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NATAL AND BREEDING DISPERSAL OF NORTHERN SPOTTED OWLS

by

ERIC D. FORSMAN, ROBERT G. ANTHONY, JANICE A. REID,
PETER J. LOSCHL, STAN G. SOVERN, MARGARET TAYLOR,
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FRANK F. WAGNER, AND D. ERRAN SEAMAN

NO. 149

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There is a perpetual need for additional funds to sponsor publication of worthwhile manuscripts in *Wildlife Monographs*. Any contribution will be accepted with gratitude by The Wildlife Society. Memorial funds collected to honor and perpetuate the names of deceased members of the profession probably could be put to no better use.

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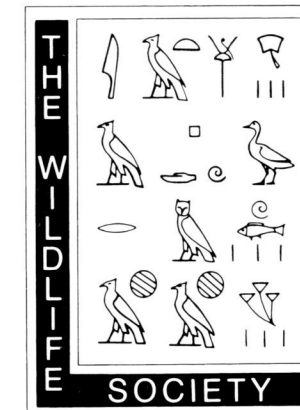
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NO. 149

OCTOBER 2002



FRONTISPIECE. A northern spotted owl dispersing in western Oregon (Photo from U.S. Forest Service files).

NATAL AND BREEDING DISPERSAL OF NORTHERN SPOTTED OWLS

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Abstract: We studied the dispersal behavior of 1,475 northern spotted owls (*Strix occidentalis caurina*) during banding and radio-telemetry studies in Oregon and Washington in 1985–1996. The sample included 324 radio-marked juveniles and 1,151 banded individuals (711 juveniles, 440 non-juveniles) that were recaptured or resighted after dispersing from the initial banding location. Juveniles typically left the nest during the last week in May and the first two weeks in June ($\bar{x} \pm SE = 8 \text{ June} \pm 0.53 \text{ days}$, $n = 320$, range = 15 May–1 July), and spent an average of 103.7 days in the natal territory after leaving the nest ($SE = 0.986 \text{ days}$, $n = 137$, range = 76–147 days). The estimated mean date that juveniles began to disperse was 19 September in Oregon (95% CI = 17–21 September) and 30 September in Washington (95% CI = 25 September–4 October). Mean dispersal dates did not differ between males and females or among years. Siblings dispersed independently. Dispersal was typically initiated with a series of rapid movements away from the natal site during the first few days or weeks of dispersal. Thereafter, most juveniles settled into temporary home ranges in late October or November and remained there for several months. In February–April there was a second pulse of dispersal activity, with many owls moving considerable distances before settling again in their second summer. Subsequent dispersal patterns were highly variable, with some individuals settling permanently in their second summer and others occupying a series of temporary home ranges before eventually settling on territories when they were 2–5 years old. Final dispersal distances ranged from 0.6–111.2 km for banded juveniles and 1.8–103.5 km for radio-marked juveniles. The distribution of dispersal distances was strongly skewed towards shorter distances, with only 8.7% of individuals dispersing more than 50 km. Median natal dispersal distances were 14.6 km for banded males, 13.5 km for radio-marked males, 24.5 km for banded females, and 22.9 km for radio-marked females. On average, banded males and females settled within 4.2 and 7.0 territory widths of their natal sites, respectively. Maximum and final dispersal distances were largely independent of the number of days that juveniles were tracked. Although statistical tests of dispersal direction based on all owls indicated that direction of natal dispersal was non-random, the mean angular deviations and 95% CIs associated with the samples were large, and r -values (vector length) were small. This led us to conclude that significant test results were the result of large sample size and were not biologically meaningful. Our samples were not large enough to test whether dispersal direction from individual territories was random.

In the sample of radio-marked owls, 22% of males and 44% of females were paired at 1 year of age, but only 1.5% of males and 1.6% of females were actually breeding at 1 year of age. At 2 years of age, 68% of males and 77% of females were paired, but only 5.4% of males and 2.6% of females were breeding. In contrast to the radio-marked owls, most juveniles that were banded and relocated at 1 or 2 years of age were paired, although few were breeding. Although recruitment into the territorial population typically occurred when owls were 1–5 years old, 9% of banded juveniles were not recaptured until they were > 5 years old. We suspect that our estimates of age at recruitment of banded owls are biased high because of the likelihood that some individuals were not recaptured in the first year that they entered the territorial population.

A minimum of 6% of the banded, non-juvenile owls on our demographic study areas changed territories each year (breeding dispersal). The likelihood of breeding dispersal was higher for females, young owls, owls that did not have a mate in the previous year, and owls that lost their mate from the previous year through death or divorce. Mean and median distances dispersed by adults were shorter than for juveniles, and did not differ between the sexes or study areas ($\bar{x} = 6.1 \text{ km}$, median = 3.5 km). Owls that were 1–2 years old tended to disperse farther than owls that were > 2 years old. The direction of post-natal dispersal did not differ from random.

The large nonforested valleys of western Oregon (Willamette, Umpqua, Rogue Valleys) acted as barriers to dispersal between the Coast Ranges and the Cascade Mountains. However, dispersal did occur between the Coast Ranges and Cascade Mountains in the forested foothills between the non-forested valleys. Forest landscapes traversed by dispersing owls typically included a fragmented mosaic of roads, clear-cuts, non-forest areas, and a variety of forest age classes ranging from young forests on cutover areas, to old-growth forests ≥ 250 years old.

Our data fit the general pattern observed in birds in that females dispersed farther than males and dispersal distances were negatively skewed towards short distance dispersers. Comparison of data from radio-marked and banded owls demonstrated that the negatively skewed distribution of dispersal distances represented the actual distribution of dispersal distances, and was not the result of small study area bias on recaptures. We found no correlation between dispersal distance and age at first breeding, which suggests that reproductive fitness is not affected by dispersal distance. We observed only 3 cases of close inbreeding (parent-offspring or sibling pairs) in thousands of pairs of spotted owls, suggesting that dispersal results in a very low incidence of close inbreeding in the spotted owl. However, inbreeding with more distant relatives was common.

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INTRODUCTION

Dispersal behavior is highly variable in birds, ranging from highly philopatric species that often settle on or near the territory where they were born (Koenig and Pitelka 1979, Stacey and Ligon 1987, Bowen et al. 1989, Russell and Rowley 1993, Daniels and Walters 2000) to species that typically disperse considerable distances before settling (Beske 1982, Newton and Marquiss 1983, Vander Wall et al. 1983, Korpimäki and Lagerström 1988, Marti 1999). Although there is great variation in dispersal patterns among and within species, a consistent trend in most birds is for females to disperse farther than males (Greenwood 1980, Newton and Marquiss 1983, Small and Rusch 1989, Ellsworth and Belthoff 1997, Marti 1999). This is the reverse of the pattern observed in most mammals, in which males tend to disperse farther than females (Baker 1978, Greenwood 1980). Greenwood (1980) suggested that sex-biased dispersal may be a function of the type of resource that is defended, with female-biased dispersal prevailing in species that defend foraging areas (most birds) and male-biased dispersal predominating in species that defend mates (many mammals). The logic underlying this hypothesis is that in species that defend for-

aging areas, males invest more time in prospecting for and defending a suitable territory, whereas females have more time to travel between multiple territories in search of a suitable male.

Sexual differences in dispersal and the highly variable nature of dispersal have stimulated an extensive debate regarding the causes of dispersal (e.g., Greenwood 1980; Shields 1982, 1983; Moore and Ali 1984; Bull et al. 1987; Arcese 1989; Johnson and Gaines 1990; Koenig et al. 1992; McPeck and Holt 1992; Holt and McPeck 1996). This discussion has tended to focus on dispersal as a mechanism for (1) avoiding inbreeding with closely related individuals (Howard 1960, Greenwood et al. 1978, Packer 1979, 1985, Greenwood 1980, Shields 1983), (2) reducing intrasexual competition for mates or resources (Murray 1967, Moore and Ali 1984, Waser 1985, Small and Rusch 1989, Tonkyn and Plissner 1991), or (3) increasing individual fitness in patchy landscapes with spatio-temporal or chaotic variation in habitat quality (Holt 1985, McPeck and Holt 1992, Holt and McPeck 1996). Because there are so many exceptions to almost every generalization regarding dispersal, some have cautioned against seeking a single causal mechanism (Koenig et al. 1992, Russell and Rowley 1993).

Regardless of the reasons for dispersal, patterns of movement and behavior of non-territorial "floaters" can have profound effects on population dynamics and may mask long-term changes in populations (Thomas et al. 1990, Stacey and Taper 1992, Lamberson et al. 1994, Rhoner 1996). In addition, dispersal is the mechanism by which genes are transmitted within populations. As a result, dispersal behavior is a primary concern in reserve design for threatened and endangered species (Murphy and Noon 1992, Harrison et al. 1993, Lamberson et al. 1994). A recent example is the Northwest Forest Plan, which resulted in the retention of an extensive network of large, old-forest reserves on federal lands in western Washington, Oregon and northern California (FEMAT 1993, USDA/USDI 1994). These reserve areas are typically spaced 10–20 km apart. They are designed to provide habitat for spotted owls, marbled murrelets (*Brachyramphus marmoratus*), and other species that utilize old forests and associated riparian areas. This reserve design was established based on the premise that spotted owls would interact as a metapopulation within and among the reserves, with adequate dispersal between reserves to maintain genetic variation and recolonize unoccupied territories (Thomas et al. 1990, Murphy and Noon 1992, FEMAT 1993, USDA/USDI 1994).

A major difficulty in the development of the Northwest Forest Plan was that information on dispersal of spotted owls was limited. Previous studies were limited to small samples of radio-marked owls, most of which were tracked for less than a year, and which rarely lived long enough to acquire territories (Allen and Brewer 1985, Gutiérrez et al. 1985, Miller and Meslow 1985, Laymon 1988, Miller 1989, Miller et al. 1997). As a result, management plans for the spotted owl, and simulation models used to evaluate those plans, necessarily included many untested assumptions regarding dispersal (e.g., Lande 1988; Doak 1989; Lamberson et al. 1992, 1994; Holthausen et al. 1995).

In this paper, we describe the dispersal

behavior of northern spotted owls based on relocations of banded owls and radio-marked owls in Oregon and Washington. Our specific objectives were to (1) investigate sexual differences in dispersal, (2) describe the chronology of natal dispersal, (3) describe integration of young owls into the territorial population, (4) describe effects of landscape features on dispersal, (5) describe social factors associated with breeding dispersal, (6) determine if estimates of dispersal parameters differed between banded and radio-marked owls, and (7) determine if dispersal distance was positively correlated with the age when owls first nested. We discuss how our results fit with previous studies of dispersal in birds and with some of the hypotheses that have been suggested regarding causes of dispersal. We also discuss our findings in the context of current management plans for the owl, and we provide suggestions that modelers might use to develop more realistic spatial simulation models for spotted owls.

Acknowledgments.—This study was a group effort that would not have been possible without the dedicated efforts of many biologists and field technicians who banded, recaptured, and radio-tracked spotted owls. The main cast of characters included L. S. Andrews, G. Arnold, D. Aubuchon, D. K. Barrett, M. Blow, R. R. Bown, M. Brown, J. A. Burns, B. R. Casler, A. D. Center, G. S. Center, N. L. Duncan, R. H. Espinosa, C. C. Foster, R. K. Forson, A. R. Giese, J. H. Guetterman, J. F. Harper, T. Hines, D. S. Hopkins, R. B. Horn, S. P. Horton, M. Kinsey, D. L. Kelso, R. Leach, J. C. Lewis, J. B. Lint, W. D. Logan, R. Lowell, D. Manson, K. J. Maurice, C. McCafferty, G. S. Miller, G. W. Mires, J. Mowdy, M. Nixon, C. Oakley, I. A. Otto, L. B. Page, J. P. Perkins, M. R. Roan, S. E. Salmons, R. Schnoes, P. A. Shaklee, G. Sitter, R. J. Straub, M. St. Peters, J. K. Swingle, M. Townsend, J. Witt, C. Zabel, and J. Zisa. In addition to helping with field work, F. M. Oliver made most of the plastic color bands that were used in our study. His craftsmanship and attention to

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STUDY AREAS

We banded and monitored owls on 12 large (1,075–15,216 km²) demographic study areas that were originally selected as long-term monitoring areas for spotted owls on federal lands in Oregon and Washington (Fig. 1) (Franklin et al. 1996). Many of these areas were adjacent to each other, such that owls banded in 1 study area were often detected in another study area after they dispersed (Fig. 1). In addition, concurrent surveys for spotted owls were conducted by timber companies, consulting firms and state agencies in many other areas in Oregon and Washington, such that banded owls were often recaptured or resighted even if they left our demographic study areas. Ultimately, therefore, our study area included much of the range of the northern spotted owl in Oregon and Washington.

All study areas were dominated by rugged mountains covered by temperate coniferous forests. Forests in more mesic regions (western Washington and northwest Oregon) were typically dominated by Douglas-fir (*Pseudotsuga menziesii*), western hemlock (*Tsuga heterophylla*), and western redcedar (*Thuja plicata*). In more xeric areas (southwestern Oregon and the east slope of the Cascades Mountains), forests were typically dominated by mixtures of grand fir (*Abies grandis*), Douglas-fir, ponderosa pine (*Pinus ponderosa*), incense cedar (*Libocedrus decurrens*), and western white pine (*Pinus monticola*). In the Klamath Mountains of southwestern Oregon, evergreen hardwoods such as tan-oak (*Lithocarpus densiflorus*), California laurel (*Umbellularia californica*), and Pacific madrone (*Arbutus menziesii*) commonly occurred in mixed-species stands with conifers, including Douglas-fir, grand fir, incense cedar, western white pine or redwoods (*Sequoia sempervirens*).

Landscapes within our study areas typically included a complex mosaic of forests, roads, clear-cuts and non-forest cover types. Age and structure of forests was highly variable, but typically included areas of old-growth and mature forest intermixed with younger forests growing on areas that had been burned or harvested. Large lowland valleys dominated by agriculture and urban development were interspersed within and among many study areas (Fig. 1).

METHODS

Field Methods

Demographic studies on the 12 study areas began in 1985–1990, and continued through 1996. Owl territories in each study area were surveyed each year to resight marked owls, band unmarked owls, locate nests, and determine the number of young produced by each resident owl (Franklin et al. 1996). Adult owls were marked with a U. S. Fish & Wildlife Service leg band and a colored leg band when first captured, so that they could be visu-

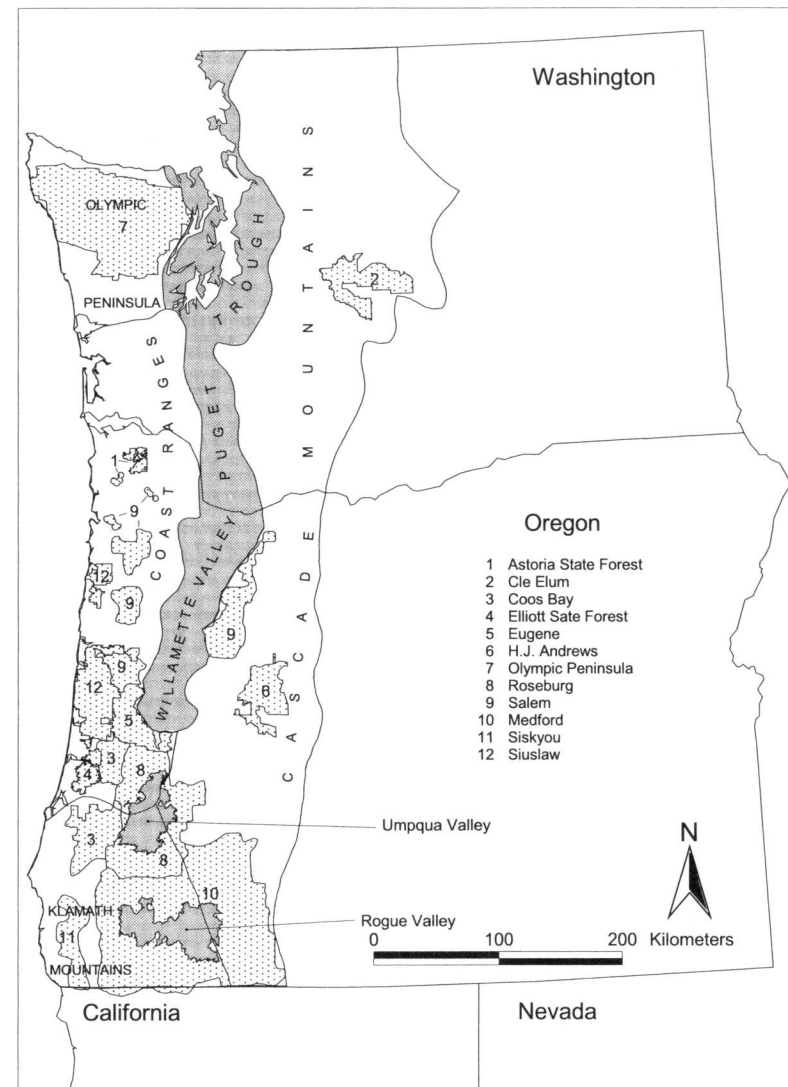


Fig. 1. Demographic study areas in Oregon and Washington where spotted owls were banded or radio-marked in 1985–1996.

ally identified in subsequent years without recapture (Forsman et al. 1996, Franklin et al. 1996). Juveniles were banded with a U. S. Fish & Wildlife Service band and a red-and-white color band. If they were resighted in subsequent years, owls banded as juveniles were recaptured, at which time their red-and-white bands were replaced with unique color bands. Spotted owls are easily captured with noose poles (Forsman 1983), so we were almost always able to recapture and identify juveniles af-

ter they were relocated on a new territory. Adults were identified by observing their color bands at close range with binoculars. Adults that dispersed were sometimes recaptured to confirm their identity or change their color bands.

We used acoustic lure and live lure surveys to resight banded owls and to locate nests and juvenile owls (Forsman 1983, Franklin et al. 1996, Reid et al. 1999). In most cases, surveys did not include a complete coverage of the entire study area but

were conducted at many different locations where there was a history of occupancy by spotted owls. Although study area boundaries changed somewhat over the years, most areas and most territories were searched each year, using a standardized protocol to confirm bands, band new owls and document the number of young produced by each owl (Franklin et al. 1996). Monitoring efforts on demographic study areas were further supplemented by surveys on adjacent areas, where private landowners and consulting firms conducted surveys or mark-recapture studies of spotted owls and occasionally resighted our banded owls. Sex of banded owls was determined from vocalizations and behavior (Forsman et al. 1984, Franklin et al. 1996) or from blood samples (Dvorák et al. 1992, Fleming et al. 1996).

In addition to observations of banded owls, we radio-marked 386 juvenile spotted owls in 1991–95 and attempted to track them for 1–2 years. Juveniles were radio-marked on the Olympic and Cle Elum Study Areas in Washington ($n = 170$) and on the Siuslaw, Eugene, and Roseburg Study Areas in western Oregon ($n = 216$) (Fig. 1). Sex of 318 of the radio-marked juveniles was determined from blood samples, necropsies, or vocalizations. Sex of 68 of the radio-marked juveniles was unknown. Transmitters weighed 5.5 g (Holohil Systems Ltd., Model RI-2C), were tied and glued to the central tail feathers in late July or August (Reid et al. 1996a), and had an expected field life of 12 months (maximum = 23 months).

We defined natal dispersal as the movement the individual makes from its birth site to the place where it reproduces or would have reproduced if it had survived and found a mate (Howard 1960). We defined breeding dispersal as any case in which a non-juvenile owl (≥ 1 year old) moved between territories where it had the opportunity to breed, regardless of whether it bred or not (Daniels and Walters 2000). Breeding dispersal could occur multiple times during the lifetime of an individual if it occupied a series of different territories or moved back-and-forth

between 2 or more distinct territories in different years. We excluded cases where movements involved use of alternate nest sites within the same territory in different years. We also excluded cases where owls were located at 2 different territories during the same summer because such movements usually involved non-breeding birds and probably represented prospecting behavior (Reed et al. 1999) rather than dispersal.

For radio-marked juveniles, we considered dispersal to have started when owls moved ≥ 2.4 km from their natal site. The only exceptions to the 2.4-km rule were 5 cases where juveniles settled on territories that were < 2.4 km from their natal sites. We used the 2.4-km cutoff for initiation of dispersal because we were reasonably sure that, once juveniles moved more than 2.4 km from the natal site, they were outside the home range of their parents (Forsman et al. 1984:21).

Dates when radio-marked owls started to disperse were estimated as the midpoint between the last location at the natal site and the first location after dispersal started. This approach was necessary because we did not relocate every owl each day. Thus there was undoubtedly some error in the estimates of individual dispersal dates. However, we had no reason to believe that individual errors were biased in 1 direction, so estimates of means should have been unbiased.

Radio-marked juveniles were relocated by triangulating with a portable receiver (Telonics model TR2) and hand-held antenna (Telonics model RA-2A) or a pair of RA-2A antennas mounted on an airplane (Guetterman et al. 1991). Locations determined by triangulation were often followed up by homing in on owls at their roosts to visually confirm that they were alive. Most relocations (98.0%) of radio-marked owls were obtained during daylight hours and thus represented roost locations.

After radio-marked juveniles started to disperse, the average interval between sequential relocations was 5.390 ± 0.092 days in Oregon ($n = 5,200$), 14.345 ± 1.014 days

on the Olympic Peninsula ($n = 368$), and 12.177 ± 0.385 days on Cle Elum ($n = 1,239$). After the first year of life (1 June–31 May) the average interval between sequential relocations of radio-marked owls increased to 9.565 ± 0.271 days in Oregon ($n = 2,742$), 34.678 ± 3.186 days on the Olympic Peninsula ($n = 174$), and 30.869 ± 2.516 days on Cle Elum ($n = 183$). We reduced the frequency of relocations after the first year of life because many owls became more sedentary and because owl trackers were busy banding, radio-marking and tracking the next cohort of juveniles.

We usually were able to follow radio-marked juveniles by tracking them from the ground, but aircraft flights were scheduled as needed to search for missing birds. Aircraft searches were typically conducted by flying a grid pattern, working outward from the last known location for distances of 30–40 km. If a missing bird was not located on 1 flight, we continued to search for it on subsequent flights when we searched for other missing birds, such that the cumulative search effort from aircraft flights typically included our study areas plus the areas 50–100 km beyond the study area boundaries.

Radio-marked juveniles were tracked until they died or until the signal was lost. Transmitters were replaced on 100 individuals during their second summer, so that they could be followed for approximately 2 years. After transmitters failed we were still able to determine the fate of some of the radio-marked owls because they were recaptured as territorial birds in our demographic studies.

To determine when juvenile owls entered the territorial population, we tried to determine the status of all radio-marked and banded owls that were relocated each year. Owls were typically relocated several times in their day roosts during the breeding season to determine if they were paired or nesting. Nesting status and pair status were determined by imitating spotted owl vocalizations (acoustic lure technique) in roost areas to see if a mate was present, and by feeding owls live mice to

see if they would deliver them to a nest or fledged young (live lure technique) (Franklin et al. 1996, Reid et al. 1999). These data were used to estimate the proportion of owls in each age cohort that were single, breeding, or paired but not breeding. We estimated recruitment rates of radio-marked owls based on the proportion of 1-year-old and 2-year-old owls that were paired. For banded owls we estimated recruitment rates as the proportion of owls first recaptured in each age class, regardless of whether they were paired or not.

To evaluate whether territorial behavior influenced movements of floaters we compared the distribution of relocations of radio-marked juveniles with the distribution of the territories of resident owls. For this evaluation we made the simplifying assumption that the area of primary use of resident owls corresponded to a 1.5 km radius around each nest site, and we limited the analysis to a portion of the Roseburg Study Area that was completely surveyed each year to locate all resident owls (Reid et al. 1996b).

Statistical Analyses

All statistical analyses were performed with program SPSS (Norušis 1990) or program SAS (SAS Institute 1997). We used 1-way ANOVA to evaluate year-effects and sex-effects on dates when owlets left the nest, number of days spent in the natal area, and dispersal dates. Dates when owlets left the nest and number of days spent in the natal area were estimated for 4 years in Oregon (1991–94) and 2 years in Washington (1991–92). Time spent in the natal area could not be computed for other cohorts of radio-marked juveniles because we did not visit nests frequently enough to determine approximate dates when owlets left the nest.

Variables measured relative to distance and direction of natal dispersal were: (1) the straight-line distance (MAXD) and azimuth (MAXAZ) to the farthest location from the natal site, (2) the straight-line distance and azimuth from the natal site to

the final location where the owl was located (FIND, FINAZ), regardless of the number of times the owl dispersed during the study or its age when last recaptured, (3) average distance moved per day (DDAY) during each time interval between sequential relocations, and (4) distance from natal site to owl at each relocation (DNEST). Estimates of DDAY were calculated by dividing the distance traveled between sequential relocations by the number of days in the interval, and were limited to cases where the interval between sequential relocations was ≤ 10 days. Average DDAY and DNEST were estimated for each weekly interval after dispersal started by averaging all estimates from all owls that were sampled in each weekly interval.

To evaluate the influence of dispersal distance on lifetime reproduction we used ANOVA to test the null hypothesis that mean dispersal distances did not differ among owls that first attempted to nest at 1, 2, 3, or 4+ years of age. This analysis was based on banded owls because the number of radio-marked owls that nested at 1 year of age was small.

For breeding dispersal the frame of reference for calculations of MAXD, MAXAZ, FIND, and FINAZ, was the initial banding location rather than the natal site. Differences in mean dispersal distances between groups were tested with 1-way ANOVA. All distances were log-transformed for analysis to improve normality.

For radio-marked juveniles we used regression analysis to examine the degree of correlation between MAXD and FIND and the number of days that owls were tracked after they initiated dispersal. For these tests we only used owls that were tracked ≥ 30 days after initiating dispersal. To determine if banded owls tended to keep moving away from their natal sites when they dispersed more than once, we tested the null hypothesis that mean FIND did not differ depending on the number of times that an owl dispersed during its lifetime. For the latter test we used 1-way ANOVA to compare mean

FIND for owls that dispersed 1, 2, or 3 times.

Shields (1983) proposed the "effective dispersal distance" (mean or median dispersal distance \div mean distance between pairs or territories in the population) as a method for comparing the relative degree of philopatry in species with different territory sizes and population densities. He defined a "philopatric" species as one in which the effective dispersal distance was ≤ 10 . To determine the denominator for calculations of effective dispersal distance, we selected a 1,011-km² area in the Roseburg Study Area that was completely surveyed every year, and divided the area by the average number of pairs detected per year in 1990–96 ($\bar{x} = 56$). This produced an estimate of 1 pair for every 1,805 ha, which, assuming that pairs were hexagonally packed, indicated an average spacing of 3.5 km between territory centers. We chose this approach because we did not have data on density of owls from all study areas, and because it was simple and repeatable.

Mean dispersal azimuths ($\bar{\alpha}$) and lengths of mean dispersal vectors (r) were calculated as described by Batschelet (1981:10). We used the mean angular deviation (s) to estimate the amount of dispersion around mean dispersal azimuths (Zar 1984:431). Confidence limits around mean azimuths were calculated as per Zar (1984:432). We tested the hypothesis that dispersal azimuths did not differ from random with a χ^2 test ($\chi^2 = 2nr^2$ with 2 df) (F. L. Ramsey, Oregon State University, personal communication). To determine if final dispersal azimuths of siblings were correlated we used a t -test to evaluate the null hypothesis that the mean difference between final dispersal azimuths of siblings did not differ from 90°, where $t = \bar{x} - 90^\circ / \sqrt{\text{var}/n} - 1$. The logic for this test was that if there was no tendency for siblings to disperse in the same direction or in opposite directions, then the average difference between dispersal azimuths of siblings should be 90°.

For non-juvenile owls we calculated a minimum estimate of the proportion of the territorial population dispersing per

Table 1. Number of spotted owls banded in Oregon and Washington that dispersed 1 or more times, 1985–1996.

No. of dispersal events per owl	No. of owls subdivided by age (in years) when first banded				Totals	
	0	1	2	3+	No.	%
1	595	60	54	252	961	83.5
2	105	9	17	7	168	14.6
3	9	2	3	5	19	1.7
4	2	0	1	0	3	0.3
Totals	711	71	75	294	1,151	100.0

year by dividing the number of owls that moved in a given year by the number of owls in the marked population that did not move or that disappeared and were never seen again. This was a minimum estimate of the annual breeding dispersal rate since we did not know if birds that disappeared were dead or had dispersed and gone undetected. For this analysis we assumed that dispersal occurred in the first year an owl was missing from its territory, regardless of when it was eventually re-observed at a new territory. This analysis was based on 4,917 records where we knew whether the owl moved, stayed on its territory, or disappeared in a given year, and where we determined the status of the mate from the previous year based on repeated field surveys. We restricted this analysis to 6 study areas where researchers provided a complete record of all field surveys between 1990–1996. We used χ^2 tests to compare proportions of owls that dispersed in different years.

We used 1-way ANOVA to conduct univariate tests of the null hypotheses that breeding dispersal was not influenced by sex, age in the previous breeding season, or social factors. Social factors (SF) that we examined were based on the status of the owl in the breeding season prior to the year in which it was found at a new territory, or the status of the owl's previous mate in the year that the owl was found at a new territory, as follows:

- 1 = owl did not have a mate in previous year.
- 2 = mate from previous year died or disappeared and was never seen again, despite repeated surveys.

3 = mate from previous year moved to new territory.

4 = mate from previous year still at the original territory.

Age in the breeding season prior to the year that an owl was relocated at a new territory (AGE) was classified as 1, 2, or 3+, with all owls that were ≥ 3 years old classified as 3+. Owls not banded as juveniles were assigned to age classes based on plumage characteristics (Forsman 1981).

In addition to univariate tests of factors related to breeding dispersal, we used 2 different logistic regression analyses to examine the simultaneous influence of sex, age, social factors and breeding status on breeding dispersal. In 1 analysis we treated dispersal as the response variable (Yes/No) with explanatory categorical variables SEX, AGE, and SF. In the other we used the same response variable, with explanatory variables SEX, AGE and nesting status (Yes/No) in the previous breeding season. The latter analysis was based on 4,877 cases where we were reasonably sure that nesting did or did not occur, based on repeated relocations of the owls in each territory. To compare the relative likelihood or "odds" of dispersal among groups with different combinations of age, sex and social factors, we computed 95% CIs on the odds ratios from the logistic regression models (Ramsey and Schafer (1997:575–577). All means are expressed as $\bar{x} \pm SE$.

RESULTS

During 1985–1996 we banded 7,682 spotted owls (3,683 juveniles, 3,999 non-

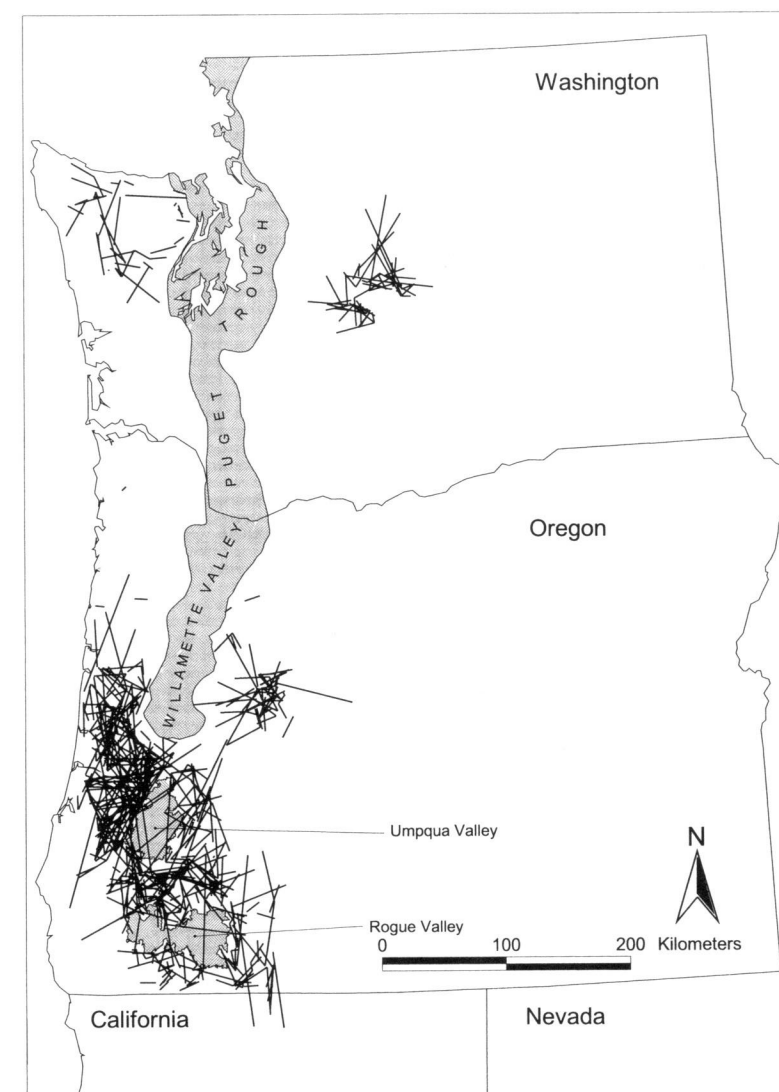


Fig. 2. Straight-line dispersal paths of 711 juvenile spotted owls banded in Oregon or Washington and recaptured after dispersing from their natal sites, 1985–1996. Shaded areas indicate lowland valleys characterized by non-forest habitat.

juveniles) and documented 1,366 dispersal events by 1,151 individuals (711 juveniles, 440 non-juveniles) (Table 1, Figs 2–3). For banded owls whose sex was known, records of dispersal were about equally distributed between males and females for juveniles (376 males, 327 females) and non-juveniles (231 males, 209 females). In most cases, we observed only 1 (83.5%) or 2 (14.6%) dispersal events per banded owl,

but there were 19 cases where owls dispersed 3 times (1.7%), and 3 cases (0.3%) where owls dispersed 4 times (Table 1).

Of the 386 juveniles that were radio-marked in 1990–95, we obtained dispersal data on 324. The other 62 juveniles either died ($n = 45$), molted their transmitters ($n = 5$), had transmitter failure ($n = 3$), or were lost due to unknown causes ($n = 9$) before initiating dispersal. Daily rates of

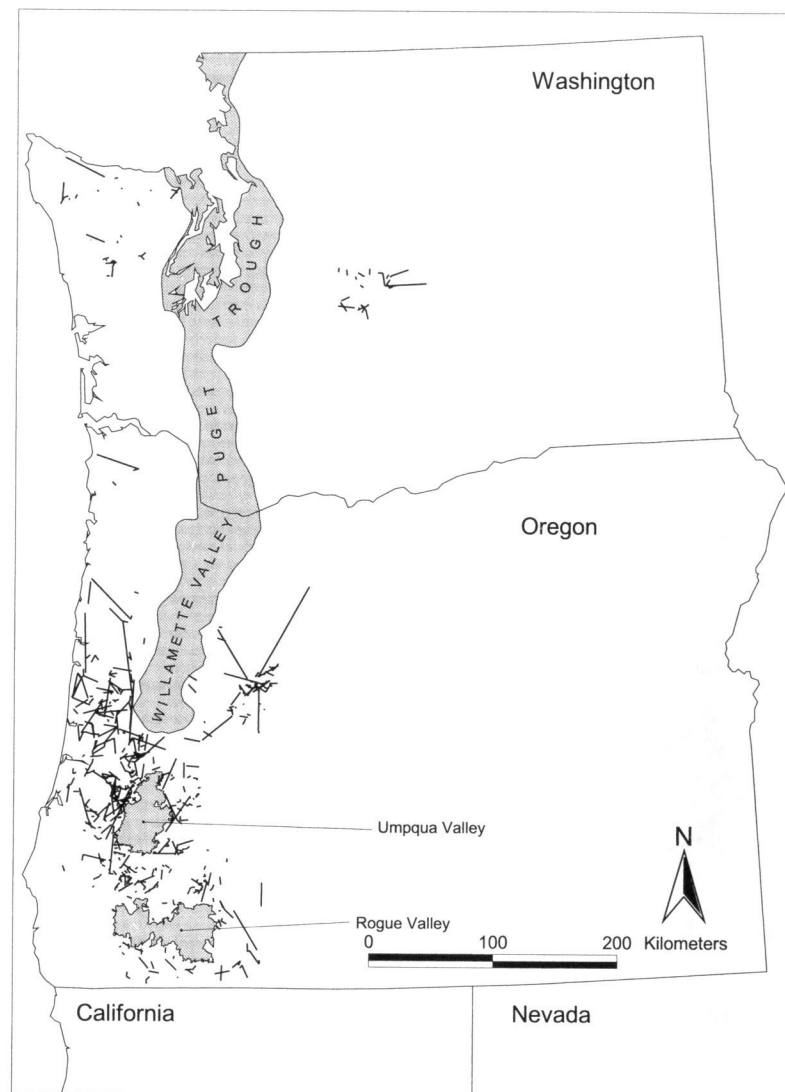


Fig. 3. Straight-line dispersal paths of 440 non-juvenile spotted owls that were banded in Oregon or Washington and recaptured or resighted after moving to new territories, 1985–1996. Shaded areas indicate lowland valleys characterized by non-forest habitat.

movement and dispersal direction were calculated for all radio-marked owls that dispersed, regardless of their sex or how many days they were tracked after they started dispersal. Estimates of mean MAXD and mean FIND of radio-marked owls were restricted to 236 individuals of known sex (114 males, 122 females) that we tracked for ≥ 30 days after they began to disperse.

Chronology of Natal Dispersal

Mean dates when juveniles were first located out of the nest were 8 June ± 0.53 days in Oregon ($n = 320$, range = 15 May–1 July) and 18 June ± 1.67 days in Washington ($n = 77$, range = 13 May–15 July). Mean dates when owlets left the nest varied among years in Oregon (range of means = 4–9 June, $F_{3,312} = 5.41$, $P =$

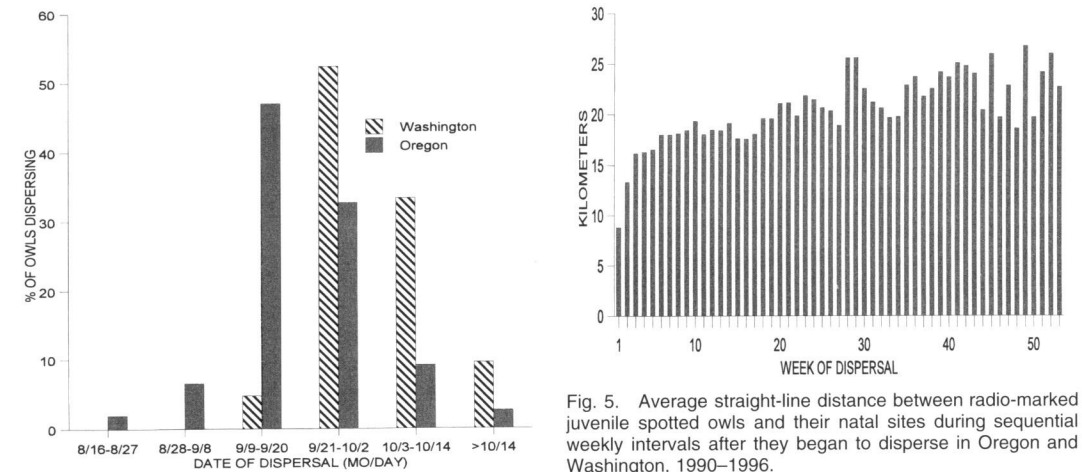


Fig. 4. Timing of dispersal of radio-marked juvenile spotted owls in Oregon and Washington, 1990–1995. Graph indicates percent of individuals initiating dispersal in different 12-day intervals. $N = 154$ in Oregon and 20 in Washington.

0.001) and Washington (range of means = 11–29 June, $F_{1,73} = 40.28$, $P < 0.001$). Because we sometimes did not find owlets until they had been out of the nest for several days, actual mean dates when owlets left the nest were probably several days earlier than our estimates.

Radio-marked juveniles spent an average of 103.7 ± 0.986 days in the natal territory after leaving the nest ($n = 137$, range = 76–147 days). Time spent in the natal area varied between the sexes ($F_{1,129} = 6.69$, $P = 0.011$) and among years ($F_{3,129} = 6.49$, $P < 0.001$), with males staying 5 days longer than females on average.

Of 287 cases where we determined approximate dispersal dates of radio-marked juveniles, 286 occurred in the period 9 August–18 December of the year of birth (Fig. 4). The exception was a male that did not disperse from his natal territory until 24 May of the year following birth (this outlier was excluded from estimates of sample means). The estimated mean date that owlets began to disperse was 19 September in Oregon (95% CI = 17–21 September) and 30 September in Washington (95% CI = 25 September–4 October) (Fig. 4). Mean dispersal dates did not differ between males and females ($F_{1,134} = 2.26$, $P = 0.14$) or among years ($F_{3,134} = 1.17$, $P =$

Fig. 5. Average straight-line distance between radio-marked juvenile spotted owls and their natal sites during sequential weekly intervals after they began to disperse in Oregon and Washington, 1990–1996.

$= 0.33$). Although we did not continuously monitor juveniles during the days immediately before dispersal started, we never saw any parental aggression towards juveniles on those occasions when we visited natal areas to check on radio-marked owls. Rather, it appeared that the adults simply stopped feeding and associating with their young in late August or September, several weeks before dispersal began.

Dispersal of radio-marked juveniles was highly variable, but was typically initiated with a series of rapid movements away from the natal site during the first few days or weeks of dispersal. On average, the straight-line distance between dispersers and their natal sites (DNEST) increased to 8.8 km during the first week of dispersal, 13.3 km during the second week of dispersal, and 16.2 km during the third week of dispersal (Fig. 5). The rapid movements that took place during the first few days or weeks of dispersal were indicated by high average daily rates of movement during September–October (Fig. 6). After the initial pulse of rapid dispersal, most juveniles settled into temporary home ranges in late October or November and remained there for several months. During this period mean daily rates of movement were comparatively low (Fig. 6), and mean DNEST stabilized at about 18–20 km (weeks 10–20 in Fig. 5). Then, in February–May, average daily rates of movement increased

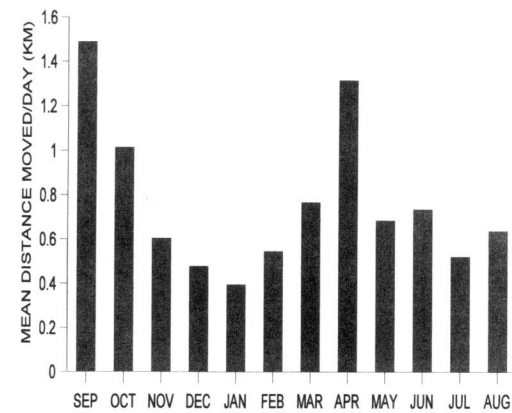


Fig. 6. Average distance moved per day by radio-marked juvenile spotted owls after they started to disperse in Oregon and Washington, 1990-1996. Data are subdivided by monthly intervals.

again (Fig. 6), and many owls moved to new areas, often dispersing considerable distances before settling in their second summer. The direction of this second pulse of natal dispersal was somewhat random relative to the natal site, and as a result, average DNEST leveled off at about 22 km after week 20 (Fig. 5).

Subsequent dispersal patterns were highly variable, with some owls settling permanently in their second summer and others occupying a series of temporary home ranges before eventually settling on territories when they were 2-5 years old (Fig. 7). Occupancy of temporary ranges was punctuated by occasional forays into adjacent areas. In some cases, these forays involved a return visit to areas near the natal site or to a temporary home range occupied during a previous period (Fig. 7). None of the banded or radio-marked juveniles settled at their natal sites, although 6.3% did settle on territories adjacent to their natal sites (males = 7.2%, females = 4.9%).

Areas traversed by dispersing juveniles typically encompassed the home ranges of multiple pairs of resident owls (Fig. 8). However, 85% of the relocations of radio-marked floaters in our Roseburg study area were > 1.5 km from the center of territories occupied by resident pairs, suggesting a strategy in which floaters inhab-

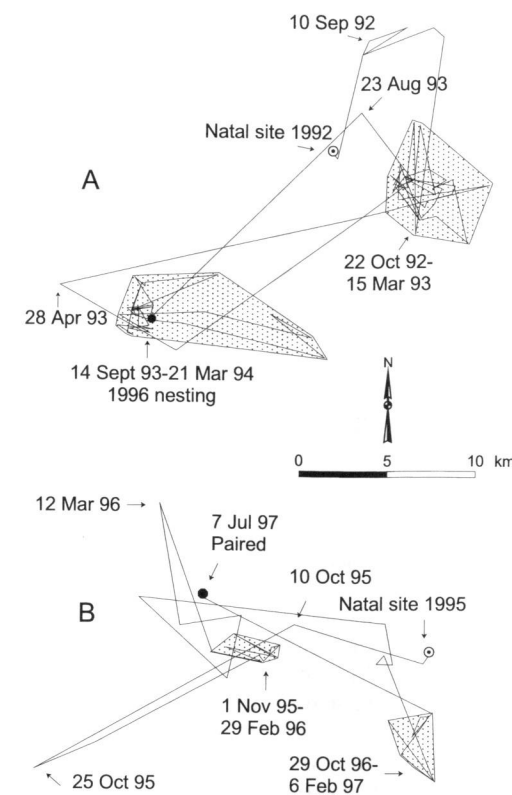


Fig. 7. Examples of movements of 2 radio-marked juvenile spotted owls during natal dispersal in Oregon. Sequential relocations are connected by straight lines. Shaded areas indicate temporary or permanent home ranges occupied by the owls.

ited the periphery of the territories of resident owls, making occasional forays into the territories to test the residents. In a few cases, we found floaters roosting within a few meters of resident pairs. We observed no cases where the floaters that associated with resident pairs were offspring of those pairs and we saw no evidence that they mated with the resident owls. Floaters did not appear to vocalize a great deal, but we did occasionally hear unsolicited vocalizations from them. In a small sample of cases where we used an acoustic lure to see if radio-marked floaters would respond to conspecific calls, we found that males responded 47% of the time ($n = 10$ males, 19 surveys) and females responded 12% of the time ($n = 5$ females, 8 surveys).

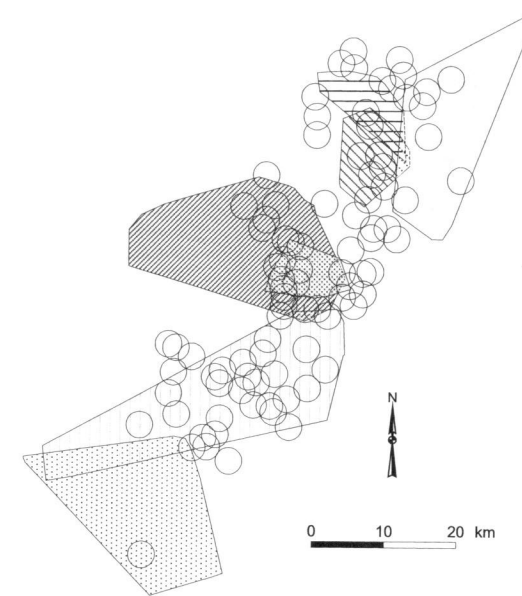


Fig. 8. Areas traversed by spotted owls during natal dispersal in the Roseburg Study Area, Oregon, 1995-1996. Minimum convex polygons indicate areas traversed by individual owls. Circles (2.4 km radius) indicate approximate home range areas of resident pairs, centered on nest trees.

Natal Dispersal Distance

All regressions of distance dispersed (FIND) on the number of days that owls were radio-tracked produced low r^2 values (0.005-0.083), indicating that little of the variation in dispersal distance was explained by the length of the tracking period. As a result, we pooled all data for

estimates of mean and median dispersal distances, the only limitation being that owls had to be tracked for ≥ 30 days after initiating dispersal. We also pooled the data for analysis regardless of whether juveniles successfully reproduced after dispersing, because there was no difference in dispersal distance (FIND) of banded owls that successfully reproduced in the year of first recapture and those that did not ($\sigma \sigma F_{1,312} = 1.272, P = 0.260$; $\sigma \sigma F_{1,290} = 0.006, P = 0.937$). As a result we did not complicate the analysis by differentiating between owls that dispersed and reproduced (genetic dispersal) and owls that dispersed but did not reproduce (ecological dispersal) (Johnson and Gaines (1990)).

Maximum dispersal distances (MAXD) ranged from 1.3-111.2 km for banded juveniles and from 5.5-122.1 km for radio-marked juveniles (Table 2). Final dispersal distances (FIND) ranged from 0.6-111.2 km for banded juveniles and from 1.8-103.5 km for radio-marked juveniles. Distributions of MAXD and FIND were skewed towards shorter distances, with only 8.7% of individuals dispersing more than 50 km (Fig. 9). Because of the skewed distribution, median estimates of MAXD and FIND were consistently lower than means (Table 2).

On average, females dispersed farther than males, regardless of whether we ex-

Table 2. Maximum (MAXD), final (FIND) and effective (EDD) dispersal distances of juvenile spotted owls in Washington and Oregon, 1985-1996.^a

	<i>n</i>	\bar{x} (km)	SE	Median	Range	EDD
Males						
MAXD banded	376	20.0	0.83	15.1	1.4-111.2	4.3
MAXD radio-marked	114	23.4	1.47	20.5	5.9-94.3	5.9
FIND banded	376	19.5	0.83	14.6	0.6-111.2	4.2
FIND radio-marked	114	18.1	1.47	13.5	2.7-93.1	3.9
Females						
MAXD banded	328	28.9	0.99	24.6	1.3-104.7	7.0
MAXD radio-marked	122	32.2	1.71	27.7	5.5-122.1	7.9
FIND banded	328	28.6	0.99	24.5	1.3-104.6	7.0
FIND radio-marked	122	26.3	1.57	22.9	1.8-103.5	6.5

^a MAXD = straight-line distance to the location farthest from the natal site. FIND = straight-line distance from the natal site to the final location where the owl settled, died, or disappeared. Effective dispersal distance (EDD) was the median dispersal distance divided by the average distance between territories of resident owls (3.5 km).

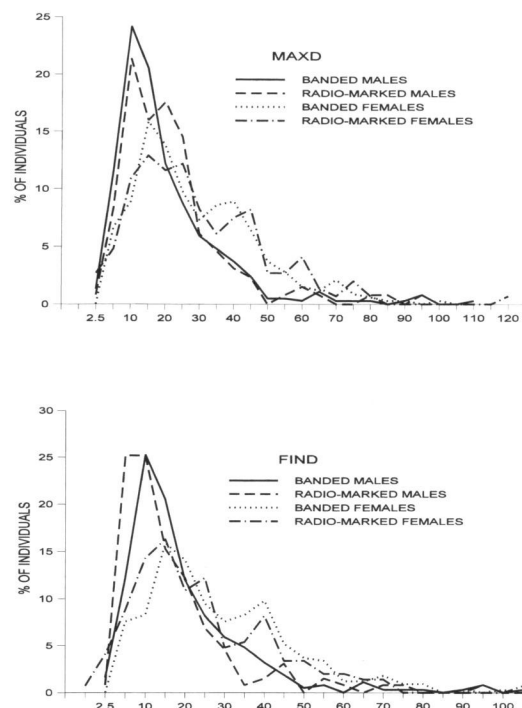


Fig. 9. Distribution of natal dispersal distances of spotted owls in Oregon and Washington, 1985–1996. Maximum (MAXD) and final (FIND) dispersal distances were straight-line distances (km) from the natal site to the farthest and final locations where owls were relocated, respectively.

amed banded owls (FIND $F_{1,703} = 64.965$, $P < 0.001$; MAXD $F_{1,934} = 74.865$, $P < 0.001$) or radio-marked owls (FIND $F_{1,234} = 18.976$, $P < 0.001$; MAXD $F_{1,234} = 14.586$, $P < 0.001$) (Table 2, Fig. 9). In the sample of banded juveniles, mean and median estimates of FIND for females were 47% and 68% greater than for males, respectively (Table 2). In the sample of radio-marked juveniles, estimates of mean and median FIND for females were 46% and 70% greater than for males, respectively (Table 2).

Estimates of mean FIND were similar for banded and radio-marked owls ($F_{1,947} = 1.777$, $P = 0.183$) (Table 2). Estimates of mean MAXD were greater for radio-marked owls than for banded owls ($F_{1,947} = 14.381$, $P < 0.001$) (Table 2), but this was expected given that we rarely relocated banded juveniles until they settled on a territory. In contrast, we were often able

Table 3. Mean natal dispersal distances (km) of banded spotted owls, subdivided based on age (in years) when owls first nested. This analysis was limited to owls that were first captured when they were ≤ 4 years old, Oregon and Washington, 1985–1996.

Age when owls first nested	Males			Females		
	<i>n</i>	\bar{x}	SE	<i>n</i>	\bar{x}	SE
1	4	20.1	4.15	6	22.2	5.88
2	25	14.9	1.81	33	31.0	3.08
3	23	17.7	2.91	20	20.9	3.00
4	40	16.7	1.75	17	28.4	4.25
5	11	16.7	3.74	12	30.9	5.41
6+	13	17.5	4.02	8	29.9	7.08
Did not nest ^a	51	22.4	2.48	39	30.2	2.82

^a Included any owls that dispersed and then did not nest before they disappeared.

to record locations of radio-marked owls at locations beyond where they eventually settled. Thus, comparisons of MAXD obtained with the 2 different methods were useful only to demonstrate that estimates from banding data underestimate maximum dispersal distances. The age when banded owls first nested did not appear to be influenced by dispersal distance for either males ($F_{6,160} = 1.129$, $P = 0.348$) or females ($F_{6,128} = 1.0113$, $P = 0.421$) (Table 3).

Estimates of effective dispersal distance were similar for banded and radio-marked juveniles (Table 2). The average effective dispersal distance for the pooled samples of radio-marked and banded owls was 4.1 for males, and 6.8 for females.

Direction of Natal Dispersal

Mean dispersal vectors (FINAZ) differed from random for banded juveniles ($\bar{x} = 262^\circ$, $s = 76^\circ$, 95% CI = 192–332°, $r = 0.121$, $\chi^2 = 21.72$, $P = 0.001$, $n = 711$) and radio-marked juveniles ($\bar{x} = 115^\circ$, $s = 77^\circ$, 95% CI = 38–192°, $r = 0.088$, $\chi^2 = 4.96$, $P = 0.010$, $n = 324$) (Fig. 10). However, the small r -values, large mean angular deviations, and large 95% CIs for both samples led us to conclude that statistical differences were due to large sample size as opposed to biologically significant variation (Fig. 10).

The mean difference between final dispersal azimuths of siblings did not differ

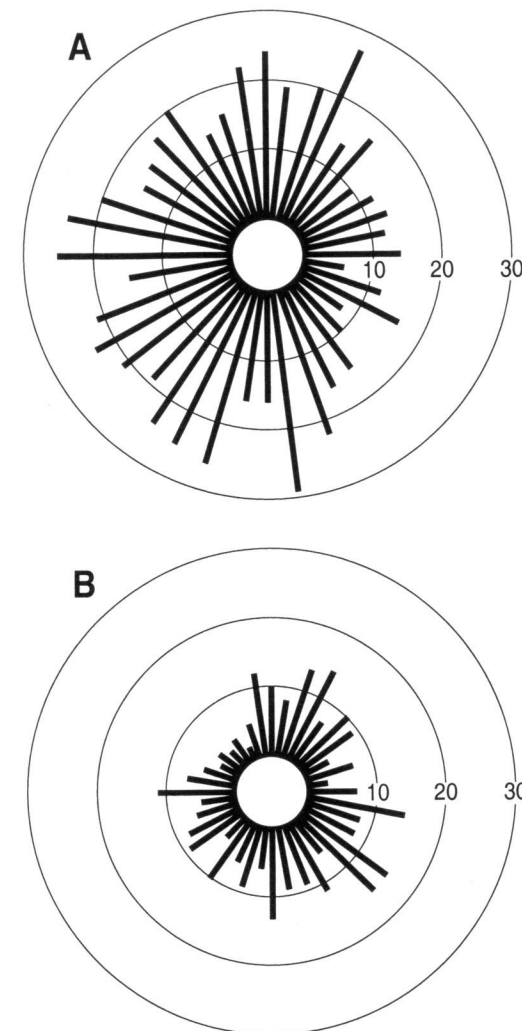


Fig. 10. Distribution of final dispersal azimuths of 1,035 juvenile spotted owls that were banded (A) ($n = 711$) or radio-marked (B) ($n = 324$) in Oregon and Washington, 1985–1996. Columns indicate number of owls dispersing in each 9° arc.

from 90° ($\bar{x} = 84.131 \pm 4.555^\circ$, $t_{144} = 1.318$, $P = 0.095$, $n = 145$ paired samples). This suggested that dispersal azimuths of siblings were not correlated. In addition, siblings were never found together while dispersing, indicating that they dispersed independently.

Social Integration of Juveniles

Age at Recruitment.—Of the radio-marked owls that were alive, 21.5% of

males and 44.2% of females were paired at age 1, and 67.6% of males and 76.9% of females were paired at age 2 (Table 4). We considered these estimates as analogous to recruitment rates, because most radio-marked owls that were single at 1–2 years of age were unsettled itinerants. Estimates from the radio-marked sample suggested that considerably more females than males were recruited into the territorial population at age 1, and that sexual differences in recruitment began to even out after year 1. Few of the radio-marked owls that were paired nested at 1–2 years of age (Table 4).

Estimates of recruitment rates of banded owls based on age at first recapture (age = 1, 2, 3, 4, or >4) were 33%, 31%, 17%, 10%, and 9%, respectively. Comparable estimates of recruitment from the radio-marked sample were 33% for 1-year-old owls and 39% for 2-year-old owls. The latter estimate was derived by subtracting the proportion of owls that were paired in year 1 from the proportion of owls paired in year 2 (Table 4). Assuming that banded owls were recruited into the territorial population when they were first recaptured, mean age at recruitment was 2.36 ± 0.07 years for males (range = 1–8, 95% CI = 2.22–2.49, $n = 375$) and 2.39 ± 0.08 years for females (range = 1–8 years, 95% CI = 2.23–2.55, $n = 327$).

Although mean estimates of recruitment from the banded and radio-marked samples were similar, the 2 methods produced very different estimates of sexual differences in recruitment and of social status of recruits. Whereas the radio-marked sample indicated that nearly twice as many females as males were recruited at 1 year of age (Table 4), the banded sample indicated that percentages of banded owls first recaptured in different age cohorts did not differ between males and females ($\chi^2_4 = 6.35$, $P = 0.175$). In addition, the social distribution of owls in the 2 samples was different (Table 4). In the banded sample, most males and over 90% of females were paired when they were first recaptured at 1–2 years of age (Table 4). In the radio-marked sample, most owls were single at

Table 4. Social status of known-age spotted owls detected in study areas in Oregon and Washington, 1985–1996. Data are expressed as the percentage of total individuals recaptured or resighted in each age class. The sample for each age cohort included all owls detected, regardless of whether the same owls were also detected in other age cohorts.

	Radio-marked owls ^a		Banded owls ^b		
	Age = 1	Age = 2	Age = 1	Age = 2	Age = 3+
Males					
Single	78.5	32.4	37.4	23.2	15.1
Paired, not breeding	20.0	62.2	56.9	57.2	50.8
Paired, breeding	1.5	5.4	5.7	19.6	34.1
Females					
Single	55.8	23.1	8.4	6.0	5.7
Paired, not breeding	42.6	74.3	83.2	60.7	54.8
Paired, breeding	1.6	2.6	8.4	33.3	39.5

^a Sample sizes were: age 1 year = 65 ♂♂, 61 ♀♀; age 2 years = 37 ♂♂, 39 ♀♀.

^b Sample sizes were: age 1 year = 123 ♂♂, 107 ♀♀; age 2 years = 138 ♂♂, 117 ♀♀; age 3+ years = 464 ♂♂, 403 ♀♀.

1 year of age, and 23% of females and 32% of males were still single at 2 years of age (Table 4).

Inbreeding.—Despite monitoring thousands of pairs of spotted owls for periods ranging from 5–13 years, we documented only 3 cases of close inbreeding, including a half-sib pair (same father), a full-sib pair, and a father-daughter pair. The half-siblings were produced on the same territory and settled 2.2 km away, where they produced 2 young in 2 different years. The full-sib pair consisted of offspring from the 1990 cohort. They nested and produced 2 young in 1992, 4.4 km from their natal site. The female disappeared after 1992. The father-daughter pair was a case where an adult male dispersed 3.5 km and paired with his 2-year-old daughter from his previous territory. They nested in 3 of the 4 years they were together, but produced only 1 young. Although inbreeding between siblings or parents and offspring was a rare event, pairings between dispersers and more distant relatives (cousins, aunts, uncles, grandparents, or great grandparents was common (Reid and Forsman, unpublished data).

Causes of Mortality

Of the 386 juveniles that we radio-marked, at least 188 (48.7%) died before or during dispersal. In 122 cases where we were able to infer cause of death from signs found at the recovery site, 83 owls

(68.0%) died from predation, 32 (26.2%) starved and 7 (5.7%) died from accidents. Of the 83 cases of predation, 67 (81%) were due to avian predators, and 16 (19%) were due to predation by mammals or unknown predators. In most of the latter cases, it was unclear whether owls were killed by predators or were scavenged after they were already dead or dying from starvation or disease. Thus, if anything, we suspect that mortality from starvation is underestimated by our analysis, whereas death from predation is probably slightly overestimated.

We suspected that great horned owls (*Bubo virginianus*) were responsible for most cases of avian predation, but we could only confirm this in 1 case where we found a transmitter in a great horned owl nest and 2 cases where we found remains in great horned owl pellets. The most common cause of accidents was collisions with vehicles ($n = 4$), but we also documented 1 case where an owl caught its wing in a narrow crevice in a tree trunk, 1 case where an owl impaled itself on a sharp stick, and 1 case where an owl was apparently killed by a falling tree in an area that was being logged.

Although starvation and predation appeared to be the ultimate cause of death in 94% of cases, parasites or disease may have been a predisposing factor in some cases. Of 48 juvenile and adult owls that we recovered intact enough for at least a

Table 5. Annual estimates of the percentage of banded non-juvenile spotted owls that dispersed to new territories (Disp.), remained on the same territory (Stayed) or disappeared and were never seen again (Gone) on study areas in Oregon and Washington, 1985–1996.^a

Year	1-year-old owls			2-year-old owls			≥ 3-year-old owls		
	Gone	Stayed	Disp.	Gone	Stayed	Disp.	Gone	Stayed	Disp.
86							17	78	4
87							16	78	6
88	20	55	25	8	92	0	14	83	3
89	38	56	6	11	69	20	26	71	3
90	35	45	20	19	70	11	16	77	7
91	36	50	14	14	71	16	16	78	6
92	39	46	15	11	66	23	15	79	6
93	30	32	39	18	68	14	23	71	6
94	29	52	19	19	71	10	13	82	5
95	30	45	25	23	57	20	20	76	4
96	33	46	21	28	61	11	16	79	5
\bar{x}	32	48	20	17	69	14	17	78	5

^a Sample sizes by year for each age class were: 1 year old (20, 16, 20, 36, 39, 44, 48, 20, 33); 2 years old (12, 45, 27, 51, 53, 57, 48, 91, 18); ≥ 3 years old (52, 107, 220, 296, 411, 697, 773, 886, 839, 841, 820).

partial necropsy, at least 32 (67%) were infected by blood parasites or intestinal parasites, or had evidence of disease. Infections with multiple species of hemoparasites and intestinal parasites were common, and 1 owl had avian cholera.

Breeding Dispersal

Proportion of non-juveniles dispersing per year.—Of the non-juvenile owls that we banded, 6.6% dispersed each year, and 18% disappeared each year and were never seen again. The annual proportion of owls that dispersed was highest for 1-year-old owls ($\bar{x} = 20\%$, 95% CI = 13.6–

27.4%), intermediate for 2-year-old owls ($\bar{x} = 14\%$, 95% CI = 8.6–19.1%), and lowest for owls that were ≥ 3 years old ($\bar{x} = 5.0\%$, 95% CI = 4.0–6.1%) ($F_{2,24} = 12.61$, $P < 0.001$) (Table 5). The proportion of owls that dispersed did not vary among years for the combined sample ($\chi^2_{10} = 8.9$, $P = 0.54$) or for any age groups (χ^2 P -values ranged from 0.156–0.48). When owls that were ≥ 3-years old were subdivided into minimum age classes based on length of tenure in our studies, annual rates of dispersal differed among age classes (Table 6, $F_{9,6,422} = 6.185$, $P < 0.001$). However, this relationship was not evident when the 2 youngest minimum age classes (3–4) were removed from the analysis ($F_{7,3,406} = 0.304$, $P = 0.952$). This suggested that annual dispersal rates of older adults (minimum age = 5–12 years) did not differ among age classes (Table 6).

We observed only 1 dispersal event for most (83%) of the banded owls that undertook breeding dispersal (363 of 440 owls). In 39 cases (9%) where owls that were ≥ 3 years old dispersed twice, 41% moved back to their previous territory on the second move. Owls that were banded at 1 or 2 years of age, and then moved twice, returned to their original territory on the second move only 11% and 24% of the time, respectively. Of 12 owls that

Table 6. Minimum percentage of banded adult northern spotted owls that dispersed each year in study areas in Oregon and Washington, subdivided by minimum age class, 1985–1996. Minimum age class indicates minimum age of owls in the previous breeding season.

Minimum age (years)	n	% dispersing	95% CI
3	1,709	8.31	7.00–9.62
4	1,309	5.19	3.99–6.40
5	1,042	4.13	2.92–5.34
6	820	3.29	2.07–4.52
7	620	3.23	1.83–4.62
8	445	3.60	1.86–5.33
9	266	2.63	0.70–4.57
10	130	3.08	0.07–6.09
11	60	3.33	0.00–8.00
12	31	3.23	0.00–0.98

Table 7. Annual percentage of banded non-juvenile spotted owls that dispersed to new territories, stayed on the same territories, or disappeared and were never seen again, relative to the status of the mate from the previous year. χ^2 results are for tests of the null hypothesis that proportions did not differ among age groups.

Status of previous mate ^a	Age in years	Percentage of owls			n	χ^2	P
		Dispersed	Stayed	Disappeared			
Dispersed	1	31	19	50	16	5.5	0.240
	2	44	36	20	25		
	3+	29	31	40	237		
Stayed	1	9	71	20	123	53.4	<0.001
	2	4	84	12	262		
	3+	1	87	12	4,855		
Gone	1	28	26	46	35	29.7	<0.001
	2	21	44	35	72		
	3+	10	60	30	921		
No mate	1	35	28	37	89	39.6	<0.001
	2	41	45	14	56		
	3+	18	58	24	388		

^a "Dispersed" = old mate moved to a new territory, "Stayed" = old mate still present at old territory, "Gone" = old mate disappeared and never seen again, "No mate" = owl did not have a mate in previous year.

were ≥ 3 years old that moved 3–4 times, 6 moved to a different territory every time, 3 moved back and forth between 2 adjacent territories, 1 moved once and then moved back and forth between 2 adjacent territories, and 2 moved back and forth between 2 territories before moving to a third territory.

Factors Associated With Breeding Dispersal.—Annual dispersal rates were higher for owls whose mates disappeared or moved to another territory than for owls whose mates were still present on the historic territory (Table 7). On average, dispersal rates of females were slightly higher than males, but the differences were significant in only 2 of 11 years examined (Table 8).

Ten percent of breeding dispersal events by owls that were ≥ 3 years old involved cases where both members of a pair moved together to an adjacent territory, 10% involved cases where pairs split up and moved to new locations, and 17.5% involved cases where an owl dispersed while its mate stayed at the original territory (Table 9). Of 118 cases where adult pairs split up, 57% appeared to be divorces, as evidenced by the fact that the previous mate was single in the year following the breakup, or was paired with a new mate on a new territory. In the other 43% of cases it was unclear if dispersal was the

result of a divorce or eviction by a competitor, since the owl that moved was immediately replaced on its old territory (Table 9).

The logistic regression analysis of breeding dispersal indicated that the likelihood of dispersal in a given year was simultaneously influenced by sex, age and social factors (SF), in the following manner:

$$\begin{aligned} \log(\text{odds of dispersal}) &= -3.705 - 0.711*\text{SEX} + 3.069*\text{SF}_1 \\ &+ 2.275*\text{SF}_2 + 3.983*\text{SF}_3 \\ &+ 1.573*\text{AGE}_1 + 0.9468*\text{AGE}_2 \end{aligned}$$

where $\text{SF}_1 = 1$ if the owl was single in the previous year, $\text{SF}_2 = 1$ if the mate from the previous year was missing or dead, $\text{SF}_3 = 1$ if the mate from previous year moved to a new territory, and $\text{AGE}_1 = 1$ if age in the previous year was 1, and $\text{AGE}_2 = 1$ if age in the previous year was 2. (Table 10). Other factors being equal (i.e., same sex and social factor), the probability of movement was greatest for 1-year-old owls, intermediate for 2-year-old owls and lowest for owls that were ≥ 3 years old (Table 10). Females were 1.6–2.6 times more likely to move than males, other factors being equal (Table 10). Owls that were single in the previous year or whose mates from the previous year disappeared or moved to a

Table 8. Minimum percentage of adult spotted owls (≥ 3 years old) that dispersed each year on study areas in Oregon and Washington, 1985–1996, subdivided by sex.^a

Year	n	Percent of owls dispersing		χ^2	P
		♂♂	♀♀		
1986	28:24	3.6	4.2	0.01	0.91
1987	64:43	1.6	14.0	6.46	0.01
1988	123:97	1.6	4.1	1.27	0.26
1989	163:133	2.5	4.5	0.95	0.33
1990	222:189	6.8	7.4	0.07	0.78
1991	374:305	4.5	8.2	3.86	0.05
1992	429:353	6.7	4.8	1.20	0.27
1993	468:418	5.8	5.5	0.03	0.86
1994	441:398	5.7	4.3	0.86	0.35
1995	435:406	4.4	3.9	0.10	0.76
1996	430:390	4.9	5.4	0.11	0.74
\bar{x}		4.4	6.0		

^a Data combined from the Cle Elum, Siuslaw, Roseburg, H. J. Andrews, Coos, Eugene, and Salem Study Areas. Owls present at the same site or missing and never seen again were counted as non-dispersers.

new site were much more likely to disperse than owls whose mates from the previous year were still present at the same territory (Table 10). The highest odds of movement were for owls whose mates moved to a new territory. In those cases, owls were 36–80 times more likely to move than owls whose mates were still present on the same territory (Table 10).

The selected logistic regression model from the analysis of dispersal relative to sex, age, and breeding status in the previous year (PNS) was:

$$\begin{aligned} \log(\text{odds of dispersal}) &= -3.0192 - 0.6848*\text{SEX}\delta \\ &+ 1.7090*\text{AGE}_1 + 1.0735*\text{AGE}_2 \\ &+ 0.5524*\text{PNS} \\ &+ 0.6673*\text{SEX}\delta*\text{PNS} \end{aligned}$$

where $\text{PNS} = 1$ if the owl did not nest in the previous year, or 0 otherwise. This model also included an interaction with sex and previous nesting status, indicating that the effect of previous nesting status differed between the sexes. Males that did not nest in the previous year were 2.6–4.3 times more likely to move than males that nested in the previous year, whereas females that did not nest in the previous year were 1.2–2.4 times more likely to move than females that nested in the previous year.

Distance and direction of Breeding Dispersal.—Mean breeding dispersal distances were considerably shorter than distances moved by natal dispersers (Table 11, Fig. 3) and did not differ between the sexes or among study areas (all P -values > 0.10). On average, young owls dispersed farther than older owls ($F_{2,435} = 3.674$, $P = 0.026$) (Table 11). Mean FIND did not differ depending on the number of times that owls dispersed for any age classes except adults. Adults that moved twice tended to move closer to their original territory

Table 9. Percentage of observed breeding dispersal events of spotted owls relative to the status of the mate from the previous territory in the year that dispersal occurred, Oregon and Washington, 1985–1996. Estimates are presented separately for owls that dispersed when they were 1, 2, or ≥ 3 years old.

Status of mate from previous territory	Percentage of dispersal events		
	Age 1	Age 2	Age ≥ 3
Owl did not have a mate at previous territory	51.4	34.2	16.8
Previous mate died (confirmed death)	1.4	1.0	2.8
Previous mate missing and never seen again	13.5	31.3	38.5
Pair moved to new territory together		5.1	10.0
Previous mate single at previous territory	6.6	1.0	5.6
Previous mate single at a new territory	2.7	1.0	1.4
Previous mate paired with new mate at same territory	12.2	16.2	11.9
Previous mate paired with new mate at new territory	9.5	6.1	8.6
Previous mate missing, but seen in later years	2.7	4.1	4.4
Total	100.0	100.0	100.0

^a Sample sizes by age group were 72, 99, 429

Table 10. Relative odds of breeding dispersal of spotted owls in Oregon and Washington in 1985–1996, based on the selected logistic regression model. In each row the 95% CI's indicate the relative odds (or likelihood) that owls with characteristics indicated under group 1 will disperse, compared to owls with characteristics indicated under group 2. The SF column indicates the status of the mate from the previous territory in the year that dispersal occurred (D = disappeared or presumed dead, M = moved to new territory, P = still present at old territory, S = the owl that dispersed did not have a mate in the year prior to dispersal). A blank variable in a row means that both groups have the same status for that variable. The table displays only a few of many possible comparisons.

Group 1			Group 2			95% CI on relative odds of dispersal (group 1 versus group 2)
Sex	Age ^a	SF	Sex	Age	SF	
♀	1		♂	3+		1.6–2.6 greater
	2			3+		
		S			P	1.8–3.7 greater
		D			P	15.2–30.4 greater
		M			P	7.1–13.3 greater
	1	S		3+	P	35.9–80.3 greater
♀	1	S	♂	3+	P	62.0–174.2 greater
♀	1	M	♂	3+	P	156.6–283.2 greater
						378.8–732.9 greater

^a Age = 1, 2, or ≥ 3 years old.

if they moved twice ($F_{2,291} = 23.09$, $P < 0.001$). That is, they tended to move back to their original territory after occupying an adjacent territory for 1 or more years. The direction of post-natal dispersal did not differ from random regardless of whether we examined the azimuth from the origin to the final location ($\bar{x} = 123^\circ$, $r = 0.011$, $\chi^2 = 0.07$, $P = 0.97$, $n = 294$) or the azimuth from the origin to the farthest recorded location ($\bar{x} = 121^\circ$, $r = 0.008$, $\chi^2 = 0.03$, $P = 0.98$, $n = 294$).

Barriers To Dispersal

The large, non-forested valleys of western Oregon (Willamette, Rogue, and Umpqua Valleys) appeared to act as barriers to dispersal between the Coastal Mountains and Cascades Mountains (Figs. 2–3). For example, we never documented any movements directly across the Willamette Valley, which separates the Oregon

Table 11. Breeding dispersal distances of banded non-juvenile spotted owls that moved from 1 territory to another in Oregon or Washington, 1985–1996.

Age of owl in years	Distance moved (km)				
	\bar{x}	SE	Median	Range	<i>n</i>
1	8.2	1.21	5.1	0.01–63.7	71
2	6.9	0.93	4.1	0.17–50.7	75
3+	6.1	0.49	3.5	0.01–85.2	294

Coast Ranges from the Cascades Mountains (Figs. 2–3). However, owls did disperse from the Coastal Mountains to the Cascades Mountains in the broad forested regions between the Willamette, Umpqua and Rogue valleys (Figs. 2–3).

Although large areas of non-forested habitat appeared to inhibit dispersal, spotted owls regularly dispersed through the highly fragmented forest landscapes that were typical of the mountain ranges in western Oregon and Washington. They also crossed highway corridors such as Interstate 5 in Oregon and Interstate 90 in Washington. Although dispersal typically occurred in fragmented forest landscapes, an analysis of the survival of dispersing owls relative to the degree of forest fragmentation was beyond the scope of our study.

We observed several owls that crossed the crest of the Cascades Mountains, dispersing through high-elevation areas of mixed subalpine forest and alpine tundra. The relative infrequency of these movements suggested that high elevation areas dominated by mixtures of subalpine forest and alpine tundra inhibited dispersal, but did not completely stop it.

Owls regularly dispersed around or over lakes and rivers, except in the case of very wide bodies of water. The most notable example was the large marine inlets (Hood

Canal and Puget Sound) that separated the Olympic Peninsula from mainland Washington (Figs. 3–4). We did not document any dispersal from the peninsula across Hood Canal or Puget Sound. We also did not observe any dispersal between the peninsula and southwestern Washington (Figs. 3–4). While the absence of recorded dispersal movements between the peninsula and southwestern Washington or the Washington Cascades may indicate that the owl population on the peninsula is relatively isolated, it could also be due to the fact that there were no demography studies of spotted owls in areas immediately adjacent to the peninsula, and thus little chance of detecting dispersal.

DISCUSSION

Natal Dispersal

Although the behavior of dispersing juveniles was highly variable, the most common pattern in our study and in all previous studies of dispersal in the spotted owl was for juveniles to move rapidly away from the natal site during September–November (Gutiérrez et al. 1985, Miller 1989, Arsenault et al. 1997, Ganey et al. 1998). Both sexes dispersed, and we never saw any cases where juveniles settled on their natal sites. After the initial surge of movement away from the natal site most individuals settled in 1 or more temporary home ranges before eventually acquiring territories. This pattern of dispersal seems to be fairly typical of non-migratory owls (Korpimäki and Lagerström 1988, Belthoff and Ritchison 1989, Bull and Henjum 1990, Taylor 1994, Ellsworth and Belthoff 1997, Rhoner 1997a, b).

Our estimates of the amount of mean time spent in the natal area prior to dispersal (103 days) and mean dates of dispersal (19–30 Sept.) are similar to estimates from previous studies (Miller 1989, Ganey et al. 1998), suggesting that these parameters do not vary much, even between populations in widely disparate areas. However, some yearly variation may occur (this study, Ganey et al. 1998). Great

horned owls are similar to spotted owls in that their young disperse primarily in September or October after spending several months at their birth site (Rhoner 1997b). In comparison, the young of some other owls spend comparatively little time at the natal site before dispersing. For example, the mean interval between fledging and initiation of dispersal was 55 ± 1.3 days for eastern screech owls (*Otus asio*) and 60 ± 2.4 days for western screech owls (*O. kennicottii*) (Ellsworth and Belthoff 1997: 156, Belthoff and Ritchison 1989:256). Barn owls (*Tyto alba*) have a particularly short period of postnatal care, typically dispersing within 2–5 weeks after leaving the nest (Seel et al. 1983, Taylor 1994).

The negatively skewed distribution of dispersal distances observed in our study is typical of natal dispersal in most organisms (Bateman 1950, Stewart 1952, Levin and Kerster 1974, Adamcik and Keith 1978, Greenwood 1980, Moore and Dolbeer 1989). A concern in banding studies is that a negatively skewed distribution of dispersal distances can result from survey bias if search effort is focused primarily in a small, finite study area (Barrowclough 1978, Moore and Dolbeer 1989, Koenig et al. 1996). Because our estimates of means and ranges of dispersal distance were similar for banded and radio-marked owls, we concluded that recaptures of banded owls were not influenced by small study area bias. This outcome was not particularly surprising because our study areas were large and because we received assistance from observers outside our study areas who were also conducting surveys of spotted owls.

Although we observed no cases where northern spotted owls dispersed >122 km, there is 1 record of a female Mexican spotted owl (*S. o. lucida*) that was recovered 187 km from her original banding location (Gutiérrez et al. 1996). In addition, we confirmed 1 case of long-distance dispersal that we did not include in our analysis because the bird was an F1 female hybrid between a spotted owl and a northern barred owl (*Strix varia*). This hybrid was banded as a juvenile in 1986 in the south-

ern Cascades of Washington (H. Allen pers. comm), and subsequently dispersed 292 km to the northwest tip of the Olympic Peninsula, where she was recaptured in 1991 and resighted in most years from 1992–2001. We do not know if this exceptionally long dispersal event was an anomaly or is indicative of stronger dispersal by hybrids or barred owls. Regardless, it is clear from our data that dispersal distances >100 km are rare for northern spotted owls.

Although few juveniles tracked in previous studies of spotted owls were monitored long enough to determine where they eventually settled (Allen and Brewer 1985, Gutiérrez et al. 1985, 1996, Laymon 1988, Miller 1989, Verner et al. 1992, U.S. Fish and Wildlife Service 1995, Arsenault et al. 1997, Miller et al. 1997, Ganey et al. 1998), mean dispersal distances in those studies were similar to our estimates from owls that were tracked for much longer periods and that eventually settled on territories. We believe this was the case because, after the initial surge of dispersal away from natal sites in September–December, the direction of subsequent movements was essentially random relative to the natal territories. As a result, mean dispersal distances stabilized within 4–6 months after dispersal began, even though many individuals continued to disperse and did not acquire territories until they were several years old. Similarly, Bairlien (1985) found that mean natal dispersal distances of barn owls stabilized after 4–5 months, even though some birds were still dispersing.

Although data from most previous studies of natal dispersal in the spotted owl were not subdivided by sex, small samples from Miller (1989) and Gutiérrez et al. (1996) are in agreement with our results, in that females dispersed farther than males. This same pattern has been reported for many other birds (Greenwood and Harvey 1982), including many birds of prey (Fuiczynski 1978, Newton 1986, Korpimäki 1988, James et al. 1989, Taylor 1994, Dietrich and Woodbridge 1994, Rosenfield and Bielfeldt 1996, Wellicome et al. 1997,

Forero et al. 1999, Marti 1999, Real and Manosa 2001). However, there are exceptions (Greenwood and Harvey 1982, Picozzi 1984). Thrailkill et al. (1997) found no sexual differences in dispersal distances of spotted owls, but their samples were very small.

In some birds there is evidence that individuals that disperse farther may settle on lower quality territories or may breed later or have smaller clutches (Newton 1986). We did not examine clutch size or territory quality, but the fact that we found no relationship between dispersal distance and age when owls first nested does not suggest a negative relationship between dispersal distance and lifetime reproduction in the spotted owl. A number of other studies have also found little correlation between reproductive performance and dispersal distance in birds (Greenwood et al. 1979, Marti 1999), and Spear et al. (1998) found that survival and reproduction were positively correlated with natal dispersal distance. Our results suggest that, in long-lived birds like spotted owls, which typically do not breed until they are several years old, dispersal distance has little influence on lifetime reproduction compared to other factors such as annual or local variation in weather (Franklin et al. 2000) or prey abundance (Carey et al. 1992, Ward et al. 1998).

Dispersal distances in owls vary greatly among species. Estimates from barn owls and great horned owls suggest that they disperse farther than spotted owls on average, and that occasional individuals undertake extremely long movements. However, the majority of barn owls and great horned owls do not disperse more than 80 km from their natal sites (Stewart 1952, 1969, Braaksma and de Bruijn 1976, Houston 1978, Adamcik and Keith 1978, Bairlien 1985, Taylor 1994, Marty 1999). Of 434 recoveries of banded great horned owls reported by Stewart (1969:156), 405 (93%) were within 80 km of the natal site. The other 29 recoveries included 16 owls that dispersed more than 160 km, including 1 that dispersed 1,370 km. Thus, it appears that great horned owls and barn

owls, while capable of very long movements, typically settle near their natal sites. Tengmalm's owls (*Aegolius funereus*) also appear to be fairly strong dispersers, often moving long distances in years of low prey abundance (Korpimäki and Lagerström 1988). In contrast, the mean dispersal distance of 31 radio-marked screech owls (*Otus kennicottii*) from the natal site to the location where the owls overwintered was only 10.6 ± 1.8 km (Ellsworth and Belthoff 1997:157). None of the above studies provided estimates of effective dispersal distances, but estimates from several species of small resident birds are similar to spotted owls (Shields 1983).

For specialist vole predators like the Tengmalm's owl, saw-whet owl (*Aegolius acadicus*), snowy owl (*Nyctea scandiaca*) and barn owl, or species that feed on cyclic populations of snowshoe hares, like the great horned owl, the tendency to disperse long distances in some years is probably a response to a highly variable prey resource (Lofgren et al. 1986, Korpimäki 1986, Hayward et al. 1993, Marks 1997, Rhoner 1997a, b, Smith 1997). In comparison, spotted owls have a rather diverse diet and their primary prey are not known to undergo large annual variations in abundance (Rosenberg et al. 1992, Ward et al. 1998). As a result, spotted owls are probably rarely faced with the almost complete collapse of their prey supply, and are less likely to exhibit migratory or nomadic behavior than are species with more irruptive or cyclic prey.

Dispersal Direction

Previous studies of natal dispersal of spotted owls have suggested that the distribution of individual dispersal azimuths is random (Miller 1989, Gutiérrez et al. 1985, Ganey et al. 1998). We also concluded that there was little evidence of a biologically significant trend in dispersal direction, even though our statistical tests on large samples suggested a non-random pattern. With samples as large as ours, even a small divergence from a random distribution can produce a significant re-

sult, which led us to question the biological relevance of the test results.

Houston (1978) and Adamcik et al. (1978) concluded that directional orientation of dispersal by great horned owls was random except in poor prey years, when a disproportionate number of juveniles dispersed long distances to the south. Whether this represented permanent dispersal or a southward migration was unclear (Adamcik et al. 1978). Bunn et al. (1982) and Taylor (1994) found that dispersal direction of barn owls in Scotland and Great Britain did not differ from random. In contrast, studies of barn owl dispersal in continental Europe and Utah indicated non-random dispersal, possibly in response to mountain ranges that acted as barriers to dispersal (Taylor 1994, Marti 1999).

Absence of strong or consistent directional tendencies in dispersal based on pooled samples from many different territories in no way implies that direction of dispersal from individual territories is random. Spotted owls in western Washington and Oregon occupy extremely heterogeneous environments where the distribution of forest habitat adjacent to individual territories is highly variable. In this situation, it is possible that dispersal direction from individual territories might be a nonrandom response to the local distribution of habitat and topography, whereas the pooled data from many different territories would suggest a random pattern. Thus, it should not be concluded from our results that owls simply move randomly away from the natal site without regard to the distribution of suitable habitat.

Although it is clear from our study that spotted owls disperse across fragmented forest landscapes, we do not know if survival rates of dispersing owls are influenced by the amount of forest fragmentation or the amount of suitable habitat encountered along the dispersal path. Lamberson et al. (1992) suggested that survival of dispersing spotted owls may be lower in fragmented forests or areas with little old forest. However, Miller (1989) found no correlation between forest fragmentation

and survival or dispersal distance of spotted owls. Observations of Mexican spotted owls (*S. o. lucida*) in the southwestern U.S. indicate that they will, at least occasionally, disperse across large areas of inhospitable habitat between isolated mountain ranges (Gutiérrez et al. 1996, Arsenault et al. 1997, Ganey et al. 1998). In an interesting contrast, however, LaHaye et al. (1994) observed no dispersal between insular populations of spotted owls in southern California. Obviously, more work is needed to evaluate the influence of habitat fragmentation and habitat quality on dispersal distance and survival of dispersing spotted owls.

Social Integration of Dispersers

The fact that most of our radio-marked owls were paired by the time they were 2 years old suggests that the majority of young spotted owls are integrated into the territorial population relatively quickly, but some (about 23% of females and 32% of males) do not acquire territories until they are ≥ 3 years old. Although they often form somewhat tenuous pair bonds and defend territories, spotted owls that are 1–2 years old rarely breed (this study, Miller et al. 1985, Burnham et al. 1996). It is unclear whether this is due to physiological immaturity, lack of experience, or both.

In our study, integration of young owls into the territorial population closely paralleled Franklin (1992). He estimated that mean age of recruitment into the territorial population was 1.9 ± 0.3 years ($n = 16$), compared to 2.4 years in our study. He also estimated that 40% of males did not enter the territorial population until they were > 2 years old (32% in our study). The main difference between his study and ours was that he reported all females were integrated into the territorial population by the time they were 2 years old. In contrast, we found that 23% of radio-marked females were still unpaired floaters when they were 2 years old, and did not enter the territorial population until they were 3–5 years old.

Some studies of owls and diurnal rap-

tors suggest that more females than males breed at 1–2 years of age (Newton 1979, Rhoner 1987a). Although our data from radio-marked owls indicated that a higher proportion of females than males were recruited into the territorial population as 1-year-olds, proportions of males and females that actually bred at 1 year of age were essentially identical, and more males nested at 2 years of age than did females. In contrast, our data from banded owls indicated no sexual differences in recruitment rates of males and females for any age classes, and proportions of females breeding at age 1 or 2 were higher than males. The difference between our results from radio-marked owls and banded owls may have been due to a sampling bias in the data from banded owls. Female spotted owls that are not radio-marked tend to be more difficult to locate than males unless they are paired or breeding, in which case they are often located by following the male to the female (Reid et al. 1999). Given this bias it is not surprising that samples based on recaptures of banded owls should include fewer single females and more females that are paired or breeding, compared to males. We do not know if this bias is unique to spotted owls or is a problem in studies of other species, as well.

In our study, the proportion of radio-marked owls that were paired or breeding at 1 year of age was much lower than in the sample of banded owls, regardless of sex. This clearly shows that studies of owls based on acoustic-lure techniques (Reid et al. 1999) are biased towards detection of owls that are paired and defending territories. This is not surprising given that there is ample evidence in the literature that non-territorial "floaters" are less detectable than are territorial birds (Rhoner 1997a, b). In spotted owls, the low detection of young owls occurs because many floaters either do not respond to acoustic-lure surveys, or respond in a very tenuous fashion such that they are difficult to capture or resight. Because of this bias, mark-recapture studies of spotted owls that rely on the acoustic-lure technique have fo-

cused on the territorial population (Burnham et al. 1994, 1996).

Because we observed no evidence of breeding by floaters, we agree with Rhoner (1997b) that floating behavior in owls is not an alternative reproductive strategy whereby non-territorial birds share mates with territorial birds. If, as Rhoner (1997b) suggested, spatial knowledge is paramount to hunting success and survival, then floaters would be expected to occupy temporary home ranges from which they could regularly sample or "prospect" (Eadie and Gauthier 1985) the underlying network of territorial pairs for opportunities to acquire a territory. In this context, floating is the result of territorial behavior, which excludes floaters from obtaining territories. The fact that many spotted owls do not obtain territories until they are 2–5 years old suggests that the number of floaters generally exceeds the number of available territories and that territorial behavior of established residents excludes floaters from the breeding population.

Causes of Mortality

In our study, predation by great horned owls and other raptors was the primary source of mortality of young owls. Starvation, mammalian predation and accidents accounted for the rest. Although we suspected great horned owls were responsible for the majority of cases of avian predation, we could only positively confirm this in 3 cases where we found remains in great horned owl nests or pellets. It is possible that some of the kills that we suspected were caused by great horned owls could have been caused by barred owls (Leskiw and Gutiérrez 1998) or other spotted owls. Forsman et al. (1984) also reported predation on juvenile spotted owls by great-horned owls. Sources of mortality reported for great gray owls (*Strix nebulosa*) by Duncan (1987:105) were similar to our data for spotted owls in that predation by great-horned owls was the primary source of mortality (56.5%), followed by mammalian predation (21.7), starvation (8.7%), accidents (4.4%), and other/unknown

(8.7%). We also observed goshawks (*Accipiter gentilis*) and red-tailed hawks (*Buteo jamaicensis*) attempting to capture spotted owls on a number of occasions, and suspected that they were responsible for some predation. The high incidence of parasitic infections that we observed in owls that were necropsied suggested that parasitism or disease may have predisposed some individuals to starvation or predation, as has been suggested by Hunter et al. (1987, 1997), Gutiérrez (1989), and Hoberg et al. (1989).

Causes of Natal Dispersal

Hypotheses regarding the evolution of dispersal in organisms fall into 3 main groups, (1) intrasexual competition, (2) inbreeding avoidance or optimal inbreeding, and (3) spatio-temporal variation in resources. The logic underlying the intrasexual competition hypothesis is that animals disperse because they are physically excluded from settling on their natal sites and other occupied territories by individuals of the same sex, including their own parents (Moore and Ali 1984, Liberg and von Schantz 1985, Waser 1985). Once they began to disperse, there is little doubt that young spotted owls are excluded from acquiring territories by resident territory holders. However, we never observed any evidence that adults evicted their offspring from the territory, and we never observed any cases where juveniles settled on their natal territories and reproduced with 1 of their parents. Instead, it appeared that juveniles voluntarily dispersed after the adults stopped feeding and associating with them. Similarly, Beske (1982) saw no sign of parent/offspring aggression prior to dispersal of juvenile harriers (*Circus cyaneus*). Moore and Ali (1984) suggested that the absence of overt aggression between adults and offspring was not necessarily a contradiction of the intrasexual competition hypothesis, because juveniles might disperse simply because they were made to feel unwelcome or were aware of the threat imposed by the presence of a dominant individual. However, it does

seem that if intrasexual competition was the primary cause of dispersal, there would be at least some occasions when juveniles would remain on their natal sites when 1 or both of their parents died or dispersed. The fact that we never observed this suggests that something other than, or in addition to, intrasexual competition may be driving dispersal in the spotted owl. In contrast to the spotted owl, male burrowing owls (*Speotyto cunicularia*) in Saskatchewan frequently returned to breed at their natal sites (Wellicome et al. 1997).

An alternative to the intrasexual competition hypothesis is that dispersal evolved because it reduces the risk of close inbreeding (Lincoln 1934, Howard 1960, Greenwood and Harvey 1976). The fact that female birds typically disperse farther than males is sometimes cited in support of the inbreeding avoidance hypothesis (Greenwood 1980). However, Moore and Ali (1984) argued that differences in dispersal between males and females could be explained based solely on the basis of intrasexual competition for mates (territories) without invoking the inbreeding reduction hypothesis. The rarity of full-sib or parent-offspring inbreeding in spotted owls (this study, Carlson et al. 1998) and barn owls (Marti 1999) suggests that dispersal in these species does result in very low rates of close inbreeding. However, the comparatively short distances dispersed by spotted owls does result in frequent pairings between more distant relatives (cousins, aunts, uncles, grandparents, or great grandparents) (Reid and Forsman, unpublished data). Similar observations with other species of birds led Shields (1983) to suggest that the philopatric nature of dispersal in most organisms was designed not to avoid inbreeding, but to insure an "optimal" level of inbreeding in which individuals are more likely to breed with relatives than with unrelated individuals.

Although some have suggested that sex-biased dispersal is a means of avoiding close inbreeding, others have argued that greater male philopatry might be a product of a resource defense mating system in

which males defend the primary resources, and females select among males (Greenwood 1980). In support of this hypothesis, Greenwood (1980) argued that males would have an advantage if they settled on or near their natal site, in that they would be more familiar with the resources in that area and would have reduced dispersal cost. Since females do not have to defend resources in this system, Greenwood argued that they could spend more time and energy searching for a suitable male, and would not be as severely penalized by unfamiliarity with the resource. Secondarily, he suggested that philopatry of males might occur if females tended to mate preferentially with males of a similar genotype. Aside from the fact that there is no evidence to suggest that female spotted owls mate preferentially with related males, the most troublesome aspect of the resource familiarity hypothesis relative to owls is that most juveniles move rapidly away from the natal area during the first few days or weeks of dispersal (Miller and Meslow 1985, Ganey et al. 1998, Belthoff and Ritchison 1989, Rhoner 1997a, b). In this situation, it is unlikely that dispersing males would initially be any more familiar with resources in territories near the natal site than areas farther away. A more plausible explanation, suggested by Small and Rusch (1989), is that males are less likely to travel as far as females simply because the intensive sampling process required to locate and defend a territory prohibits males from sampling large areas quickly, whereas females are free to travel widely, sampling many territories to find a suitable mate.

Another explanation for the ubiquitous nature of dispersal in organisms is that spatio-temporal or chaotic variation in fitness values of habitat patches may favor dispersal in patchy environments (Holt 1985, McPeck and Holt 1992, Holt and McPeck 1996). As a general explanation for dispersal this hypothesis seems reasonable for spotted owls, which evolved in forest landscapes that were regularly impacted by fire, windstorms, and other natural disturbances. However, it does not address

the causes of sex-biased dispersal. Also, if we assume that natal patches typically have high fitness values, it seems odd that juvenile spotted owls almost never settle at their natal site, even when there is a turnover event that removes 1 or both of their parents.

Breeding Dispersal

Spotted owls seem to fit the general pattern for long-lived birds that occupy relatively stable environments in that they have high site fidelity from 1 year to the next, and site fidelity tends to increase with age (Richdale 1957, Darley et al. 1977, Newton and Marquiss 1982, Saurola 1987). In contrast, site fidelity of owls that occupy more variable habitats is less predictable. For example, annual site fidelity of breeding barn owls in Scotland was >95% (Taylor 1994:198), but was apparently much lower in Germany and Holland where >40% of banded adults dispersed from their initial banding locations (Bairlien 1985, as summarized by Taylor 1994:199). Great gray owls and boreal owls may remain on the same territories from 1 year to the next in good prey years, but many individuals change territories in poor prey years, often moving long distances before breeding again (Duncan 1987, Hayward et al. 1993).

Our data suggest that spotted owls were more likely to undertake breeding dispersal if (1) they were female, (2) they were young, (3) they did not nest in the previous year, (4) they did not have a mate in the previous year, or (5) their mate from the previous year died or moved to a new territory. These results generally agree with other studies of birds that have shown that rates of breeding dispersal were higher for females, young birds, birds that lost a mate through death or divorce, or birds that failed at nesting (Coulson 1966, Newton and Marquiss 1982, Greenwood and Harvey 1982, Greig-Smith 1982, Bowen et al. 1989, Taylor 1994, Wellicome et al. 1997, Marti 1999, Daniels and Walters 2000). One hypothesis for higher rates of female breeding dispersal is that, in a ter-

ritorial defense system in which the male locates and defends the territory, it may be more difficult for males to switch territories than it is for females to switch mates (Emlen and Oring 1977, Greenwood and Harvey 1982). A possible explanation for higher rates of breeding dispersal by young birds is that there may be strong competition for high-quality territories, which results in many young birds initially settling on lower-quality sites and then moving to higher-quality sites as they grow older (Greenwood and Harvey 1982).

Although many adult movements followed the death or disappearance of a mate, many also involved cases of divorce or territory switching by pairs. This suggests a strategy in which owls attempted to increase their fitness by switching to better territories or more fecund mates or both (Korpimäki 1988, Goodburn 1991, Newton and Willie 1992, Ens et al. 1996, Daniels and Walters 2000). Tests of these hypotheses were beyond the scope of this paper. In addition, we caution against the assumption that divorce always represents a voluntary choice on the part of the individual that moves, because floaters sometimes displace residents (Forsman 1975, Choudhury 1995).

Spatially Explicit Simulation Models of Dispersal

Simulation models used to evaluate dispersal typically include numerous simplifying assumptions regarding search patterns of dispersers and rates of territory vacancy (e.g., Wasser 1985, Lande 1988, Doak 1989, Noon and Biles 1990, Tonkyn and Plissner 1991, Lamberson et al. 1992, Boyce et al. 1994, Dunning et al. 1995). Most researchers who have attempted to model spotted owl populations have assumed that juveniles perish fairly quickly if they do not acquire territories, and that the search for available territories occurs in 1 of 2 ways: (1) the animal searches territories that are intersected by a randomly assigned straight line radiating outward from the natal site, or (2) the animal searches all territories within a certain ra-

dius of the natal site (Wasser 1985, Lande 1988, Tonkyn and Plissner 1991, Lamber-son et al. 1992). Contrary to these simplifying assumptions, our data suggest that at least some juveniles disperse and persist for ≥ 5 years as floaters in the population, and that dispersers use a series of temporary home ranges to systematically sample or "prospect" the underlying network of resident territories along a somewhat erratic dispersal path. Rhoner (1997b) described similar dispersal patterns in young great horned owls. These results suggest that more realistic spatial population models for spotted owls might be developed in which it is assumed that natal dispersers can search for potential territories for 5 or more years and that search patterns of individuals are highly variable, ranging from some individuals that sample only a few territories near the natal site to a small minority of individuals that sample large numbers of territories out to about 120 km from the natal territory. Obviously, the sexual differences in dispersal distances that we observed should also be assumed in any model.

MANAGEMENT IMPLICATIONS

Distances moved by young spotted owls are such that genes can travel long distances in only a few generations. Thus, it is not surprising that recent genetic studies have found little evidence of meta-population structure in the northern spotted owl (Barrowclough et al. 1999, Haig et al. 2001). Our results also suggest that a conservation strategy that consists of numerous, closely spaced reserves of old forest (e.g., the Northwest Forest Plan) is not likely to result in genetic or demographic isolation of local populations, simply because dispersal between reserves will be a common occurrence, even if landscapes between the reserves consist of highly fragmented forests. Thus, we believe that concerns regarding genetic or demographic isolation of spotted owls that might result from a management plan like the Northwest Forest Plan are largely unfounded, except for areas isolated by large

natural barriers (e.g., the Olympic Peninsula), or by extensive areas of intensively managed young forest (e.g., the coastal mountains of northwest Oregon and southwest Washington). Even if some areas are somewhat isolated, this may not be of particular concern from a genetic or demographic standpoint if populations within those areas are large, as is the case on the Olympic Peninsula (Holthausen et al. 1995).

In recent efforts to develop management plans for the northern spotted owl it has been assumed that forested regions between the large lowland valleys of western Oregon function as dispersal pathways for spotted owls between the Coastal Mountains and Cascades Mountains (Thomas et al. 1990, FEMAT 1993). Our data clearly demonstrate that this is the case, and that concerns regarding the importance of these areas as dispersal "corridors" for spotted owls are warranted.

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