	1.6
Age = Adult	505	3.8
Age = Subadult	63	11.1
Reproductive status = Fledged ≥ 1 young in year t	328	1.5
Reproductive status = 0 young fledged in year t	202	9.4
Sex = Female	292	5.5
Sex = Male	276	3.6

^a N = number of potential dispersal occasions observed within the indicated category. Potential dispersal occasions occurred when a marked owl was observed in both years t and $t + i$, where i = the number of intervening years.

Distance moved between territories averaged 5.1 km for female owls (95% CI = 3.1–7.0 km, range = 2.1–15.7 km, $n = 17$) and 3.6 km for male owls (95% CI = 2.2–5.1 km, range = 1.6–9.0 km, $n = 11$). Most owls of both sexes dispersed < 5 km, and no males were observed to disperse > 9 km (Fig. 1). Most observed dispersal events (57.1%) involved owls moving to a territory adjacent to the territory occupied in year t . Males were slightly more likely than females to move to an adjacent territory (63.6% versus 52.9%), but the difference was not statistically significant (Fisher's exact test, $P = 0.705$).

Characteristics of Breeding Dispersal Events.—Twenty-two dispersing owls (78.6%) were first

observed in their new territory in year $t + 1$, whereas five owls were not relocated on new territories until year $t + 2$ and one owl was not relocated until year $t + 4$. All dispersing owls were paired the first year they were observed on their new territory. In contrast, 75% of single owls that did not disperse and 92.7% of mated owls that apparently lost their mate but did not disperse were paired the following year. In 75% of observed dispersal events, the dispersing owl mated with an owl in year $t + i$ that was known to be present in the territory in year $(t + i) - 1$. Dispersing owls fledged significantly more young (Wilcoxon signed-ranks test, $P < 0.001$; $n = 20$) in year $t + i$ (median = 1.5 young, interquartile

TABLE 4. Model results for generalized linear models of breeding dispersal distance evaluated for Mexican Spotted Owls in the Sacramento Mountains, New Mexico, 2003–2011. Models are sorted by ΔAIC_c^a .

Model ^b	ΔAIC_c	w^c
Sex	0.000	0.408
Null	0.949	0.254
Sex + Reproductive status	2.749	0.103
Reproductive status	3.474	0.072
Sex + Social status	3.508	0.071
Age + Sex	5.018	0.033
Social status	5.485	0.026
Age	5.766	0.023
Age + Reproductive status	8.759	0.005
Age + Sex + Social status	10.049	0.003
Age + Social status	11.454	0.001
Age + Social status + Reproductive status + Sex	14.268	< 0.001
Age + Social status + Reproductive status	15.247	< 0.001
Global	49.511	< 0.001

^a Change in AIC_c (Akaike's Information Criterion corrected for small sample size, Burnham and Anderson) from the model with the lowest AIC_c value.

^b Variables and levels included in models were: Age (adult, subadult); Social status (single owl, mated owl whose mate disappeared or moved after year t , mated owl whose mate remained on territory in year $t + 1$); Reproductive status (0 young fledged, ≥ 1 young fledged); and Sex (female, male). The null model included no covariates, and the global model included all covariates.

^c Akaike model weights (Burnham and Anderson 2002).

TABLE 5. Parameter estimates (with standard errors and 95% confidence intervals) from the top-ranked generalized linear model of breeding dispersal distance for Mexican Spotted Owls in the Sacramento Mountains, New Mexico, 2003–2011.

Model/parameter	Estimate ^a	SE	95% CI ^b
Intercept	1.055	0.165	0.718–1.391
Sex = Female	0.409	0.211	–0.020–0.838

^a Estimates are relative to the reference category Sex = Male.
^b Profile likelihood confidence intervals.

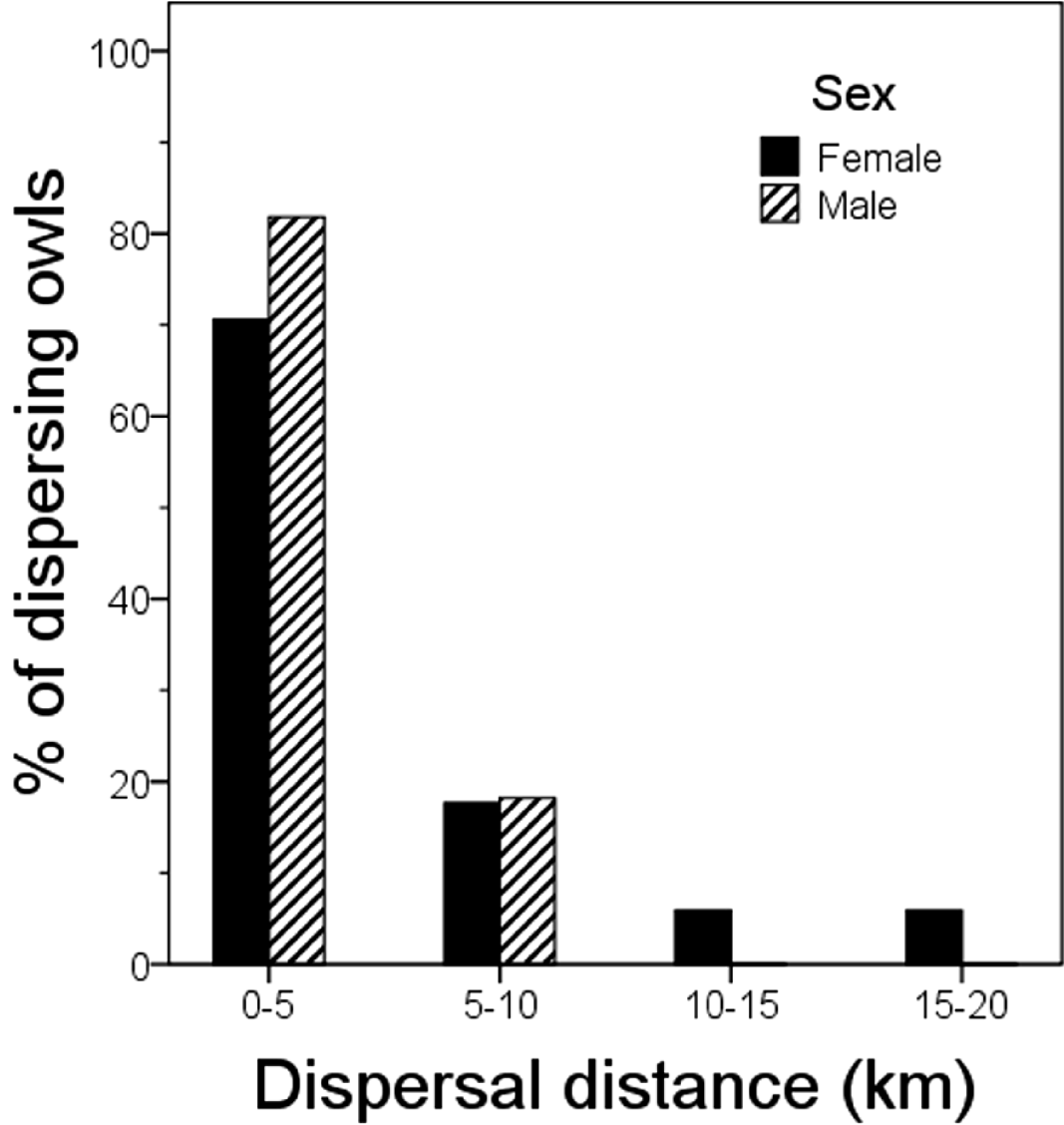


FIG. 1. Dispersal distances of Mexican Spotted Owls in the Sacramento Mountains, New Mexico, 2003–2011; $n = 17$ female and 11 male owls.

range [IQR] = 0.0–2.0) than in year t (median = 0.0 young, IQR = 0.0–0.0), and the difference in reproductive output pre-and post-dispersal did not differ between dispersing subadults and adults (Mann-Whitney test, $P = 0.58$). Only 12.5% of dispersing owls that were paired in year t ($n = 24$) fledged young in that year, versus 59.1% in year $t + i$.

Most owls (87.5%) that dispersed did so only once during the study, but four owls (two females, two males) dispersed twice. Two of these owls (one male, one female) dispersed (in separate events) from the territory occupied in year t to an adjacent territory in year $t + 1$, then back to the original territory in year $t + 2$. The other two dispersed (in separate events) from their original territory in year t to a second territory in year $t + 1$, and then later dispersed to a third territory. Because six dispersing owls were not relocated until 2–4 years following disappearance from their original territory, we may have underestimated the number of dispersal events for these owls.

DISCUSSION

Breeding dispersal probability among Mexican Spotted Owls in the Sacramento Mountains was influenced by social status, age class, reproductive status, and sex. Most studies in other subspecies of Spotted Owls also found support for the effect of social status and age class on breeding dispersal probability (Forsman et al. 2002, Blakesley et al. 2006, Seamans and Gutiérrez 2007). In contrast, there is less consistency among studies with respect to effects of reproductive success and sex on dispersal probability. Owls in our study and in studies by Forsman et al. (2002) and Blakesley et al. (2006) were more likely to disperse if they failed to reproduce in year t , and owls studied by Gutiérrez et al. (2011) were more likely to disperse if their mean pre-dispersal reproductive output was less than the average for the population. In contrast, Seamans and Gutiérrez (2007) found little support for a reproductive effect on breeding dispersal probability. Similarly, Forsman et al. (2002) reported that females were more likely than males to disperse and both Gutiérrez et al. (2011) and this study also showed support for this pattern. In contrast, Blakesley et al. (2006) found little evidence for a sex effect on dispersal probability. The reasons for observed differences among studies are largely unclear.

Our results suggest that breeding dispersal occurs regularly but at relatively low rates among Mexican Spotted Owls in the Sacramento Mountains. Our overall estimate of breeding dispersal probability (4.9%) was slightly lower than estimates reported for northern and California Spotted Owls by Forsman et al. (2002), Blakesley et al. (2006) (~7% in both studies), and Seamans and Gutiérrez (2007; 9%). Proportions dispersing per year in our study (0–9%) and proportions of females (17.7%) and males (10.7%) dispersing at least once during the study also were lower than values reported by Gutiérrez et al. (2011; 0–13% per yr and 29 and 19% of female and male owls, respectively) for California Spotted Owls. Dispersal distances observed in this study generally were within the range observed in other studies of breeding dispersal in Spotted Owls (Forsman et al. 2002, Blakesley et al. 2006, Gutiérrez et al. 2011), and in all studies many dispersing owls moved to an adjacent territory. We observed evidence for an effect of sex on breeding dispersal distance in this study, although mean dispersal distances were similar among female and male owls. In contrast, sex did not appear to influence dispersal distance in owls studied by either Forsman et al. (2002) or Blakesley et al. (2006). This runs contrary to the general pattern in birds for females to disperse farther than males (Greenwood 1980, Marti 1999).

Reasons for these differences among studies remain largely unknown. Gutiérrez et al. (2011) worked with a population assumed to be closed to emigration; however, other studies, including ours, occurred in areas where dispersal into and out of the study population was possible. Because dispersing owls may leave these open study areas and not be resighted, both breeding dispersal probability and breeding dispersal distances may be underestimated in these studies. If females disperse greater distances than males, they would be more likely to leave the study area, and the extent of this bias thus would be greater for female than for male owls. There is evidence that territorial female Mexican Spotted Owls may undertake long distance movements (Gutiérrez et al. 1996: 187 km, Ganey and Jenness 2013: 462 km; this study: >15 km), but no similar evidence exists for male Mexican Spotted Owls.

Both Blakesley et al. (2006) and Gutiérrez et al. (2011) found evidence that dispersing owls moved to higher quality territories, as rated by indices of reproductive success. We did not model territory quality directly, but all dispersing owls in our

study were paired in year $t + i$, whereas 75% of dispersing owls in our study either were single in year t or lost their mate between year t and year $t + i$. Partly as a result of these differences in social status, dispersing owls fledged significantly more young immediately following than before dispersal. Thus, dispersal appeared to be adaptive in our study as well, with dispersing owls typically improving both their social status and reproductive success.

How dispersing owls select new territories remains unknown. In our study, at least 75% of dispersing owls moved to territories that were occupied by an owl of the opposite sex in year $(t + i) - 1$, implying that presence of a potential mate may be an important factor in selecting a new territory. Almost 79% of the dispersing owls in our study were settled in their new territory by year $t + 1$, and >50% settled in an adjacent territory. This implies that (1) most dispersing owls settled relatively quickly, and (2) dispersing owls may have settled in the first territory they encountered that was occupied by a potential mate and lacking a resident owl of the same sex (although we cannot rule out eviction of the former territory holder; see Choudhury [1995]). This suggests that dispersal did not involve a lengthy exploration period that would allow dispersing owls to assess territory quality throughout the area.

In summary, owls in the Sacramento Mountains typically dispersed from territories where they either were unmated or were mated but failed to reproduce successfully in year t , and to territories occupied by a potential mate where many reproduced successfully in year $t + i$. Thus, most dispersing owls were leaving unfavorable social and/or reproductive situations and were able to improve their situation, at least in the short term, by dispersing. In this context, breeding dispersal can be adaptive (Blakesley et al. 2006, Gutiérrez et al. 2011) without requiring dispersing owls to have knowledge of relative habitat quality, which may vary over time, in multiple territories.

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LITERATURE CITED

- ARSENAULT, D. P., A. HODGSON, AND P. B. STACEY. 1997. Dispersal movements of juvenile Mexican Spotted Owls (*Strix occidentalis lucida*) in New Mexico. Pages 47–57 in *Biology and conservation of owls of the northern hemisphere* (J. R. Duncan, D. H. Johnson, and T. H. Nicholls, Editors). USDA Forest Service General Technical Report NC-190.
- BAKER, R. R. 1978. *The evolutionary ecology of animal migration*. Hodder and Stoughton, London, UK.
- BLAKESLEY, J. A., D. R. ANDERSON, AND B. R. NOON. 2006. Breeding dispersal in the California Spotted Owl. *Condor* 108:71–81.
- BURNHAM, K. P. AND D. R. ANDERSON. 2002. *Model selection and inference. A practical information-theoretic approach*. Second Edition. Springer-Verlag, New York, New York, USA.
- CHOUDHURY, S. 1995. Divorce in birds: a review of the hypotheses. *Animal Behavior* 50:413–429.
- CONOVER, W. J. 1999. *Practical nonparametric statistics*. Third Edition. John Wiley & Sons, New York, New York, USA.
- DANIELS, S. J. AND J. R. WALTERS. 2000. Between-year breeding dispersal in Red-cockaded Woodpeckers: multiple causes and estimated cost. *Ecology* 81:2473–2484.
- DUNCAN, R. B. AND S. M. SPEICH. 1995. Spotted Owl banding in sub-Mogollon Arizona, dispersal and movement: current knowledge. *North American Bird Bander* 20:151.
- FORSMAN, E. D. 1983. *Methods and materials for locating and studying Spotted Owls*. USDA Forest Service General Technical Report PNW-162.
- FORSMAN, E. D., E. C. MESLOW, AND H. M. WIGHT. 1984. *Distribution and biology of the Spotted Owl in Oregon*. Wildlife Monographs 87:1–64.
- FORSMAN, E. D., A. B. FRANKLIN, F. M. OLIVER, AND J. P. WARD JR. 1996. A color band for Spotted Owls. *Journal of Field Ornithology* 67:507–510.
- FORSMAN, E. D., R. G. ANTHONY, J. A. REID, P. J. LOSCHL, S. G. SOVERN, M. TAYLOR, B. L. BISWELL, A. ELLINGSON, E. C. MESLOW, G. S. MILLER, K. A. SWINDLE, J. A. THRAILKILL, F. W. WAGNER, AND D. E. SEAMAN. 2002. Natal and breeding dispersal of Northern Spotted Owls. *Wildlife Monographs* 149:1–35.
- FRANKLIN, A. B., D. R. ANDERSON, E. D. FORSMAN, K. P. BURNHAM, AND F. W. WAGNER. 1996. Methods for collecting and analyzing demographic data on the Northern Spotted Owl. *Studies in Avian Biology* 17:12–20.
- GANEY, J. L. 1990. Calling behavior of Mexican Spotted Owls in Arizona. *Condor* 92:485–490.

- GANNEY, J. L. AND J. A. DICK. 1995. Habitat relationships of Mexican Spotted Owls: current knowledge. Chapter 4:1–42 in *Recovery plan for the Mexican Spotted Owl (*Strix occidentalis lucida*)*, Volume II - Technical supporting information. U.S. Fish and Wildlife Service, Albuquerque, New Mexico, USA.
- GANNEY, J. L. AND J. S. JENNESS. 2013. An apparent case of long distance breeding dispersal by a Mexican Spotted Owl in New Mexico. USDA Forest Service Research Note RMRS-RN-53WW.
- GANNEY, J. L., W. M. BLOCK, J. K. DWYER, B. E. STROHMEYER, AND J. S. JENNESS. 1998. Dispersal movements and survival rates of juvenile Mexican Spotted Owls in northern Arizona. *Wilson Bulletin* 110:206–217.
- GREENWOOD, P. J. 1980. Mating systems, philopatry, and dispersal in birds and mammals. *Animal Behavior* 28:1140–1162.
- GREENWOOD, P. J. AND P. H. HARVEY. 1982. The natal and breeding dispersal of birds. *Annual Review of Ecology and Systematics* 13:1–21.
- GUTIÉRREZ, R. J., A. B. FRANKLIN, W. LAHAYE, V. J. MERETSKY, AND J. P. WARD. 1985. Juvenile Spotted Owl dispersal in northwestern California: preliminary results. Pages 39–49 in *Ecology and management of Spotted Owls in the Pacific Northwest* (R. J. Gutiérrez and A. B. Carey, Editors). USDA Forest Service General Technical Report PNW-185.
- GUTIÉRREZ, R. J., A. B. FRANKLIN, AND W. S. LAHAYE. 1995. Spotted Owl (*Strix occidentalis*). The birds of North America, Number 179. The Academy of Natural Sciences Philadelphia and the American Ornithologists Union, Washington, D.C., USA.
- GUTIÉRREZ, R. J., M. E. SEAMANS, AND M. Z. PEERY. 1996. Intermountain movement by Mexican Spotted Owls (*Strix occidentalis lucida*). *Great Basin Naturalist* 56:87–89.
- GUTIÉRREZ, R. J., W. S. LAHAYE, AND G. S. ZIMMERMAN. 2011. Breeding dispersal in an isolated population of Spotted Owls *Strix occidentalis*: evidence for improved reproductive output. *Ibis* 153:592–600.
- HOSMER, D. W. AND A. LEMESHOW. 2000. *Applied Logistic Regression*. Second Edition. John Wiley and Sons, New York, New York, USA.
- HOWARD, W. E. 1960. Innate and environmental dispersal of individual vertebrates. *American Midland Naturalist* 63:152–161.
- IBM SPSS SOFTWARE. 2009. PASW Statistics. Version 17.0. www-01.ibm.com/software/analytics/spss/ (accessed 15 Dec 2013).
- KAUFMANN, M. R., L. S. HUCKABY, C. M. REGAN, AND J. POPP. 1998. Forest reference conditions for ecosystem management in the Sacramento Mountains, New Mexico. USDA Forest Service General Technical Report RMRS-GTR-19.
- LAHAYE, W. S., R. J. GUTIÉRREZ, AND J. R. DUNK. 2001. Natal dispersal of the Spotted Owl in southern California: dispersal profile of an insular population. *Condor* 103:691–700.
- MARTI, C. D. 1999. Natal and breeding dispersal in Barn Owls. *Journal of Raptor Research* 33:181–189.
- MILLER, G. S. 1989. Dispersal of juvenile Northern Spotted Owls in western Oregon. M.S. Thesis, Oregon State University, Corvallis, Oregon, USA.
- MOEN, C. A., A. B. FRANKLIN, AND R. J. GUTIÉRREZ. 1991. Age determination of subadult Northern Spotted Owls in northwest California. *Wildlife Society Bulletin* 19:489–493.
- SEAMANS, M. E. AND R. J. GUTIÉRREZ. 2007. Habitat selection in a changing environment: the relationship between habitat alteration and Spotted Owl territory occupancy and breeding dispersal. *Condor* 109:566–576.
- U.S. FISH AND WILDLIFE SERVICE. 1993. Endangered and threatened wildlife and plants: final rule to list the Mexican Spotted Owl as a threatened species. *Federal Register* 58:14248–14271.
- U.S. FISH AND WILDLIFE SERVICE. 2012. Final Recovery Plan for the Mexican Spotted Owl. First Revision. U.S. Fish and Wildlife Service, Albuquerque, New Mexico, USA.
- WARD JR., J. P., A. B. FRANKLIN, S. E. RINKEVICH, AND F. CLEMENTE. 1995. Distribution and abundance of Mexican Spotted Owls. Pages 1–14 in *Recovery Plan for the Mexican Spotted Owl (*Strix occidentalis lucida*)*, Volume II - Technical supporting information, U.S. Fish and Wildlife Service, Albuquerque, New Mexico, USA.
- WILLEY, D. W. AND C. VAN RIPER III. 2000. First-year movements by juvenile Mexican Spotted Owls in the canyonlands of Utah. *Journal of Raptor Research* 34:1–7.