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NATAL DISPERSAL OF THE SPOTTED OWL IN SOUTHERN CALIFORNIA: DISPERSAL PROFILE OF AN INSULAR POPULATION

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Abstract. We studied the dispersal patterns of an insular population of California Spotted Owls (*Strix occidentalis occidentalis*) in southern California from 1987–1998. The study area encompassed the entire San Bernardino Mountains and included a nested, 535-km^2 study area which we used to evaluate the effects of study area size on dispersal parameter estimation. One hundred and twenty-nine of the 478 banded juvenile owls (27%) had entered the territorial population by 1998. Over half of the successful dispersers became territorial within one year. Additionally, all females and 95% of the males occupied territories within three years. Twenty-three sibling pairs and one set of triplets dispersed successfully. Sibling dispersal distances were not correlated. Sixty-seven males and 62 females dispersed 2.3–36.4 km (mean ± SD = 10.1 ± 7.6 km) and 0.4–35.7 km (mean ± SD = 11.7 ± 8.1 km), respectively. The difference between male and female mean dispersal distances was not significant. Dispersal distance and first-year survival were underestimated when using data collected within the smaller, nested study area. The presence of conspecifics may play a key role in the settling process. Seventy-eight percent of the dispersers settled in territories that were occupied by either pairs or single owls the previous year, 16% settled in vacant territories next to occupied sites, and 6% settled at sites of unknown occupancy. No owls settled at unoccupied sites that were not adjacent to occupied sites.

Key words: conspecific attraction, dispersal, floaters, landscape composition, recruitment, Spotted Owl, Strix occidentalis occidentalis.

Dispersión Natal de *Strix occidentalis occidentalis*: Descripción de la Dispersión de una Población Insular

Resumen. Estudiamos los patrones de dispersión de una población insular de lechuza moteada californiana (*Strix occidentalis occidentalis*) en el sur de California, desde 1987–1998. El área de estudio comprendió las montañas de San Bernardino e incluyó un sito de estudio de 535 km^2 incluído en esta zona el cual usamos para evaluar el efecto del tamaño del área de estudio para la estimación de los parámetros de dispersión. Hasta 1998, 129 de las 478 lechuzas juveniles marcadas (27%) habían entrado a la población territorial. Más la mitad de los dispersores exitosos se hicieron territoriales al cabo de un año. Adicionalmente, todas las hembras y el 95% de los machos ocuparon territorios al cabo de tres años. Veintitrés pares de hermanos y un triplete se dispersaron exitosamente. La distancia de dispersión entre hermanos no se correlacionó. Sesenta y siete machos y 62 hembras se dispersaron 2.3–36.4 km (media = 10.1 ± 7.6 km) y 0.4–35.7 km (media = 11.7 ± 8.1 km), respectivamente. La diferencia entre la media de la distancia de dispersión entre hembras y machos no fue significativa. La distancia de dispersión y supervivencia del primer año fueron subestimadas cuando se utilizaron los datos colectados en la subárea de estudio de menor tamaño. La presencia de conespecíficos puede representar un factor clave en el proceso de asentamiento. Setenta y ocho por ciento de los dispersores se asentaron en territorios que habían estado ocupados por parejas o lechuzas no emparejadas el año anterior, el 16% en territorios no ocupados próximos a sitios ocupados, y el 6% se asentó en sitios con ocupación desconocida. Ninguna lechuza se asentó en sitios desocupados que no estuvieran adyacentes a un sitio ocupado.

INTRODUCTION

Dispersal is a fundamental aspect of the life history of all living things (Comins et al. 1980). It is the mechanism by which a species maintains its current distribution (Greenwood 1980), reoccupies vacated habitats, and expands its range (Howard 1960, Comins et al. 1980, Paradis et al. 1998). Dispersal also allows species to have discontinuous distributions (Howard 1960) and is a fundamental contributor to population synchrony (Paradis et al. 1998), population regula-

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tion (Greenwood 1980), and reduced extinction probability (Comins et al. 1980). Dispersal also influences population genetics by influencing gene flow, inbreeding, and outbreeding (Howard 1960, Greenwood 1980, Dobson and Jones 1985, Tonkyn and Plissner 1991, Paradis et al. 1998).

The Spotted Owl (*Strix occidentalis*) is a forest-dwelling species that ranges from southwestern Canada to central Mexico (Gutiérrez et al. 1995). It has been intensively studied for nearly three decades (Forsman et al. 1984, Verner et al. 1992, Franklin et al. 2000). This is primarily due to the owl's affinity for forests of high commercial value (USDI 1990, 1993). Logging often makes these forests unsuitable for Spotted Owls (Forsman et al. 1984). This has left many of the remaining suitable habitat patches isolated in highly fragmented landscapes (USDI 1990, 1993). Dispersal is a key demographic process that is critical for understanding the population dynamics of this species, particularly in fragmented landscapes.

One major problem associated with the measurement of dispersal is study area size (Barrowclough 1978, Baker et al. 1995, Koenig et al. 2000). Most study areas are not large enough to provide an adequate sample of the longest dispersal distances. Unless the potential for recoveries is uniformly distributed for all distances and directions, estimates of dispersal will be biased (Barrowclough 1978). In addition, the likelihood of a disperser leaving the study area increases the closer a natal site is to the study area boundary (Barrowclough 1978). These same issues are relevant when estimating survival (Baker et al. 1995). Koenig et al. (2000) reasoned that the most reliable dispersal data is recorded in isolated populations or extremely large study areas where the edge to interior ratio is minimized. We report dispersal distances, survival of dispersing owls, and settlement patterns observed during a long-term demographic study of a large, insular population of California Spotted Owls (*S. o. occidentalis*) in southern California.

METHODS

STUDY AREA

The study area is located in the San Bernardino Mountains (34°10′N, 117°00′W) approximately 140 km east of Los Angeles, California. Elevations range from 800 m to 3500 m. The climate is Mediterranean with most of the precipitation falling during the winter months (Fujioka et al. 1998). Annual precipitation ranges from 50–100 cm depending on location, elevation, and topography (Minnich 1988).

The San Bernardino Mountains are one of a series of mountain ranges that rise above extensive desert (Vasek and Barbour 1988) and semidesert (Mooney 1988) vegetation types in Southern California (Noon and McKelvey 1992, LaHaye et al. 1994). These mountain ranges are mesic compared to the surrounding lowlands, which allows them to support a diverse assemblage of shrub and forest vegetation types (Minnich 1998). Vegetation types most commonly used by Spotted Owls in southern California are mixed evergreen (Sawyer et al. 1988) and montane forests (Thorne 1988). These forests occur as isolates above ~1200 m elevation (Noon and McKelvey 1992, LaHaye et al. 1994) and occupy ~2% of the southern California landscape (Fig. 1; Scott et al. 1993).

We established two sampling areas within the study area. In 1987, we established the 535-km^2 Big Bear Study Area (BBSA) centered on the majority of the Spotted Owl locations known at that time. In 1989, we established the 2137-km^2 San Bernardino Mountains Study Area (SBMSA), which encompassed the entire mountain range, including the BBSA (Fig. 1).

SURVEY EFFORT

Each year we systematically surveyed all previously occupied Spotted Owl locations as well as all other forested vegetation. Nighttime surveys were conducted by imitating Spotted Owl vocalizations for a minimum of 15 min at each call point (spaced ~0.8 km apart) or by calling continuously while walking designated survey routes (Forsman 1983, Franklin et al. 1996). The locations of nighttime surveys were chosen systematically to cover all forested habitat a minimum of three times per year. We typically performed about 500 nighttime surveys annually.

Upon detecting an owl, we recorded the time of the response, sex of the owl, and its location. We returned to the area of each response at dawn and attempted to relocate the owl(s). When an owl was relocated, standard techniques were used to determine its social status (paired or single) and number of young produced (Forsman 1983, Franklin et al. 1996). We performed ap-

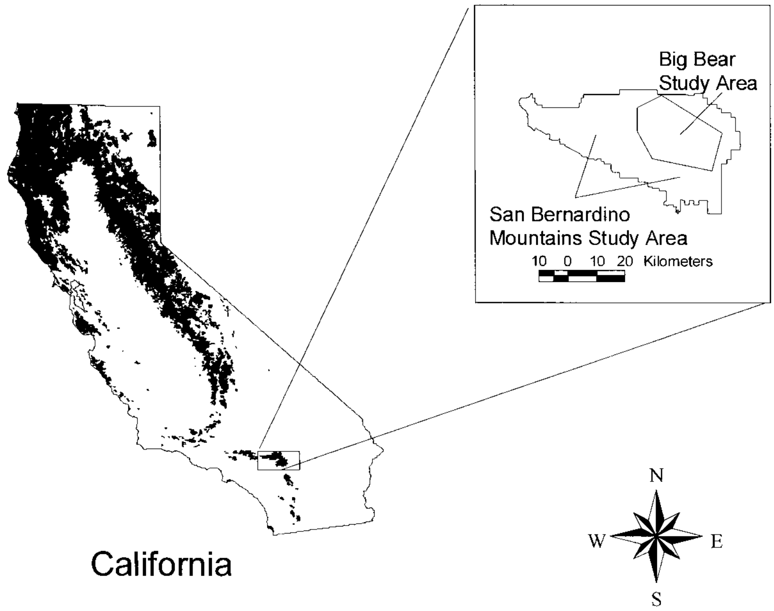

FIGURE 1. The distribution of the vegetation types that support Spotted Owls in California, and the Big Bear and San Bernardino Mountain Spotted Owl study areas. Vegetation data from Scott et al. (1993).

proximately 575 owl encounter surveys annually.

BANDING

We attempted to capture and band all Spotted Owls located using a noose pole or mist net. All owls captured were banded with locking, aluminum leg bands. Additionally, we banded adult and subadult owls with a combination colorband and tab that uniquely identified each individual. Juveniles were fitted with a color band unique to each cohort. Owls originally banded as juveniles were recaptured and fitted with a unique color band when they entered the territorial population. We identified previously colorbanded owls using binoculars and determined the sex of nonjuvenile owls by voice, behavior, or morphological measurements (Forsman 1983, Franklin et al. 1996). Sex of juvenile owls was not determined until they were recaptured.

STATISTICAL ANALYSES

Time to recruitment. We examined the capture histories of dispersing owls and the occupancy histories of territories where recruitment occurred to estimate time (years) to recruitment. Owls with uncertain capture histories and territories with ambiguous occupancy histories were removed from the analysis. Mean time to settling between sexes was compared using a *t*-test.

Dispersal distance. We used Pearson correlation coefficients to evaluate the correlation between sibling dispersal distances. Male and female mean dispersal distances were compared using a *t*-test. Successful dispersal has been defined as occupying a territory and becoming reproductively active (Howard 1960). Because some of our dispersed owls had successfully reproduced and others had not, we compared the mean dispersal distances between successful owls and owls which had not fledged young using a *t*-test.

Because all territories in the study area were within the maximum dispersal range recorded for this species (Gutiérrez et al. 1985, Miller and Meslow 1985, Gutiérrez et al. 1996, Ganey et al. 1998), we calculated the distances between all known territory centers and considered the distribution of interterritory distances to represent the potential distribution of random dispersal distances. Territory centers were defined by nest locations or by roost locations when no nests were known for a territory. The most central nest or roost was used as the territory center when multiple nests or roosts were known. The distributions of interterritory and dispersal distances were compared using chi-square analysis.

Study area size. We evaluated the effect of study area size on estimates of time to settling and dispersal distances by comparing data collected within the BBSA to all other data from the SBMSA using a *t*-test. We evaluated immigration, emigration, and recruitment by comparing natal and post-dispersal settling locations.

We estimated survival using program MARK (White and Burnham 1999) with three different data sets to evaluate the effect of study area size on estimates of survival. We modeled first-year survival using fledglings originally banded and recaptured within the BBSA, fledglings banded in the BBSA that were recaptured anywhere within the SBMSA, and first-year survival using all fledglings banded and recaptured within the entire SBMSA. We did not assess the fit of the data or estimate ''c-hat'' to correct for overdispersed variance (Anderson et al. 1994) because we were mainly interested in the relative differences in survival estimates among the various study area sizes and not in model selection or accuracy of the estimates. Model notation followed Lebreton et al. (1992), survival and recapture probability were modeled identically for all three data sets, and the structure of the model was (ϕ_{s1+a}, $P_{s1+s2+a}$), where ϕ = apparent survival, P = recapture probability, $s1$ = first year subadults, $s2$ = second year subadults, and a = adults.

Settling behavior. We evaluated the hypothesis of social facilitation in settling by examining the previous year's occupancy and social status of occupants at sites where owls settled. Spotted Owls exhibit high fidelity to their breeding sites and are relatively long-lived (Forsman et al. 1984, Gutiérrez et al. 1995). Thus, we felt this evaluation provided a reasonable approximation of social status of owls occupying territories near the time of recruitment. We compared occupancy in the previous year and social status of occupants at territories where settlement occurred to overall territory occupancy and social status in the SBMSA for all years using chi-square analysis.

Some sites were only occasionally occupied by Spotted Owls. We labeled these sites ''frequently vacant'' and defined them as sites that were unoccupied in at least 50% of the seasons they were surveyed. We then assessed reproduction at these sites to evaluate their potential to support breeding Spotted Owls.

Landscape analysis. We used a vegetation classification produced from Landsat imagery (Smith et al., in press) to derive a habitat map that consisted of four categories: owl nesting and roosting habitat, owl foraging habitat, nonforested habitat, and other non-owl habitats. We used this classification to estimate the proportion of the study area supporting owl nesting and foraging habitat. All *t*-tests were two-tailed, means are reported ± SD except where noted, and significance is set at $P < 0.05$.

RESULTS

SURVEYS, BANDING, AND RELOCATION OF OWLS

Between 1987 and 1998, we surveyed up to 148 territories annually (Table 1). The percentage of territories occupied varied from 59% to 95% and the number of pairs monitored ranged from 32 to 90. Between 1992 and 1998, the percentage of the territorial population that was banded prior to each field season averaged 92 ± 3% (range 86–96%, Table 1).

Between 1987 and 1997 we located 524 fledglings and banded 478 of them. Sixteen of the 46 unbanded owlets were either found dead or we suspected they died prior to capture attempts and dispersal. Thus, we banded 94% (478 of 508) of the fledglings we detected during the study period.

We recaptured 129 (27%, 62 females and 67 males) territorial owls initially banded as fledglings. Dispersing owls took up to four years to enter the territorial population. However, 61% of recruited females (n = 46) and 62% of recruited males (n = 59) occupied a territory within one year of fledging. Settling time was similar between sexes (t_{104} = 0.5, P = 0.63). All females and 95% of males occupied territories within three years.

DISPERSAL DISTANCE

Twenty-three sibling pairs and one set of triplets successfully dispersed. Sibling dispersal distances were not correlated (r = 0.17, P = 0.43). There was no difference between mean dispersal distances of owls which had successfully reproduced and owls which had not reproduced (t_{127} = -0.4, P = 0.7). Thus, successful and unsuccessful owls were pooled for the remainder of the analyses. Mean dispersal distances were 10.1

TABLE 1. Spotted Owl survey effort and banding activity between 1987 and 1998 in the San Bernardino Mountains of southern California.

	Territories		Territorial owls			
Year	Number surveyed	% occupied	Number pairs	Number singles	% banded[a]	Juveniles number banded
1987	42	95	32	8	0	15
1988	78	95	56	18	42	16
1989	115	90	81	23	42	52
1990	127	86	90	19	72	47
1991	132	76	86	12	79	44
1992	136	65	78	11	91	49
1993	141	63	78	11	90	52
1994	143	68	84	13	86	70
1995	145	70	86	15	93	38
1996	146	67	89	9	93	54
1997	147	62	80	11	96	41
1998	148	59	76	11	95	23

[a] Percent of the territorial population banded prior to each field season, including newly recruited territorial owls.

± 7.6 km (range 2.3–36.4 km) for males and 11.7 ± 8.1 km (range 0.4–35.6 km) for females (Fig. 2). No owls settled in their natal territories and dispersal distances were similar for both sexes ($t_{127} = 1.1$, $P = 0.25$).

The distribution of potential dispersal distances (mean = 24.3 ± 14.1 km, range 0.4–71.8 km, n = 10 731), estimated from the distribution of interterritory distances, was different than the distribution of actual dispersal distances (mean = 10.9 ± 7.8 km, n = 129; $\chi^2_4 = 164.9$, $P < 0.01$). Dispersal distances occurred more frequently than expected in the shorter distance classes and less often than expected in the longer distance classes.

EFFECT OF STUDY AREA SIZE

Estimates of time to settling within the BBSA and all other dispersals in the SBMSA were similar ($t_{102} = 0.57$, $P = 0.57$). The mean dispersal distance of owls that fledged and settled within the BBSA (9.9 ± 5.8 km) was different than the mean dispersal distance of owls that dispersed beyond the BBSA boundary (13.6 ± 6.8 km; $t_{75} = -2.6$, $P = 0.01$).

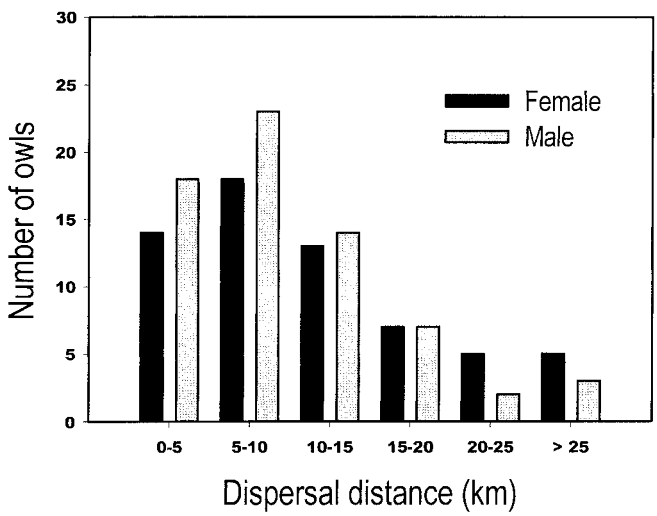

FIGURE 2. Distribution of dispersal distances for female and male Spotted Owls in the San Bernardino Mountains, California, 1988–1998.

SURVIVAL, SETTLING BEHAVIOR, AND SUITABLE HABITAT

First-year apparent survival was 0.219 (SE = 0.030) for juveniles that fledged and settled within the BBSA, 0.262 (SE = 0.032) for juveniles fledged in the BBSA that were recaptured anywhere within the SBMSA, and 0.318 (SE = 0.025) for all juveniles banded and settling within the SBMSA. During the period of study, owls that fledged within the BBSA accounted for 68% (n = 66) of known-age recruits within the BBSA.

Sixty-six percent of the dispersers settled at sites that were occupied by a pair of owls the previous year, 15% settled at sites that were vacant the previous year, 12% settled at sites that were occupied by a single owl, and 6% settled at sites where the previous year's occupancy was unknown. Thus, 78% of the dispersers settled at sites that were known to be occupied the previous year. This ratio (101:28) was different ($\chi^2_1 = 6.9$, $P < 0.01$) than the expected mean occupancy ratio estimated from all known Spotted Owl territories for all years (87:42). Thus, owls were more likely to settle at sites that were occupied the previous year. In addition, all previously vacant territories (n = 20) where owls settled were adjacent to occupied sites.

We identified 39 owl sites that were frequently vacant during the study period. Sixty-one percent of these sites fledged young in at least one year and 28% fledged young in two or more years. Thus, many frequently vacant sites were capable of supporting reproduction when occupied. Nineteen percent of the SBMSA was potentially suitable nesting or roosting habitat and an additional 6% was suitable foraging habitat. Thus, approximately 24% of the SBMSA supported potential Spotted Owl habitat.

DISCUSSION

Vegetation types that support Spotted Owls in southern California are rare and occur in isolates on only 2% of the landscape (Fig. 1). In addition, it is not known how effectively Spotted Owls disperse across the extensive matrix of desert and urbanized environments that currently exist between mountain ranges. Despite having conducted Spotted Owl surveys in the two mountain ranges nearest the SBMSA (Gutiérrez and Pritchard 1990, LaHaye et al. 1994), we know of no intermountain dispersals for this species in this region. This insular setting provided an exceptional opportunity for studying Spotted Owl dispersal.

While it is possible that some of the juveniles from the SBMSA settled in adjacent mountain ranges, we believe such dispersal events are rare. However, we assume some movement between mountain ranges must occasionally occur if a Spotted Owl metapopulation exists in the region (Noon and McKelvey 1992, LaHaye et al. 1994, Gutiérrez and Harrison 1996). Thus, it is possible this population has a bimodal distribution for dispersal distance. Alternatively, extensive environmental changes (e.g., urbanization, habitat conversion for agriculture, water diversion, wind-driven electric power generation, etc.) that have occurred in southern California during the past century may have reduced the rate of intermountain dispersal.

TIME TO SETTLING

Approximately 40% of the dispersing owls during this study required two to four years to become territorial. Franklin (1992) reported a similar estimate for male Northern Spotted Owls (*S. o. caurina*) in northwestern California. However, all of the females during his study settled by age two. Raphael et al. (1996) reported that 40% of banded, juvenile Northern Spotted Owls in Washington and Oregon were resighted one year after banding. The remaining 60% were resighted at 2–5 years of age. Thus, some individuals in all three studies remained floaters for multiple years.

Because some owls took four years to become territorial, we have complete data from only the first several cohorts. Thus, it is likely that our results exaggerate recruitment in the first two years of life and underestimate total recruitment from later cohorts. Early recruitment may have been further amplified due to this population's apparent decline during the last decade (LaHaye et al. 1994). That is, the increased territory vacancies may have enhanced earlier recruitment. Alternatively, settling may have been postponed due to lack of mates (see our discussion of conspecific attraction below).

DISPERSAL DISTANCE

Dispersal distances for Spotted Owls in other populations range from 5.8 km (Ganey et al. 1998) to 56 km (Gutiérrez et al. 1996). However, comparing dispersal characteristics between populations was not possible due to the small sample sizes in those studies. Several studies of Spotted Owl dispersal using radio-telemetry (Miller et al. 1997, Ganey et al. 1998, Willey and van Riper 2000) reported median, maximum, or net dispersal distances which ranged from 0.6 to 72.1 km. These distances reflected not only owls that survived and settled, but also owl deaths, transmitter failures, and lost signals. Thus, direct comparisons between these distances and our results are not appropriate.

Keppie (1980), Newton and Marquiss (1983), and Massot et al. (1994) found that sibling dispersal distances were highly correlated in grouse, Sparrowhawks (*Accipiter nisus*), and vertebrates in general, respectively. These authors suggested that analyses should compensate for the problem of nonindependence of sibling data. However, sibling dispersal distances were not correlated in our study.

In contrast to many bird studies (Greenwood 1980, Liberg 1985, Pusey 1987, Ellsworth and Belthoff 1999), we did not detect female-biased dispersal distances. Clarke et al. (1997) showed that not all species exhibit sex-biased dispersal, and they reported that sex-biased dispersal should not be considered constant, even within a species. Thus, while sex-biased dispersal does not appear to exist in this population, it may occur in the Northern Spotted Owl (E. Forsman, pers. comm.; A. Franklin, pers. comm.). However, we are unaware of any other published results addressing this issue for this species.

EFFECT OF STUDY AREA SIZE

Spotted Owls in the San Bernardino Mountains had a mean dispersal distance that was roughly half the mean interterritory distance. Although dispersal distances for this species appeared longer in other studies (Gutiérrez et al. 1996, Miller et al. 1997, Ganey et al. 1998, Willey and van Riper 2000), this difference may be due to the insular nature of our study area, undetected movements to adjacent mountain ranges, or differences in methodologies among studies. However, Dale (2001) suggested that natal philopatry (i.e., reduced dispersal distances) may be the optimal dispersal strategy for isolated populations.

Study area size may affect estimation of dispersal distance and survival (Barrowclough 1978, Baker et al. 1995, Koenig et al. 2000). This was true in our study; estimates of dispersal distance increased nearly 40% when we included owls dispersing beyond the BBSA boundary. In addition, our estimates of survival increased 20% and 60% when we included recaptures from progressively larger areas. However, we minimized most of the problems associated with small study area size by conducting our research on an entire, relatively large, insular population.

SETTLING BEHAVIOR

Nearly two-thirds of the frequently vacant sites had records of successful fledging. Thus, the majority of these sites were not only capable of supporting owls, but were also capable of supporting reproduction when occupied. Therefore, we did not believe that these sites remained vacant simply because they were incapable of supporting Spotted Owls. Consequently, it was not clear why dispersing owls remained floaters when numerous vacant territories were available.

The majority of dispersing owls settled in or adjacent to sites that were occupied the previous year. Additionally, owls at some consistently occupied sites failed to fledge young, while several frequently vacant sites supported high survival and reproduction when they were occupied. Thus, the presence of unoccupied, suitable habitat did not necessarily promote settling, and the presence of a territorial conspecific did not guarantee that a site would support reproduction. Both of the above indicated that finding a mate may take priority over selecting the ''best'' available territory when settling. This suggests that conspecific attraction may play a vital role in the recruitment of dispersing Spotted Owls in this population.

Conspecifics may provide cues to the existence of suitable habitat and mates (Kiester 1979, Stamps 1987, Muller et al. 1999). This may be crucial for species like the Spotted Owl which occupy large home ranges and spatially variable habitats (Gutiérrez et al. 1995, Smith et al., in press). Thus, individuals may disperse preferentially to occupied sites (Ray et al. 1999, Stephens and Sutherland 1999). Additionally, vacant sites may indicate that the habitat is unsuitable for long-term occupancy (Smith and Peacock 1990). Ultimately, cueing on conspecifics may lead to increased success of dispersing individuals (Ray et al. 1999).

Given the numerous vacant territories and high turnover rates we recorded previously (LaHaye et al. 1992), we may have observed dispersal during a period with above average opportunities for recruitment. Alternatively, if conspecific attraction explained settling patterns in this population, higher territory occupancy rates might have promoted increased recruitment. The latter suggests that recruitment may have been below average during this study.

LANDSCAPE COMPOSITION

Numerous workers have modeled the effect of the proportion of suitable habitat on dispersal success (Lande 1988, Doak 1989, Noon and McKelvey 1992, Lamberson et al. 1992, 1994, Ruckelshaus et al. 1997). The consensus is that the likelihood of successful dispersal increased with the proportion of suitable habitat in the landscape. Harrison et al. (1993) reviewed most of the habitat modeling work done on the Spotted Owl and estimated that the critical threshold for the proportion of suitable habitat was around 20%. Additionally, Lamberson et al. (1992) indicated that their modeling determined that the problems associated with site and mate search became insurmountable once suitable habitat fell below 15%.

Potential Spotted Owl habitat constituted 24% of our study area. This was very near the threshold values estimated from models of Spotted Owl persistence in the Pacific Northwest (Lande 1988, Doak 1989, Lamberson et al. 1992, Murphy and Noon 1992). Interestingly, the San Bernardino Mountains probably contained a higher percentage of potential Spotted Owl habitat than most of the other mountain ranges in Southern California where Spotted Owls occur. Noon and McKelvey (1992) recognized this and suggested that many of the subpopulations have an insular structure at both landscape and local scales.

Spotted Owls have been recorded from southern California (Xantus 1859) and northern Baja California (Bryant 1889, Anthony 1893) for more than a century. Yet, with landscapes so depauperate in suitable habitat it is difficult to explain this species' regional persistence. Behavioral adaptations such as natal philopatry, lack of sex-biased dispersal distance, and conspecific attraction may be several adaptations that have aided this species' survival in the isolated patches of forest found in southern California.

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