



Breeding dispersal in an isolated population of Spotted Owls *Strix occidentalis*: evidence for improved reproductive output

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Breeding dispersal among territorial species is of interest to population biologists because leaving a territory carries fundamental risks to the dispersing individuals, and this may not outweigh the costs of maintaining the territory. Most studies of breeding dispersal have focused on species inhabiting spatially open populations, in which undetected emigration could impart a negative bias to estimates of dispersal. We studied breeding dispersal in an isolated (spatially closed) population of California Spotted Owl *Strix occidentalis occidentalis* in southern California for 12 years to assess factors that might correlate with breeding dispersal. Twenty-nine per cent ($n = 47$) of territorial females and 19% ($n = 35$) of territorial males dispersed at least once during the study. Annually, 0–13% of the territorial females and 0–12% of the territorial males dispersed. Among a set of *a priori* and *post hoc* models related to breeding dispersal, the top *a priori* model indicated that birds having higher reproductive output relative to the population average were less likely to disperse. A *post hoc* model based on an index of territory quality was ranked higher than the top *a priori* model and indicated that birds occupying higher quality territories were less likely to disperse. These two models were correlated and represented short- and long-term reproductive performance, respectively. Birds that dispersed also failed to fledge young in the year prior to dispersal, but the failure to fledge young did not, by itself, explain dispersal. Because Spotted Owls are long-lived, they may ultimately improve their reproduction by dispersing given that they would have future opportunities to breed over the long term. Birds whose mates are likely to have died tended to improve their reproductive success, whereas the relationship between reproductive success of birds that divorced was less clear. Substantial variation in breeding dispersal was unexplained by our analysis so it is likely that the motivation to disperse was a complex process in this population.

Keywords: California Spotted Owl, isolated population, *Strix occidentalis occidentalis*.

Dispersal is a basic life-history trait that is fundamental to population and evolutionary dynamics (Greenwood 1980, Greenwood & Harvey 1982). Breeding dispersal has been defined as the movement between successive breeding locations or

social groups (Greenwood & Harvey 1982, Clobert *et al.* 2001a). Numerous hypotheses have been proposed to explain breeding dispersal in birds. These include inbreeding avoidance, heritability, mate choice, site choice, nest-site quality, predation risk, breeding success, social constraints, rapid re-nesting, resource depletion and resource competition (for reviews of these hypotheses, see Greenwood & Harvey 1982, Korpimäki 1987, 1993, Jackson *et al.* 1989, Payne & Payne 1993, Gowaty & Plissner 1997, Daniels & Walters 2000, Clobert *et al.* 2001b). Some of these hypotheses can be

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examined simultaneously using model selection if appropriate data are available (Burnham & Anderson 1998, Blakesley *et al.* 2006). Here we examine a set of plausible *a priori* and *post hoc* hypotheses that could explain breeding dispersal of California Spotted Owls *Strix occidentalis occidentalis*. Spotted Owls are long-lived and do not breed every year, and the study was not sufficiently long to determine all breeding fates of all marked territorial individuals that dispersed during this 12-year period. Therefore, we considered breeding dispersal within the context of movement from an established territory to a new territory (i.e. social group, in this case a pair, Clobert *et al.* 2001a). Because Spotted Owls can engage in natal dispersal over several years, we took particular care to distinguish between natal dispersal and breeding dispersal (see below).

Most studies of breeding dispersal have been conducted in spatially open populations (i.e. study areas of finite size within larger areas of suitable habitat); our study of California Spotted Owls was unique among Spotted Owl studies and indeed most other studies of avian dispersal because it was an isolated population (i.e. a spatially closed population separated from other populations by large expanses of unsuitable habitat; LaHaye *et al.* 1994, 2001). Moreover, we colour-marked over 95% and annually detected over 82% of the territorial population, presenting a unique opportunity to assess breeding dispersal of these birds with little bias due to undetected movements (Barrowclough 1978, LaHaye *et al.* 2004, Zimmerman *et al.* 2007). Given the relative rarity of breeding dispersal events in Spotted Owls, our specific objective was to compare hypotheses about factors that may be correlated with breeding dispersal rather than estimating the probability that any given individual would disperse in a particular year.

METHODS

Study area

The study area (2140 km²) was approximately 140 km east of Los Angeles, California, and encompassed the San Bernardino Mountains. Elevations ranged from 800 to 3500 m. The climate was Mediterranean, most precipitation falling during the winter months (Minnich 1986). Elevation, aspect and topography within the mountain

range strongly influenced annual precipitation, which varied from < 500 to > 10 000 mm (Minnich 1988).

The San Bernardino Mountains are one of many isolated mountain ranges in southern California that rise above surrounding desert (Vasek & Barbour 1988), semi-desert (Mooney 1988) and urban landscapes. These ranges support a diverse assemblage of shrub and forest vegetation types not found at lower elevations (Minnich 1998). Spotted Owls within our study area are forest obligates and mostly use mixed evergreen (Sawyer *et al.* 1988) and montane forests (Thorne 1988, Gutiérrez *et al.* 1995). Thus, forests capable of supporting Spotted Owls are isolated on mountains within this region (Noon & McKelvey 1992, LaHaye *et al.* 1994). The nearest mountain ranges to our population are approximately 10 km to the west and 20 km to the south, both separated from the study area by chaparral and desert habitats unsuitable for Spotted Owls and likely to represent important barriers to dispersal (Noon & McKelvey 1992, Zimmerman *et al.* 2007).

Owl detection surveys

The objective was to locate and mark every Spotted Owl detected in this mountain range. Thus, each year we systematically surveyed all forest areas (including patches as small as 20 ha) that could potentially harbour Owl nest-sites or roost sites. We conducted surveys at night by imitating Owl vocalizations for a minimum of 15 min at 'call points' or by calling regularly while walking survey routes (Forsman 1983, Franklin *et al.* 1996). We established call points along roads and trails approximately every 0.9 km and recorded the time of response, sex and location of all Owls detected. We attempted to capture all Spotted Owls located and ringed them with numbered locking aluminium leg-rings. Adult and subadult (i.e. non-juvenile) Owls were ringed with a combination colour-ring and tab that uniquely identified each individual (Franklin *et al.* 1996). We attempted to capture all juvenile Owls and mark them with a colour-ring unique to their cohort. The sex of non-juvenile Owls was identified by voice, behaviour or morphology; we never recorded an error in assignment of sex using these characteristics during multiple observations of birds over time (Gutiérrez *et al.* 1995).

Identification of dispersal and reproductive events

In the study we captured and ringed the majority of Owls in the first year. We estimate that we had captured > 95% of the Owl population by year 3 of the study because we encountered < 2% of unmarked Owls in our annual surveys and most of these could be accounted for by the number of juveniles that we failed to capture in previous years. Thus, we had close to a complete enumeration of the entire Spotted Owl population after the first few years of the study (LaHaye *et al.* 2001, 2004). We assigned colour-ringed Owls to individual territories based on the locations of their nest-sites and roost sites over time, presence of suitable habitat, and social interactions between individual male and female Owls (e.g. courtship, territory defence). Spotted Owls often used different nest-sites within the territory (Gutiérrez *et al.* 1995), but over time nest-sites and roost sites of ringed birds accurately defined the general limits of the core area for territorial birds. Spotted Owls are obligate natal dispersers (LaHaye *et al.* 2001, Forsman *et al.* 2002). Following initiation of natal dispersal, juveniles usually attempt to establish a home-range within a year, but may continue dispersal if they do not successfully establish a territory in their first year (Forsman *et al.* 2002). Thus, based on observing Owls defend territories and knowing they show obligate natal dispersal, we defined a breeding dispersal event for our analysis as occurring when a ringed bird was detected on an established territory (i.e. it exhibited territorial behaviour with or without a mate (singleton)) and then moved to a different territory that had a history of occupancy by other Owls or a new location with no known history of Owl occupancy (usually they moved into a different canyon or > 5 km). We excluded all first- and second-year sub-adult Owls from the analysis if they were singletons because we could not be certain that they had actually established a territory as a singleton or were still in the process of natal dispersal. We included sub-adults if they formed part of a territorial pair.

The reproductive history of every subadult and adult Spotted Owl was used in the analysis. In general, we were able to assess the reproductive output of > 95% of individual Owls each year by following Owls to their nests or young after we had fed them live mice (Forsman 1983, Franklin

et al. 1996). This technique also allowed us to ascertain an Owl's social status (paired or not paired). Tail shape and colour pattern allowed classification of Owls into four age classes (juvenile, first-year sub-adult, second-year sub-adult, adult; Moen *et al.* 1991). Our study was not sufficiently long to analyse the influence of age as a continuous covariate on dispersal. Instead, we used the general categorical ages of sub-adults and adults. When birds were located in each year, we estimated their location in Universal Transverse Mercator coordinates (UTMs) using topographic maps, a compass and elevation in years before the availability of global positioning systems (GPS), and GPS units thereafter. Owl nests were usually located substantial distances from each other (> 1.4 km), so based on location, a high sampling proportion of birds and individual colour rings we were able to ascertain with certainty the reproductive success of individual Owls.

Statistical analyses

We aimed to assess the factors that were correlated with the probability that an individual would disperse. An alternative approach would be to estimate the probability that any given bird will disperse in the population and assess the factors that could predict those dispersals. The second approach requires substantially more data than we had in our study and would require a different analytical design (e.g. repeated sampling and incorporating individual detection probabilities each year for each bird). We already knew that the probability of a particular territorial individual dispersing in a given year is extremely low (see below), so our primary interest in this analysis was to compare hypotheses that ranged from those that change temporally (e.g. breeding success during a given year) to those that do not change at all through time (e.g. sex). To account for these different variables accurately, we would have to consider models with different hierarchies (*sensu* Royle & Dorazio 2008) because sex is an attribute of an individual whereas reproductive success is an attribute of individual by year. Models with different statistical hierarchies are difficult to compare directly (Royle & Dorazio 2008, Link & Barker 2010). Therefore, we used a non-repeated-measures logistic regression (Agresti 1996) to assess the factors that were correlated with the probability that an individual would disperse, which was an

appropriate approach given our objectives, data and study design (Bennetts *et al.* 2001). Our response variable was binary: 1 = individuals that dispersed and 0 = individuals that did not disperse. If an individual dispersed more than once, we randomly selected one dispersal event to include in the analysis. We used sex, age, reproductive performance and mate loss, which were all based on the year prior to dispersal, as predictor variables. For non-dispersers, we randomly selected a year from among all years that non-dispersers were on territories as a reference year to calculate predictor variables. We also calculated the relative (i.e. relative to the rest of the population) reproductive performance of each individual prior to dispersal as an additional predictor variable. Relative reproductive performance was estimated as the average annual reproduction from all years that individual birds were on their initial territory for dispersers (or reference year for non-dispersers) rather than the single year prior to dispersal. We defined mate loss as the disappearance of a mate that was never detected again, whereas divorce was the dissolution of a pair bond and both individuals were detected later on different territories.

We used model selection based on information theory (Burnham & Anderson 1998) to assess the relative strength of 12 hypotheses that we developed *a priori* to the analysis and one *post hoc* model (Table 1; see Discussion for details of the *post hoc* model). We developed hypotheses for which we had data (sex, age, reproductive success, mate loss) to assess factors that might influence breeding

dispersal. These factors have all been suggested to influence dispersal in other studies. We predicted that females were more likely to disperse to new territories than males because males are more vocal in territory defence. Thus, males may have greater investment in maintaining a particular territory rather than dispersing. We also predicted that young birds (first- and second-year sub-adults) were more likely to disperse than adults, again because of experience or investment. Because we could not monitor Spotted Owls continuously, we often did not know whether a bird's failure to fledge young was due to its failure to nest or to the failure of its nesting attempt. Therefore, we estimated the number of young fledged (reproductive output) as our basic measure of reproductive success. We estimated two measures of reproductive success because either one could influence dispersal. First, we assigned individuals a value of 1 if they fledged ≥ 1 young the year prior to dispersal and 0 if they fledged no young the year prior to dispersal as a measure of short-term reproductive success. We predicted that individuals that failed to breed in a given year were more likely to disperse to a new territory the following year than ones that successfully fledged young. Second, we estimated the effect of long-term reproductive success on the probability of dispersal by estimating the mean annual reproductive output for each individual prior to dispersal minus the mean annual reproductive output of the entire population across all years of the study. We predicted that individuals with lower than average long-term

Table 1. Proportion of California Spotted Owls dispersing to new breeding territories (total number of observed individuals for each year, including dispersers and non-dispersers in parentheses) by sex and age class, and year, in the San Bernardino Mountains, USA, 1987–1997.

Year*	Adult		Sub-adult	
	Female	Male	Female	Male
1987	0.00 (21)	0.03 (29)	0.00 (1)	0.00 (0)
1988	0.11 (38)	0.13 (48)	0.00 (2)	0.00 (1)
1989	0.05 (62)	0.08 (64)	0.00 (2)	0.13 (8)
1990	0.10 (69)	0.06 (67)	0.22 (9)	0.13 (8)
1991	0.10 (61)	0.05 (60)	0.21 (19)	0.06 (16)
1992	0.05 (55)	0.02 (56)	0.11 (9)	0.00 (6)
1993	0.04 (54)	0.03 (64)	0.00 (11)	0.18 (11)
1994	0.02 (56)	0.02 (66)	0.06 (17)	0.00 (13)
1995	0.03 (63)	0.02 (57)	0.38 (8)	0.07 (14)
1996	0.06 (62)	0.02 (53)	0.25 (12)	0.33 (6)
1997	0.02 (61)	0.03 (60)	0.00 (4)	0.00 (8)

*We deleted 1998 data from the table because dispersal events could not be estimated for the last year of the study.

reproductive output were more likely to disperse than those with average or above average reproductive output. We were unable to estimate lifetime reproduction because these Owls are long-lived relative to the length of our study and we had few complete life histories to quantify this life-history trait.

We used the corrected Akaike information criterion (AIC_c) to rank the models relative to their ability to support the data (Burnham & Anderson 1998) and a 95% likelihood ratio confidence interval of regression coefficient estimates to assess whether individual parameter estimates were correlated with the probability of dispersal. Confidence intervals that did not include zero indicated a strong correlation between that predictor variable and breeding dispersal. The Hosmer and Lemeshow goodness-of-fit test (Hosmer & Lemeshow 2000) was used to assess the fit of a global model (the model including additive effects of age, sex, reproductive failure and pre-dispersal reproductive success). We estimated an overdispersion parameter by dividing the Pearson chi-square value of a global model by its degrees of freedom. If this parameter was > 1 , we adjusted variances and covariances for overdispersion from a binary distribution (Burnham & Anderson 1998). We estimated a rescaled coefficient of determination using techniques described by Nagelkerke (1991) to evaluate the overall performance of our best model (as opposed to the relative performance of models identified with AIC_c). All model selection analyses used SAS (Proc LOGISTIC: SAS Institute, 2000). Paired t -tests were used to examine differences in reproductive output before and after dispersal.

RESULTS

We ringed and colour-marked 342 (182 males and 160 females) territorial and non-juvenile Spotted Owls from 1987 to 1998. Forty-three females dispersed once, three dispersed twice and one dispersed three times. Thirty-two males dispersed once, six dispersed twice and one dispersed three times. We randomly selected one dispersal event for those birds that dispersed more than once. Of the 86 Owls that dispersed, we had sufficient information to compare individual traits (i.e. known age, sex and reproductive status) of 47 individual females and 35 individual males that dispersed (29 and 19% of ringed females and males, respectively, for which we had sufficient

reproductive history data for analysis). Annually, 0–12% of males and 0–13% of females dispersed (Table 1). Sixteen females (34%) and nine males (26%) that dispersed were also involved in divorce. In four cases, a pair dispersed together to occupy a neighbouring, unoccupied territory (i.e. the location was a former territory of an Owl pair, but was unoccupied at the time of these dispersal events). In the remainder of the birds that dispersed, their mates were never seen again and were presumed dead, or the birds were singletons when originally found before they dispersed. In the latter case, singletons used in our analysis were adult birds that we detected defending a territory (see above). They could have been a bird establishing a new territory or a bird whose mate had died, but we were unaware of this death. Hence, these were cases of breeding dispersal and not natal dispersal.

The Hosmer and Lemeshow test ($P = 0.72$) indicated that the global model fitted the data. The estimated dispersion parameter was 1.02, so we adjusted variances and covariances accordingly. A model representing the long-term reproductive performance prior to dispersal was the top ranked *a priori* model correlated with breeding dispersal (Table 2). The best *a priori* model indicated that birds whose mean reproductive output was higher than the overall average of the entire population were less likely to disperse than those with lower than average reproductive output ($\hat{\beta}_{\text{reproduction}} = -1.01$, 95% confidence interval (CI) = -1.53 to -0.54). A closely competing *a priori* model suggested weak support for the hypothesis that females were more likely to disperse than males ($\hat{\beta}_{\text{sex}} = -0.59$, 95% CI = -1.22 to $+0.04$). Although this second ranked model included an interaction between average reproductive output and sex, the interaction was not strongly supported ($\hat{\beta}_{\text{reproduction} \times \text{sex}} = -0.38$, 95% CI = -1.39 to $+0.64$). Birds that lost their mates (i.e. birds whose mates probably died) and subsequently dispersed improved their reproductive output following dispersal ($\bar{x}_{\text{pre}} = 0.36$, $\bar{x}_{\text{post}} = 0.79$, $n = 30$; $t = 2.13$, $P = 0.04$). Although our analysis suggested that divorced birds might not have statistically improved their reproductive output if they dispersed ($\bar{x}_{\text{pre}} = 0.23$, $\bar{x}_{\text{post}} = 0.52$, $n = 25$; $t = 1.68$, $P = 0.11$), the point estimate of reproduction for divorced birds was over twice as high following dispersal. This simple comparison is likely to be confounded by the substantial annual variation in reproductive output of Spotted Owls regardless of

Table 2. Results of logistic regression modelling of breeding dispersal of California Spotted Owls in the San Bernardino Mountains, California, USA, 1987–2005.

Model*	–2 Log likelihood	No. of parameters	AIC _c	ΔAIC _c	AIC _c weight
Pre-dispersal reproductive success	340.48	2	344.52	0.00	0.07
Pre-dispersal reproductive success × sex interaction	336.91	4	345.04	0.52	0.05
Pre-dispersal reproductive success × age interaction	340.18	4	348.30	3.78	0.01
Reproductive failure	345.05	2	349.08	4.57	0.01
Reproductive failure × sex interaction	342.15	4	350.28	5.76	0.00
Mate loss	346.26	2	350.30	5.78	0.00
Reproductive failure × age interaction	343.89	4	352.01	7.50	0.00
Pre-dispersal reproductive success × sex × age interaction	336.07	8	352.51	8.00	0.00
Reproductive failure × sex × age interaction	340.17	8	356.61	12.10	0.00
Sex	356.54	2	360.57	16.06	0.00
Age	357.86	2	361.90	17.38	0.00
Age × sex interaction	354.34	4	362.46	17.95	0.00

*Global model used for goodness-of-fit test not included in this model set.

dispersal (Franklin *et al.* 2004). Thus, we believed there was some evidence for a reproductive benefit associated with both mate loss and divorce.

DISCUSSION

Birds in spatially open populations can disperse beyond the boundaries of a study area of finite size, thus precluding their detection (Barrowclough 1978), and hence potentially leading to biased estimates of dispersal. Our study avoids this important confounding issue because the population is essentially spatially closed (Zimmerman *et al.* 2007). Twenty-five per cent of all marked individuals dispersed at least once during the 12-year study and when they did disperse they did not disperse far from their original territory (mean breeding dispersal distances = 3.65 km, *sd* = ±4.85 km, *n* = 95). This was similar to Forsman *et al.*'s (2002) observations for Northern Spotted Owls *S. o. caurina*. In addition, Zimmerman *et al.* (2007) showed for our study population that estimates of adult survival were unbiased by undetected emigration.

Birds having higher reproductive output were less likely to disperse. We based our inference on our top *a priori* model, although it was outperformed by a *post hoc* model. Subsequent to our initial analysis, Blakesley *et al.* (2006) published a model that was based on a metric depicting territory quality, which was informative in their study of a spatially open population of Spotted Owls in the Sierra Nevada, California. This metric was the relative reproductive output of Owls on each territory summed across years. Therefore, we conducted *post hoc* analysis using Blakesley *et al.*'s

(2006) territory quality model. Blakesley *et al.*'s (2006) *post hoc* model was ranked 4.95 AIC_c units better than our best *a priori* model with an AIC_c weight of 0.85. Nevertheless, this *post hoc* model indicated similar patterns to the top-ranked *a priori* model, because territory quality and long-term reproductive performance were correlated ($r = 0.49$, $P < 0.01$). Specifically, birds were less likely to disperse from higher quality territories, based on relative reproductive output of all Owls occupying a territory ($\beta_{\text{quality}} = -2.27$, 95% CI = –3.26 to –1.27). Thus, reproduction either with respect to an individual bird's performance on a territory or with respect to all birds occupying a particular territory (i.e. the index of territory quality) was correlated with breeding dispersal, as observed in other bird populations (Greenwood 1980, Jackson 1994, Murphy 1996, Gowaty & Plissner 1997, Haas 1998, Forero *et al.* 1999, Daniels & Walters 2000), including a non-isolated population of California Spotted Owls (Blakesley *et al.* 2006). Studies of the mechanisms motivating breeding dispersal have often focused on predictions that involve improving reproduction. For example, Drilling and Thompson (1988) and Forero *et al.* (1999) reported improved reproduction after dispersal, whereas Payne and Payne (1993), Murphy (1996) and Robinson and Oring (1997) did not. It was not clear in our population that breeding dispersal always improved reproductive success, and our results regarding improvement of reproduction following dispersal were different from those expected. For example, we expected that if a bird's mate died and the bird dispersed, its chances for improved reproduction would be

lower because it would have both a new mate and a new territory, both of which might require experience before attaining successful reproduction; we found the opposite. On the other hand, if a bird divorced, we expected that a divorcer would improve its reproductive output but not the divorcee, which would result in no net gain because the behaviour of divorce was confounded with dispersal (i.e. we could not determine who precipitated the divorce). However, birds that divorced did have a higher point estimate for reproductive output following dispersal. Forsman *et al.* (2002) reported that females and younger birds had higher breeding dispersal in Northern Spotted Owls, but we only found weak support for a sex effect with our data using a model selection framework.

Studies of dispersal in several bird taxa, including Spotted Owls, have suggested there is a tendency for males to be more site faithful than females (James *et al.* 1989, Payne & Payne 1993, Jackson 1994, Forsman *et al.* 2002). Korpimäki (1987, 1988, 1993) reported that male Tengmalm's Owls *Aegolius funereus* tend to stay on a territory for life but females regularly disperse in an apparent attempt to locate males that had more breeding experience and higher quality territories. Forsman *et al.* (2002) and Blakesley *et al.* (2006) did not find the same relationship between sex and the likelihood of breeding dispersal in Spotted Owls. Forsman *et al.* (2002) reported that female Northern Spotted Owls were more likely to disperse than males, whereas Blakesley *et al.* (2006) did not detect this pattern. Our model did not explain any variation in dispersal, but there was weak support for females being more likely to disperse than males based on information theoretic ranking and a parameter 95% CI that slightly overlapped zero.

Age of dispersers also has been a factor of interest in dispersal because younger birds in many studies tended to disperse more often than adults (Payne & Payne 1993, Morton 1997, Daniels & Walters 2000), including Northern Spotted Owls (Forsman *et al.* 2002). We did not find this relationship in our modelling. Although sub-adults often dispersed, it appeared that this was associated with low reproductive output. That is, younger Owls in general had lower reproductive output than adults (Franklin *et al.* 2004, LaHaye *et al.* 2004), but dispersal was more strongly correlated with breaking of pair bonds (death or divorce) and territory quality (long-term reproductive output) than with age alone.

The decision by territorial birds to disperse is critical given the inherent risks associated with abandoning a familiar territory, particularly the very large territories and home-ranges occupied by Spotted Owls (Gutiérrez *et al.* 1995). Although many hypotheses have been proposed to account for such dispersal, it was evident from our study that some of the factors (age, sex and their interactions with measures of reproductive success), often invoked as reasons for dispersal in birds, were not informative in our study. If examined by themselves, some of these factors might have shown apparently statistically significant relationships, but our comparative modelling approach showed that most were relatively uninformative. The *post hoc* modelling of an index of territory quality (long-term reproductive success) derived by Blakesley *et al.* (2006) explained a slightly higher proportion of variation in our data regarding dispersal than the short-term reproductive success. The re-scaled coefficients of determination were 0.09 and 0.11 for the top-ranked *a priori* and *post hoc* models, respectively, which indicated that these models explained 9 and 11% of the variation in breeding dispersal. Also of interest was the fact that birds whose mates died improved their reproductive output, whereas it was not entirely clear whether birds that divorced did so. In addition, because our best model explained only 9% of the variation in dispersal, other factors must be contributing to breeding dispersal among California Spotted Owls. For example, prey availability (Ward 2001) may have provided a more direct measure of territory quality that could have explained a much greater proportion of variation in breeding dispersal probability. The conditional inferences of our results suggested that dispersing birds usually went through a divorce or lost a mate, but that mate loss or divorce by itself was probably less important than the correlation between long-term reproductive success and dispersal. Nevertheless, because both our top *a priori* and *post hoc* models considering reproduction did not explain much variation in the data it was clear that more factors were probably involved in dispersal than the ones we examined.

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REFERENCES

- Agresti, A.** 1996. *An Introduction to Categorical Data Analysis*. New York: Wiley.
- Barrowclough, G.F.** 1978. Sampling bias in dispersal studies based on finite area. *Bird-Banding* **49**: 333–341.
- Bennetts, R.E., Nichols, J.D., Leberton, J.-D., Pradel, R., Hines, J.E. & Kitchens, W.M.** 2001. Methods for estimating dispersal probabilities and related parameters using marked animals. In Clobert, J., Danchin, E., Dhondt, A.A. & Nichols, J.D. (eds) *Dispersal*: 3–17. Oxford: Oxford University Press.
- Blakesley, J.A., Anderson, D.R. & Noon, B.R.** 2006. Breeding dispersal in the California Spotted Owl. *Condor* **108**: 71–81.
- Burnham, K.P. & Anderson, D.R.** 1998. *Model Selection and Inference: A Practical Information-theoretic Approach*. New York: Springer.
- Clobert, J., Wolff, E.J.O., Nichols, J.D., Danchin, E. & Dhondt, A.A.** 2001a. Introduction. In Clobert, J., Danchin, E., Dhondt, A.A. & Nichols, J.D. (eds) *Dispersal*: xvii–xxi. Oxford: Oxford University Press.
- Clobert, J., Danchin, E., Dhondt, A.A. & Nichols, J.D.** (eds) 2001b. *Dispersal*. Oxford: Oxford University Press.
- Daniels, S.J. & Walters, J.R.** 2000. Between-year breeding dispersal in Red-Cockaded Woodpeckers: multiple causes and estimated cost. *Ecology* **81**: 2473–2484.
- Drilling, N.E. & Thompson, C.F.** 1988. Natal and breeding dispersal in House Wrens (*Troglodytes aedon*). *Auk* **105**: 480–491.
- Forero, M.G., Donazar, J.A., Blas, J. & Hiraldo, F.** 1999. Causes and consequences of territory change and breeding dispersal distance in the Black Kite. *Ecology* **80**: 1298–1310.
- Forsman, E.D.** 1983. *Methods and materials for locating and studying Spotted Owls*. Portland, OR: US Forest Service. Gen. Tech. Rep. PNW-GTR-162.
- Forsman, E.D., Anthony, R.G., Reid, J.A., Loschl, P.J., Sovern, S.G., Taylor, M., Biswell, B.L., Ellingson, A., Meslow, E.C., Miller, G.S., Swindle, K.A., Thraikill, J.A., Wagner, F.F. & Seaman, D.E.** 2002. Natal and breeding dispersal of Northern Spotted Owls. *Wild. Monogr.* **149**: 1–35.
- Franklin, A.B., Anderson, D.R., Forsman, E.D., Burnham, K.P. & Wagner, F.W.** 1996. Methods for collecting and analyzing demographic data on the Northern Spotted Owl. In Forsman, E.D., DeStefano, S., Raphael, M.G. & Gutiérrez, R.J. (eds) *Studies in Avian Biology*, vol. 17: 12–20. Lawrence, KS: Allen Press.
- Franklin, A.B., Gutiérrez, R.J., Nichols, J.D., Seamans, M.E., White, G.C., Zimmerman, G.S., Hines, J.E., Munton, T.E., LaHaye, W.S., Blakesley, J.A., Steger, G.N., Noon, B.R., Shaw, D.W.H., Keane, J.J., McDonald, T.L. & Britting, S.** 2004. Population dynamics of the California Spotted Owl: a meta-analysis. *Ornith. Monogr.* **54**: 1–54.
- Gowaty, P.A. & Plissner, J.H.** 1997. Breeding dispersal of Eastern Bluebirds depends on nesting success but not on removal of old nests: an experimental study. *J. Field Orn.* **68**: 323–330.
- Greenwood, P.J.** 1980. Mating systems, philopatry and dispersal in birds and mammals. *Anim. Behav.* **28**: 1140–1162.
- Greenwood, P.J. & Harvey, P.H.** 1982. The natal and breeding dispersal of birds. *Ann. Rev. Ecol. Syst.* **13**: 1–21.
- Gutiérrez, R.J., Franklin, A.B. & LaHaye, W.S.** 1995. Spotted Owl (*Strix occidentalis*). In Poole, A. & Gill, F. (eds) *The Birds of North America*, No. 179: 1–28. Washington, DC: Academy of Natural Sciences, and Philadelphia: and American Ornithologists' Union.
- Haas, C.A.** 1998. Effects of prior nesting success on site fidelity and breeding dispersal: an experimental approach. *Auk* **115**: 929–936.
- Hosmer, D.W. & Lemeshow, S.** 2000. *Applied Logistic Regression*, 2nd edn. New York: Wiley.
- Jackson, D.B.** 1994. Breeding dispersal and site-fidelity in three monogamous wader species in the Western Isles, U.K. *Ibis* **136**: 463–473.
- Jackson, W.M., Rohwer, S. & Nolan, V. Jr** 1989. Within-season breeding dispersal in Prairie Warblers and other passerines. *Condor* **91**: 233–241.
- James, P.C., Warkentin, I.G. & Oliphant, L.W.** 1989. Turn-over in dispersal in urban Merlins *Falco columbarius*. *Ibis* **131**: 426–429.
- Korpimäki, E.** 1987. Selection for nest-hole shift and tactics of breeding dispersal in Tengmalm's owl *Aegolius funereus*. *J. Anim. Ecol.* **56**: 185–196.
- Korpimäki, E.** 1988. Effects of territory quality on occupancy, breeding performance and breeding dispersal in Tengmalm's owl. *J. Anim. Ecol.* **57**: 97–108.
- Korpimäki, E.** 1993. Does nest-hole quality, poor breeding success or food depletion drive the breeding dispersal of Tengmalm's owls? *J. Anim. Ecol.* **62**: 606–613.
- LaHaye, W.S., Gutiérrez, R.J. & Akçakaya, H.R.** 1994. Spotted owl metapopulation dynamics in southern California. *J. Anim. Ecol.* **63**: 775–785.
- LaHaye, W.S., Gutiérrez, R.J. & Dunk, J.R.** 2001. Natal dispersal of the Spotted Owl in southern California: dispersal profile of an insular population. *Condor* **103**: 691–700.
- LaHaye, W.S., Zimmerman, G.S. & Gutiérrez, R.J.** 2004. Temporal variation in the vital rates of an insular population of Spotted Owls (*Strix occidentalis occidentalis*): contrasting effects of weather. *Auk* **121**: 1056–1069.
- Link, W.A. & Barker, R.J.** 2010. *Bayesian Inference with Ecological Applications*. Amsterdam: Academic Press.
- Minnich, R.A.** 1986. Snow levels and amounts in the mountains of southern California. *J. Hydrol.* **89**: 37–58.
- Minnich, R.A.** 1988. The biogeography of fire in the San Bernardino Mountains of California: a historical study. *University of California Publications in Geography*, Vol. 28. Los Angeles: University of California Press.

- Minnich, R.A.** 1998. Vegetation, fire regimes, and forest dynamics. In Miller, P.R. & McBride, J.R. (eds) *Oxidant Air Pollution Impacts in the Montane Forests of Southern California: A Case Study of the San Bernardino Mountains*: 44–80. New York: Springer.
- Moen, C.A., Franklin, A.B. & Gutiérrez, R.J.** 1991. Age determination of subadult northern Spotted Owls in northwest California. *Wildl. Soc. Bull.* **19**: 489–493.
- Mooney, H.A.** 1988. Southern coastal scrub. In Barbour, M.G. & Major, J. (eds) *Terrestrial Vegetation of California*, 2nd edn: 471–490. Sacramento: California Native Plant Society.
- Morton, M.L.** 1997. Natal and breeding dispersal in the Mountain White-Crowned Sparrow *Zonotrichia leucophrys oriantha*. *Ardea* **85**: 145–154.
- Murphy, M.T.** 1996. Survivorship, breeding dispersal and mate-fidelity in Eastern Kingbirds. *Condor* **98**: 82–92.
- Nagelkerke, N.J.D.** 1991. A note on a general definition of the coefficient of determination. *Biometrika* **78**: 691–692.
- Noon, B.R. & McKelvey, K.S.** 1992. Stability properties of the Spotted Owl metapopulation in southern California. In Verner, J., McKelvey, K., Noon, B.R., Gutiérrez, R.J., Gould, G.I. Jr & Beck, T.W. (eds) *The California Spotted Owl: A Technical Assessment of its Current Status: PSW-GTR-133*: 187–206. Albany, CA: Pacific Southwest Research Station, Forest Service, US Department of Agriculture.
- Payne, R.B. & Payne, L.L.** 1993. Breeding dispersal in Indigo Buntings: circumstances and consequences for breeding success and population structure. *Condor* **95**: 1–24.
- Robinson, J.A. & Oring, L.W.** 1997. Natal and breeding dispersal in American Avocets. *Auk* **114**: 416–430.
- Royle, J.A. & Dorazio, R.M.** 2008. *Hierarchical Modeling and Inference in Ecology. The Analysis of Data from Populations, Metapopulations, and Communities*. Amsterdam: Academic Press.
- SAS Institute.** 2000. *Version 8.01*. Cary, NC: SAS Institute, Inc.
- Sawyer, J.O., Thornburgh, D.A. & Griffin, J.R.** 1988. Mixed evergreen forest. In Barbour, M.G. & Major, J. (eds) *Terrestrial Vegetation of California*, 2nd edn: 359–382. Sacramento: California Native Plant Society.
- Thorne, R.F.** 1988. Montane and subalpine forests of the transverse and peninsular ranges. In Barbour, M.G. & Major, J. (eds) *Terrestrial Vegetation of California*, 2nd edn: 537–558. Sacramento: California Native Plant Society.
- Vasek, F.C. & Barbour, M.G.** 1988. Mojave desert scrub vegetation. In Barbour, M.G. & Major, J. (eds) *Terrestrial Vegetation of California*, 2nd edn: 835–868. Sacramento: California Native Plant Society.
- Ward, J.P. Jr** 2001. *Ecological responses by Mexican Spotted Owls to environmental variation in the Sacramento Mountains*. PhD Thesis, Colorado State University.
- Zimmerman, G.S., Gutiérrez, R.J. & LaHaye, W.S.** 2007. Finite study areas and vital rates: sampling effects on estimates of spotted owl survival and population trends. *J. Appl. Ecol.* **44**: 963–971.

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