



## FEATURE ARTICLES

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### BREEDING DISPERSAL IN THE CALIFORNIA SPOTTED OWL

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**Abstract.** Spotted Owls (*Strix occidentalis*) are territorial, generally nonmigratory, and strongly philopatric. Nevertheless, California Spotted Owls (*S. o. occidentalis*) exhibited breeding dispersal during 7% of interannual observations of banded individuals ( $n = 54$  of 743 occasions). Based on ecological theory and published literature, we made *a priori* predictions about the factors associated with the probability of breeding dispersal and breeding dispersal distance, and about the consequences of dispersal. Breeding dispersal probability was higher for younger owls, single owls, paired owls that lost their mates, owls at lower quality sites, and owls that failed to reproduce in the year preceding dispersal. Sex had little effect on the probability of breeding dispersal. Dispersal distance was similar for female and male owls (median = 7 km, range = 1–33 km). We found no strong relationships between dispersal distance and any of the conditions that were associated with the probability of breeding dispersal. Dispersal resulted in improved territory quality in 72% of cases. These results indicate that breeding dispersal was condition-dependent and adaptive.

**Key words:** *dispersal consequences, dispersal distance, dispersal probability, mate loss, Spotted Owl, Strix occidentalis occidentalis, territory quality.*

#### Dispersión Reproductiva en *Strix occidentalis occidentalis*

**Resumen.** *Strix occidentalis* es una especie territorial, generalmente no es migratoria, y es marcadamente filopátrica. Sin embargo, *S. o. occidentalis* mostró dispersión reproductiva en el 7% de las observaciones interanuales de individuos anillados ( $n = 54$  de 743 ocasiones). Basados en la teoría ecológica y en la literatura publicada, hicimos predicciones *a priori* acerca de los factores asociados con la probabilidad de dispersión reproductiva, con la distancia de dispersión y con las consecuencias de la dispersión. La probabilidad de dispersión reproductiva fue mayor en las lechuzas jóvenes, las solitarias, las que habían perdido a su pareja, aquellas en lugares de menor calidad y en las que tuvieron un fracaso reproductivo en el año previo a la dispersión. El sexo tuvo poco efecto en la probabilidad de dispersión. La distancia de dispersión fue similar en lechuzas hembras y machos (mediana = 7 km, rango = 1–33 km). No observamos una fuerte relación entre la distancia de dispersión y cualquiera de las circunstancias asociadas con la probabilidad de dispersión. La dispersión resultó en una mejoría de la calidad del territorio en el 72% de los casos. Estos resultados indican que la dispersión reproductiva dependió de las circunstancias y que tuvo un sentido adaptativo.

#### INTRODUCTION

Breeding dispersal in birds is commonly defined as territory or nest change between breeding

attempts. If breeding dispersal is adaptive, it should result in increased fitness, including successful breeding, of dispersing individuals

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("effective" dispersal of Greenwood and Harvey 1982). Adaptive hypotheses for breeding dispersal include inbreeding avoidance, mate choice, site choice, social constraints, and heritability (Payne and Payne 1993, Daniels and Walters 2000). Inbreeding avoidance is assumed to be a primary reason for natal dispersal (Greenwood 1980), and is relevant to breeding dispersal primarily in cooperatively breeding species in which closely related individuals occupy the same territory (Daniels and Walters 2000). Mate choice and site choice imply that an individual disperses to obtain a better mate or nesting site, respectively, than it had previously. Reproductive failure may indicate a poor mate or poor site or both, and may often be a condition triggering breeding dispersal (Haas 1998). Mate and site choice are often confounded in monogamous species, especially for females (Warkentin et al. 1991). Predation avoidance and prey density hypotheses (Jackson et al. 1989, Korpimäki 1993) are a subset of site choice hypotheses. Social constraint hypotheses include the predictions that younger birds disperse at higher rates and greater distances than older birds (Forsman et al. 2002), or that dispersal is dependent on population density (Newton and Wyllie 1992, Wiklund 1996). Finally, heritability assumes that dispersal behavior is genetically based (Payne and Payne 1993).

Before evaluating the preceding alternative hypotheses with respect to dispersal of Spotted Owls (*Strix occidentalis*), we considered the constraints imposed by the species' life history. The majority of Spotted Owls are nonmigratory; consequently, territories are not vacated seasonally, which likely reduces the ability of a new owl to displace the current territory holder. Both male and female Spotted Owls are territorial, strongly philopatric, and generally pair for life (Gutiérrez et al. 1995). Nevertheless, some individuals undergo breeding dispersal and occasionally sever pair bonds (Forsman et al. 2002). Spotted Owl populations can have high annual variability in reproduction, with 7%–91% of pairs producing young in northeastern California each year from 1990 to 1999 (Blakesley et al. 2001). Spotted Owls rarely re-nest within a breeding season, and if they do, it is within the same territory (Lewis and Wales 1993).

In Spotted Owls and other long-lived species that breed infrequently, increased productivity postdispersal may not be immediately apparent. The fitness consequences of dispersal are ideally determined by measuring lifetime reproductive success (Newton 1989). Territory change could fail to increase an owl's average annual fecundity, yet increase lifetime reproductive success by increasing the owl's survival probability. However, Spotted Owls can live >16 years in the wild (Gutiérrez et al. 1995) making it difficult to obtain sufficient samples of lifetime reproductive success. As an alternative, site quality, measured as productivity of a territory over time, may indicate the potential of an owl to reproduce within a given territory (Forero et al. 1999).

Breeding dispersal consists of three interdependent stages (Ims and Hjermann 2001). For Spotted Owls, these are: emigration from the original territory, transient movement, and immigration to the new territory. Dispersal movement was not directly observed in this study. We evaluated hypotheses corresponding to conditions prior to breeding dispersal and postdispersal by Spotted Owls.

The objectives of this study were: (1) to identify factors associated with Spotted Owl breeding dispersal; (2) to determine whether these factors affected breeding dispersal distance; and (3) to evaluate the consequences of breeding dispersal.

## METHODS

We formulated *a priori* hypotheses regarding the probability of breeding dispersal, dispersal distance, and consequences of dispersal. We predicted that dispersal probability would be higher for: (1) females than males (Greenwood 1980, Warkentin et al. 1991, Rosenfield and Bielefeldt 1996, Wiklund 1996, Clarke et al. 1997, Forero et al. 1999, Serrano et al. 2001, Forsman et al. 2002); (2) younger owls than older owls (Newton and Wyllie 1992, Forero et al. 1999, Serrano et al. 2001, Forsman et al. 2002, Winkler et al. 2004); (3) single owls than paired owls (Forsman et al. 2002); (4) owls that lost their mate than those that did not (Forero et al. 1999, Forsman et al. 2002); (5) owls that failed to breed than those that successfully bred, especially females (Newton and Wyllie 1992, Payne and Payne 1993, Wiklund 1996, Forero et al. 1999, Winkler et al. 2004); and (6) owls in

low quality territories than those in high quality territories (Forero et al. 1999). Furthermore, we expected that a higher quality site might override the tendency to disperse for owls that lost their mate or failed to breed. We predicted that dispersal distances would be farther for: (1) females than males (Greenwood 1980, Wiklund 1996, Clarke et al. 1997); (2) younger than older owls (Forero et al. 1999, Forsman et al. 2002); and (3) owls from poorer than higher quality territories (Forero et al. 1999). Finally, we predicted that, for dispersing individuals, (1) single owls that dispersed would be paired following dispersal at a higher rate than single owls that did not disperse (Payne and Payne 1993); (2) owls that lost their mate and dispersed would be paired following dispersal at a higher rate than owls that lost their mate and did not disperse; and (3) postdispersal territory quality would be higher than predispersal territory quality (Forero et al. 1999).

#### STUDY AREA

The Lassen study area encompassed 2200 km<sup>2</sup> of the Lassen National Forest and adjacent forested land in northeastern California (40°00'–40°50'N, 120°30'–121°40'W). See Blakesley et al. (2001) for a detailed description of the study area.

#### DATA COLLECTION

We studied California Spotted Owls (*S. o. occidentalis*) from April–August, 1990–2001, collecting the following data annually from individual color-banded owls: sex, age, territory location, pair status, and fledglings produced. Demographic parameters of the population and associations with forest stand characteristics are reported elsewhere (Blakesley et al. 2001, Blakesley et al. 2005). We followed a standardized field protocol to locate, capture, band, and resight owls and to determine owl reproductive status (Blakesley et al. 2001). We determined owl gender based on the pitch of their calls. We ascertained owl age at the time of first capture as first-year subadult (1 < S1 < 2 years old), second-year subadult (2 < S2 < 3 years old), or adult (A ≥ 3 years old) based on plumage characteristics (Forsman 1981, Moen et al. 1991).

We observed Spotted Owls at 57–74 sites annually, and were able to determine territory centers by mapping the locations of nest and

roost trees. We conducted nighttime surveys throughout much of the study area where territorial owls were absent. This provided us with knowledge of the locations of adjacent territories. The distance from one territory center to the nearest adjacent territory center varied from 1.2 to >5 km. Therefore, dispersal was determined through knowledge of all owls' nest and roost locations rather than defined by the distance an owl moved.

#### STATISTICAL ANALYSES

For each interval between observations of an individual owl (interval length = 1 year, 2 years, etc.), we recorded whether or not the owl dispersed to a new territory, and if the owl dispersed, we recorded the distance moved between territories. For each owl in each interval, we recorded the following associated predictor variables when available: age class (S1, S2, A), juveniles produced (0 = none, 1 = 1–3 fledged), pair status (paired or single), territory quality at the beginning of the interval, territory quality at the end of the interval, and mate loss during the interval. We assumed mate loss had occurred during an interval if we never again observed the mate during our study. Because pair status and mate loss were confounded, we combined these two binary variables into a single multinomial variable when modeling dispersal probability and dispersal distance. The multinomial variable is hereafter referred to as social status (Y = paired and lost mate; N = paired and did not lose mate; S = single).

In this owl population, apparent survival probability was positively correlated with reproductive output (Blakesley 2003). Therefore, we used mean reproductive output of a territory (1990–2001) as the measure of territory quality,  $Q_i$ . Because data were missing for various territories each year and because population-wide reproduction had high annual variability (Blakesley et al. 2001), we estimated territory quality for territory  $i$ ,  $Q_i$ , as follows:

$$Q_i = \left[ \sum_j (x_{ij} - \bar{x}_j) \right] / n_i,$$

where  $x$  = number of juveniles produced,  $i$  = territory,  $j$  = year for which reproductive data were available for territory  $i$ , and  $n$  = number of years for which reproductive data were available.

**Breeding dispersal probability.** We modeled the probability of breeding dispersal,  $P_{BD}$ , as a function of sex, age class, reproduction, social status, and predispersal territory quality with logistic regression using PROC LOGISTIC in program SAS v.8 (SAS Institute 2000). We also modeled the interactions between territory quality and age class, territory quality and social status, and sex and reproduction. In addition to the global model, we ran all possible subsets of the predictor variables to discover whether or not a reduced-parameter model would be more parsimonious.

We used Akaike's information criterion corrected for small sample size ( $AIC_c$ ) for model selection after checking for overdispersion in the data; overdispersion is indicated when deviance  $df^{-1}$  of the global model  $> 1$ . Akaike weights,  $w_i$ , estimate the relative predictive strength of each model and may be viewed as the weight of evidence in support of model  $i$  (Burnham and Anderson 2002:75). Because the same variable may appear in several competing models, we estimated the relative importance of each variable by calculating  $w_+(j)$ , where  $w_+(j)$  is the sum of  $w_i$  across all models in the set in which variable  $j$  occurred (Burnham and Anderson 2002:168).

For logistic regression, the maximum of  $R^2 < 1$ . Therefore, we measured the proportion of variance explained by a model using  $\bar{R}^2$ , the maximum-rescaled  $R^2$ , where  $\bar{R}^2 = R^2/\max(R^2)$  (Nagelkerke 1991).

**Breeding dispersal distance.** We modeled breeding dispersal distance ( $D$ ) as a function of age class, social status, sex, predispersal territory quality, and postdispersal territory quality. We modeled dispersal distance with general linear models using PROC GENMOD in program SAS v.8 (SAS Institute 2000) and used  $AIC_c$  for model selection. We linearized dispersal distance data with a logarithmic transformation.

**Consequences of breeding dispersal.** We compared the quality of each owl's predispersal territory with its postdispersal territory, separately for each sex and age class. We compared the pair status in year  $t + 1$  of single owls in year  $t$  that dispersed with single owls in year  $t$  that did not disperse, using a  $\chi^2$  test. Similarly, we compared the pair status of owls that lost their mates and dispersed with owls that lost their mates and did not disperse.

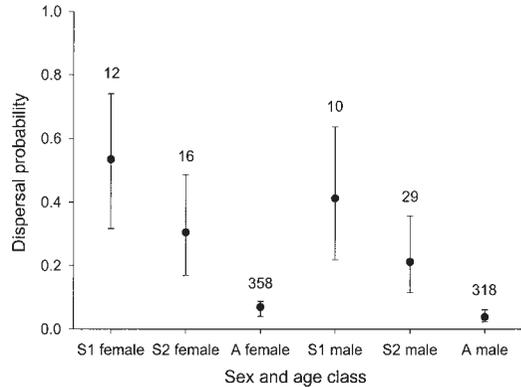


FIGURE 1. Estimated breeding dispersal probabilities of California Spotted Owls in northeastern California, 1990–2001. Error bars represent profile likelihood 95% confidence intervals. Key to age classes: S1 = first-year subadult; S2 = second-year subadult; A = adult. Sample sizes appear above error bars.

Values reported are means  $\pm$  SE. Chi-square tests were evaluated at  $\alpha = 0.10$ .

## RESULTS

Of 279 banded nonjuvenile owls on the study area from 1990–2001, 203 were seen in two or more years, yielding 946 owl-year observations. Breeding dispersal occurred in 54 of the resulting 743 intervals (7% of potential occasions), including four cases of pair bond separation. In each case of pair bond separation, the female owl moved to a new territory and the male remained on the old territory. In 23 cases, owls dispersed to adjacent territories, including the only two cases in which paired owls dispersed together. First-year subadults (S1) exhibited the highest dispersal probability ( $0.45 \pm 0.10$ ), followed by second-year subadults ( $0.24 \pm 0.06$ ) and adults ( $0.05 \pm 0.01$ ; Fig. 1). In 32 cases, owls were missing for one or more years before being resighted (12 philopatric and 20 dispersing owls). Sufficient data were available to model dispersal probability for 27 dispersal events and 508 cases of territory fidelity.

### BREEDING DISPERSAL PROBABILITY

The best model of breeding dispersal probability included age class, reproduction, mate loss, territory quality, and interactions between reproduction and territory quality and social status and territory quality, and had an  $\bar{R}^2 =$

TABLE 1. Models (95% confidence set) of breeding dispersal probability ( $P_{BD}$ ) for California Spotted Owls ( $n = 535$ ) in northeastern California, 1990–2001. Models are ordered by  $AIC_c$  and rescaled  $R^2$  of the best model = 0.40.  $\log(\mathcal{L})$  is the log-likelihood,  $K$  is the number of parameters,  $\Delta AIC_c$  is the difference in Akaike's information criterion from the top model, and  $w_i$  is the model weight.

Model <sup>a</sup>	$\log(\mathcal{L})$	$K$	$\Delta AIC_c$	$w_i$
$P_{BD}(\text{Age} + \text{Repro} + \text{Social} + \text{Quality} + \text{Repro} * \text{Quality} + \text{Social} * \text{Quality})^b$	-69.05	10	0.00	0.18
$P_{BD}(\text{Sex} + \text{Age} + \text{Repro} + \text{Social} + \text{Quality} + \text{Repro} * \text{Quality} + \text{Social} * \text{Quality} + \text{Sex} * \text{Repro})$	-67.09	12	0.25	0.16
$P_{BD}(\text{Age} + \text{Social} + \text{Quality} + \text{Social} * \text{Quality})$	-71.55	8	0.85	0.12
$P_{BD}(\text{Sex} + \text{Age} + \text{Repro} + \text{Social} + \text{Quality} + \text{Repro} * \text{Quality} + \text{Social} * \text{Quality})$	-68.66	11	1.31	0.09
$P_{BD}(\text{Age} + \text{Repro} + \text{Social} + \text{Quality} + \text{Social} * \text{Quality})$	-71.12	9	2.06	0.06
$P_{BD}(\text{Sex} + \text{Age} + \text{Social} + \text{Quality} + \text{Social} * \text{Quality})$	-71.24	9	2.32	0.06
$P_{BD}(\text{Sex} + \text{Age} + \text{Repro} + \text{Social} + \text{Quality} + \text{Social} * \text{Quality} + \text{Sex} * \text{Repro})$	-69.23	11	2.45	0.05
$P_{BD}(\text{Sex} + \text{Age} + \text{Repro} + \text{Social} + \text{Quality} + \text{Repro} * \text{Quality} + \text{Sex} * \text{Repro})$	-70.41	10	2.73	0.05
$P_{BD}(\text{Age} + \text{Repro} + \text{Social} + \text{Quality} + \text{Repro} * \text{Quality})$	-72.59	8	2.94	0.04
$P_{BD}(\text{Sex} + \text{Age} + \text{Repro} + \text{Social} + \text{Quality} + \text{Social} * \text{Quality})$	-70.81	10	3.52	0.03
$P_{BD}(\text{Age} + \text{Social} + \text{Quality})$	-75.05	6	3.74	0.03
$P_{BD}(\text{Sex} + \text{Age} + \text{Repro} + \text{Social} + \text{Quality} + \text{Repro} * \text{Quality})$	-72.09	9	4.01	0.02
$P_{BD}(\text{Sex} + \text{Age} + \text{Repro} + \text{Social} + \text{Quality} + \text{Sex} * \text{Repro})$	-72.17	9	4.17	0.02
$P_{BD}(\text{Age} + \text{Repro} + \text{Social} + \text{Quality})$	-74.27	7	4.25	0.02
$P_{BD}(\text{Sex} + \text{Age} + \text{Social} + \text{Quality})$	-74.61	7	4.91	0.02
$P_{BD}(\text{Sex} + \text{Age} + \text{Repro} + \text{Social} + \text{Quality})$	-73.83	8	5.41	0.01
$P_{BD}(\text{Sex} + \text{Repro} + \text{Social} + \text{Quality} + \text{Repro} * \text{Quality} + \text{Social} * \text{Quality} + \text{Sex} * \text{Repro})$	-71.93	10	5.76	0.01

<sup>a</sup> Abbreviations for model parameters: Age = age class; Repro = reproduction; Social = social status (a combination of pair status and mate loss); Quality = territory quality.

<sup>b</sup>  $AIC_c$  of top model = 158.51.

0.40 (Table 1). Parameter estimates of the best model (Table 2) indicated the probability of dispersal increased for first-year subadults (S1), and to a lesser extent for second-year subadults (S2), increased for single owls, and decreased for paired owls that did not lose their mates. Although territory quality and reproduction each had  $SE(\hat{\beta}) > \hat{\beta}$ , the interaction between these variables had a strong influence on dispersal probability;  $SE(\hat{\beta}) \approx 0.5 * \hat{\beta}$ . The interaction term (reproduction\*territory quality) indicates owls that did not reproduce were less likely to disperse with increasing territory quality. The estimate for age class S2 also had  $SE(\hat{\beta}) > \hat{\beta}$ , but the estimate for S1 had  $SE(\hat{\beta}) \approx 0.5 * \hat{\beta}$ . This may be explained by the smaller difference in breeding dispersal proba-

bility between second-year subadults and adults than between first-year subadults and adults (Fig. 1).

The global model (including all variables and interaction terms) was the second-best model, and was closely competitive with the top model ( $\Delta AIC_c = 0.25$ ), with  $\bar{R}^2 = 0.42$  (Table 1). The interaction between sex and reproduction indicated that females that did not reproduce were more likely to disperse than males that did not reproduce ( $\hat{\beta} = 0.553 \pm 0.334$ ). The sex effect alone was insignificant ( $\hat{\beta} = -0.081 \pm 0.333$ ). The third-best model was also a closely competing model ( $\Delta AIC_c = 0.85$ ) and consisted of four fewer parameters than the global model, containing only age class, social status, territory quality and the interaction between social status

TABLE 2. Parameter estimates ± standard errors (SE) for the top logistic regression model of breeding dispersal probability of California Spotted Owls in northeastern California, 1990–2001.

Parameter		Estimate ± SE
Intercept		-1.25 ± 0.59
Age class	S1 <sup>a</sup>	1.07 ± 0.69
Age class	S2 <sup>a</sup>	0.38 ± 0.55
Reproduction	0	0.39 ± 0.40
Social status	N <sup>b</sup>	-2.15 ± 0.43
Social status	S <sup>b</sup>	1.78 ± 0.60
Territory quality		0.26 ± 1.45
Reproduction*Territory quality	0	-2.52 ± 1.27
Social status*Territory quality	N <sup>b</sup>	-3.76 ± 1.52
Social status*Territory quality	S <sup>b</sup>	4.92 ± 2.10

<sup>a</sup> Codes for age class: S1 = first-year subadult, S2 = second-year subadult.

<sup>b</sup> Codes for social status: N = paired and did not lose mate, S = single.

and territory quality (Table 1). This model had an  $\bar{R}^2 = 0.38$ . Relative variable importance (Table 3) confirmed very strong support for social status, territory quality, and age class, and strong support for reproduction and the interaction between social status and territory quality.

BREEDING DISPERSAL DISTANCE

Median dispersal distances for adult females, adult males, subadult females, and subadult males were 9, 8, 4, and 10 km, respectively (Fig. 2). Median dispersal distance for all owls combined was 7 km (range = 1–33 km). Forty-three percent of dispersal events (92% of dispersals <6 km) were to adjacent territories. A dispersing owl’s new territory was often already occupied by an owl of the opposite sex that was present the previous year. There was no evidence that owls displaced territory

holders; e.g., when a male owl from territory *a* in year *t* was found in territory *b* in year *t* + 1, we did not find the male from territory *b* in year *t* anywhere in the study area in year *t* + 1.

The best model of dispersal distance was {*D*(predispersal territory quality)},  $\beta = 0.991 \pm 0.535$ ,  $\bar{R}^2 = 0.10$  (Table 4). The intercept-only model, however, was closely competitive ( $\Delta AIC_c = 1.05$ ), providing evidence in addition to the low rescaled  $R^2$  that predispersal territory quality was a poor predictor of dispersal distance. All of the remaining models had  $\Delta AIC_c >$  the intercept only model, and we did not consider them to be informative. Breeding dispersal distances were distributed evenly relative to each of the independent variables (Fig. 3).

TABLE 3. Relative importance ( $w_+$ ) of variables in models of breeding dispersal probability of California Spotted Owls ( $n = 535$ ) in northeastern California, 1990–2001.

Variable	$w_+$
Social status	1.00
Territory quality	0.99
Age class	0.96
Reproduction	0.78
Social status*Territory quality	0.76
Reproduction*Territory quality	0.57
Sex	0.54
Sex*Reproduction	0.30

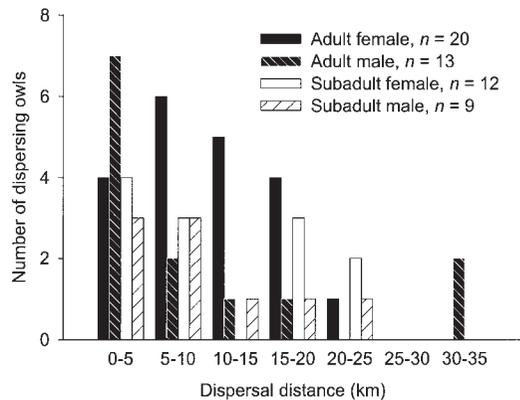


FIGURE 2. Breeding dispersal distances of California Spotted Owls in northeastern California, 1990–2001.

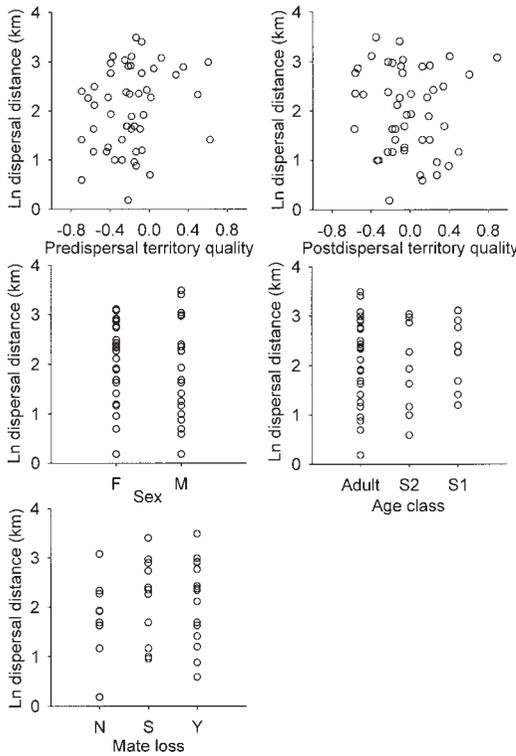


FIGURE 3. Breeding dispersal distance (log-transformed) as a function of territory quality, sex, age class, and social status for California Spotted Owls in northeastern California, 1990–2001. Territory quality was based on reproductive output of a site relative to all other sites. Key to age classes: S1 = first-year subadult; S2 = second-year subadult. Key to mate loss: N = paired and did not lose mate, S = single, Y = paired and lost mate.

CONSEQUENCES OF BREEDING DISPERSAL

Territory quality data were available for 39 of the owls that dispersed. Owls that dispersed tended to improve their territory quality, with 72% of dispersal movements to a territory of higher quality than the original territory (Fig. 4).

Of single owls that dispersed, 86% were paired following dispersal ( $n = 7$ ), whereas 57% of single owls that did not disperse were paired the following year ( $n = 14$ ,  $\chi^2 = 1.7$ ,  $P > 0.10$ ). Among owls that apparently lost their mates, 13 of 16 (81%) were paired following dispersal and the social status of the remaining three owls was unknown. Of owls that lost their mates and did not disperse, 73 of 78 (94%) were paired the following year. Differences between dispersing and philopatric owls that lost their mates were not significant regardless of whether we assumed the three owls with unknown fates were paired ( $\chi^2 = 1.1$ ) or single ( $\chi^2 = 2.6$ ).

DISCUSSION

BREEDING DISPERSAL PROBABILITY

California Spotted Owls exhibited a low rate of breeding dispersal (7%). As we hypothesized, the probability of breeding dispersal was higher for younger owls, single owls, paired owls that lost their mates, owls at lower quality sites, and owls that failed to reproduce in the year preceding dispersal. In contrast to our hypothesis, sex had little effect on the probability of breeding dispersal. Rates of pair bond separa-

TABLE 4. Models of breeding dispersal distance ( $D$ ) for California Spotted Owls ( $n = 37$ ) in northeastern California, 1990–2001. Models are ordered by  $AIC_c$ . First- and second-year subadult age classes were combined in this analysis.  $\log(\mathcal{L})$  is the log-likelihood,  $K$  is the number of parameters,  $\Delta AIC_c$  is the difference in Akaike’s information criterion from the top model, and  $w_i$  is the model weight.

Model	$\log(\mathcal{L})$	$K$	$\Delta AIC_c$	$w_i$
$D$ (Predispersal territory quality) <sup>a</sup>	-46.08	3	0.00	0.43
$D$ (Intercept only)	-47.80	2	1.05	0.25
$D$ (Age class)	-47.58	3	3.00	0.10
$D$ (Sex)	-47.71	3	3.26	0.08
$D$ (Postdispersal territory quality)	-47.78	3	3.40	0.08
$D$ (Social status)	-46.66	4	3.68	0.07
$D$ (Sex + Age class + Social status + Predispersal territory quality + Postdispersal territory quality)	-44.97	8	12.18	0.00

<sup>a</sup>  $AIC_c$  of top model = 98.89.

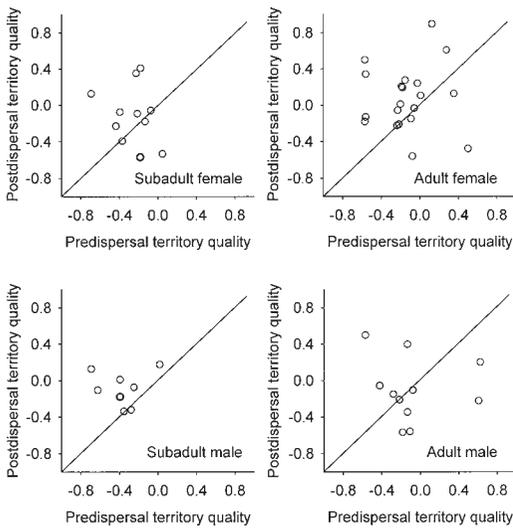


FIGURE 4. Pre- and postdispersal territory quality for California Spotted Owls in northeastern California, 1990–2001. Territory quality was based on reproductive output of a site relative to all other sites. Circles above the diagonal line represent owls that improved their territory quality by dispersing. Circles below the diagonal line represent owls that moved to territories of lower quality.

tion in California Spotted Owls were low and females moved in all observed cases of pair bond separation. The sex bias in dispersal of owls that separated pair bonds may indicate that male Spotted Owls have stronger site fidelity than female Spotted Owls; however, our sample size was quite small.

Average annual rates of breeding dispersal in California Spotted Owls were similar to those of Northern Spotted Owls: first-year subadults 32%, second-year subadults 20%, adults 8%, overall 8% ( $n > 5000$ ; Forsman et al. 2002; data adjusted to the calculations used herein). These relatively low rates of dispersal for adult Spotted Owls may reflect a high cost of breeding dispersal relative to the benefits of philopatry. Animals that disperse must compete with conspecifics for vacant territories, search for resources in unfamiliar areas, and possibly traverse suboptimal habitat with increased risk of starvation or predation. Philopatry, on the other hand, is presumed to provide more efficient exploitation of food resources and refugia from predators, and competitive advantage in territorial disputes (Greenwood and Harvey 1982).

Breeding dispersal rates among other raptor species were highly variable. In a 16-year study of Cooper's Hawks (*Accipiter cooperii*) in Wisconsin, zero males and 15% of females dispersed ( $n = 98$  and 71, respectively; Rosenfield and Bielefeldt 1996). Breeding dispersal rates for nonmigratory Barn Owls (*Tyto alba*) in Utah were approximately 4% annually ( $n > 500$ ; Marti 1999). In three populations of Sparrowhawks (*Accipiter nisus*) in Scotland and England with different population trends, approximately 30% of birds dispersed annually ( $n = 799$ ; Newton and Wyllie 1992). Among migratory Black Kites (*Milvus migrans*) in Spain, 26% of males and 33% of females changed territories annually ( $n = 121$  and 122, respectively; Forero et al. 1999). Similarly, among migratory Lesser Kestrels (*Falco naumanni*) in Spain, 19% of males and 34% of females dispersed annually ( $n = 173$  and 313, respectively; Serrano et al. 2001). Thirty-nine percent of male and 72% of female Merlins (*Falco columbarius*) in Saskatchewan dispersed in a mostly nonmigratory population ( $n = 28$  and 39, respectively; Warkentin et al. 1991).

The conditions associated with dispersal in California Spotted Owls were similar to those found for other raptors. In nonmigratory populations of Sparrowhawks, breeding failure was followed by increased dispersal of females (Newton and Wyllie 1992, Newton 2001). Nest predation increased breeding dispersal in Merlins (Wiklund 1996). Among Black Kites, the probability of breeding dispersal was higher from low-quality sites and following both breeding failure and mate loss (Forero et al. 1999). Both sexes showed an increasing tendency with age to stay on a territory in Northern Spotted Owls (Forsman et al. 2002), Sparrowhawks (Newton and Wyllie 1992, Newton 2001), and Black Kites (Forero et al. 1999). In Lesser Kestrels, the decreasing probability of dispersal with age was explained by decreasing probability of leaving a colony with increasing breeding experience in the colony (Serrano et al. 2001).

We found a negligible sex effect on the probability of breeding dispersal by California Spotted Owls even though female-biased dispersal was found in the Northern Spotted Owl (Forsman et al. 2002). This may be due in part to our smaller sample size compared to that of

Forsman et al. (2002;  $n = 440$ ). Additional studies have shown female-biased dispersal in Black Kites (Forero et al. 1999), Merlins (Warkentin et al. 1991, Wiklund 1996), Lesser Kestrels (Serrano et al. 2001), Cooper's Hawks (Rosenfield and Bielefeldt 1996), and Northern Goshawks (*Accipiter gentilis*, Detrich and Woodbridge 1994). However, the only raptor showing male-biased dispersal probability among seven species reviewed by Clarke et al. (1997) was the Northern Goshawk. Many of the studies reviewed by Clarke et al. (1997) reported that sex biases in dispersal probabilities were found only with individual birds that lost their mates or severed pair bonds.

#### BREEDING DISPERSAL DISTANCE

The median dispersal distance of California Spotted Owls was 7 km. Forty-three percent of dispersal events (92% of dispersals <6 km) were to adjacent territories. Our hypotheses regarding dispersal distance were not supported; subadult and single owls did not move farther than other owls.

In contrast to California Spotted Owls, younger Northern Spotted Owls moved farther than older owls (Forsman et al. 2002). In Merlins, females moved farther than males, and male breeding dispersal distance decreased with increasing population density (Wiklund 1996).

Breeding dispersal distance estimates would be biased toward shorter distances if owls moved beyond the study area boundary (Koenig et al. 1996). This bias was probably small for the following reasons. Breeding dispersal distances for only two owls were >23 km, whereas 50% of observed natal dispersal distances among the same territories were >23 km (range 3–76 km,  $n = 36$ ; JAB, unpubl. data). Owls undertaking natal and breeding dispersal had equal probability of being detected as residents on their new territories within the study area. Therefore, it is unlikely that dispersing nonjuvenile owls moved farther than recorded and remained undetected. Furthermore, median breeding dispersal distance for Northern Spotted Owls of both sexes within and between contiguous study areas in Oregon and Washington was 3.5 km ( $n = 440$ ), compared to median natal dispersal distance of approximately 14 km for males ( $n = 450$ ) and 23 km for females ( $n = 490$ ) in the same

study (Forsman et al. 2002). Natal dispersal distances were also greater than breeding dispersal distances for 61 of 69 terrestrial bird species reviewed by Paradis et al. (1998).

Home ranges of Spotted Owl pairs overlap (Forsman et al. 1984, Zabel et al. 1992), providing the opportunity for owls to easily discern vacancies in adjacent territories. For owls not moving into adjacent territories, it is unknown how far or what route the owls actually traveled before finding a territory vacancy; straight-line dispersal distances likely underestimate actual distances traveled in these cases (Wiens 2001).

#### CONSEQUENCES OF BREEDING DISPERSAL

Postdispersal territory quality was higher than predispersal territory quality for most owls, as hypothesized. Although we were unable to directly measure fitness pre- and postdispersal, owls that moved to higher quality territories increased their potential for reproducing. Similarly, female Black Kites that changed territories had increased reproductive success following dispersal (Forero et al. 1999). Our use of reproductive output as a measure of territory quality confounded the inherent reproductive abilities of individual owls with characteristics of the territories they occupied. That we found a change in territory quality for dispersing owls despite this confounding strengthens the evidence that owls were able to improve their potential fitness by dispersing.

Some owls, however, moved to sites of lower quality, as defined by mean reproductive output. This may reflect owls dispersing for reasons other than improved reproductive potential; e.g., in response to predators, habitat loss, or some other factor we did not measure.

The small sample of single owls was insufficient to reveal differences between dispersing and philopatric single owls in their subsequent social status. Although mate loss increased the probability of dispersal, pair status did not differ between dispersing and philopatric owls that previously lost their mates.

The timing and duration of breeding dispersal in Spotted Owls is unknown. Very few philopatric owls went unobserved when presumably they were present in their territories (<2% of intervals between observations were >1 year). In contrast, 36% of dispersing owls

were not seen for  $\geq 1$  year. This time lag may reflect that, for some owls, the dispersal process takes  $>1$  year. Some owls may enter a floater (nonterritorial) population before finding a vacancy in a suitable territory. While nonbreeding as a floater may be a cost of breeding dispersal (Danchin and Cam 2002), this cost may be offset by increasing the probability of obtaining a higher quality territory in the future.

Barred Owls (*Strix varia*) expanded their range into California from the north in 1981 (Dark et al. 1998). Only one Barred Owl was detected through 2001 on the Lassen study area, although several Spotted  $\times$  Barred Owl hybrids were observed holding territories and paired with Spotted Owls, beginning in 1999, and continuing through 2005 (JAB, unpubl. data). The range expansion of Barred Owls in Oregon and Washington appeared to displace Spotted Owls when Barred Owls were detected within 0.8 km of Spotted Owl territory centers (Kelly et al. 2003). If Barred Owls and hybrid owls continue to increase in the Lassen study area, this study will provide a baseline for comparison of future Spotted Owl dispersal rates, causes for, and consequences of dispersal. For example, if Spotted Owls are displaced by Barred Owls through competitive exclusion, we would expect to observe increased rates of dispersal by older and reproductively successful Spotted Owls. Furthermore, we may observe that dispersing owls move to lower quality territories.

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