



RETURN RATE, FIDELITY, AND DISPERSAL IN A BREEDING POPULATION OF FLAMMULATED OWLS (*OTUS FLAMMEOLUS*)

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ABSTRACT.—We estimated annual return rate, fidelity, and breeding dispersal in a migratory population of Flammulated Owls (*Otus flammeolus*) in central Colorado. Return rates, based on capture–recapture histories of 39 males and 52 females from 1981 to 2003, were higher for males (84%) than for females (45%). Annual recapture probability was higher for females, because breeders are easier to capture than nonbreeders and females always attempted to nest, whereas some males were unpaired (did not nest) for up to four years. Territory fidelity was male biased (92%, vs. 56% for females, adjusted for undetected emigration), and mean tenure on territories was more than twice as long for males as for females. Females, but not males, had lower return rates to territories in the year following nesting failure compared with females whose nests were successful. Most males appeared to occupy one territory their entire reproductive lives, countering predictions of habitat-selection models that individuals should move to higher-quality habitats when they become available. We estimated that 74% of pairs retained the same mate in consecutive nesting attempts, but mates that bred together for multiple years had no reproductive advantages over mates that bred together for the first time. In most cases, females dispersed from territories if their mates did not return. When females dispersed, they went to territories where total productivity over the study and lifetime reproductive success of new mates were higher than on original territories, which supports the hypothesis that dispersal by females increases individual fitness. Received 8 April 2005, accepted 15 February 2006.

Key words: breeding dispersal, Flammulated Owl, mate fidelity, *Otus flammeolus*, return rates, site fidelity, territory fidelity.

Tasa de Retorno, Fidelidad y Dispersión en una Población Reproductiva de *Otus flammeolus*

RESUMEN.—Estimamos la tasa de retorno anual, la fidelidad y la dispersión reproductiva en una población migratoria de *Otus flammeolus* en el centro de Colorado. Las tasas de retorno, basadas en las historias de captura-recaptura de 39 machos y 52 hembras desde 1981 a 2003, fueron mayores para los machos (84%) que para las hembras (45%). La probabilidad anual de recaptura fue mayor para las hembras, debido a que las aves reproductivas son más fáciles de capturar que las aves no reproductivas y que las hembras siempre procuran nidificar, mientras que algunos machos permanecieron sin pareja (no nidificaron) por períodos de hasta cuatro años. La fidelidad al territorio estuvo sesgada hacia los machos (92%, vs. 56% para las hembras, ajustado por la emigración no detectada), y la ocupación media de los territorios fue más de dos veces más prolongada para los machos que para las hembras.

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Las hembras, no los machos, presentaron tasas de retorno más bajas a los territorios en el año que siguió el fracaso del nido, comparado con las hembras cuyos nidos fueron exitosos. La mayoría de los machos pareció ocupar un mismo territorio durante la totalidad de sus vidas reproductivas, contradiciendo las predicciones de los modelos de selección de hábitat que indican que los individuos deberían moverse a ambientes de mayor calidad cuando éstos se vuelven disponibles. Estimamos que el 74% de las parejas mantuvieron el mismo consorte en intentos de nidificación consecutivos, pero los consortes que nidificaron juntos por múltiples años no tuvieron ventajas reproductivas sobre los que nidificaron juntos por primera vez. En la mayoría de los casos, las hembras se dispersaron de los territorios si sus consortes no retornaron. Cuando las hembras se dispersaron, se fueron a territorios en donde la productividad total a lo largo del estudio y el éxito reproductivo total de vida de los nuevos consortes fueron mayores que en los territorios originales, lo que apoya la hipótesis de que la dispersión por parte de las hembras aumenta su adecuación biológica individual.

IN STABLE ENVIRONMENTS, many birds annually return to the same breeding sites and retain the same breeding partners (Greenwood 1980). Particularly for migratory species, site fidelity confers benefits that may include increased knowledge of locations of requisite nesting resources and improved chances of maintaining a breeding territory and securing a mate (Shields 1984; Pärt 1994, 1995). If neighbors return annually, site-faithful individuals may also reduce costs of contesting territory boundaries (Krebs 1982). Mate fidelity may improve coordination between mates, prolong biparental investment, and reduce the costs of mate sampling (Black 1996). In addition, studies have shown that mates that bred together previously initiate nesting earlier, have larger clutches, and have higher nesting success than newly formed pairs (Bradley et al. 1990, Orell et al. 1994, Murphy 1996).

Mate and site fidelity also involve costs. Site faithfulness may increase the probability of inbreeding (Walters et al. 1988) and may lower chances for reproductive success if habitat quality declines (Greenwood et al. 1978, Oring and Lank 1984). For migratory species, costs of mate fidelity include waiting for mates to return or searching for new mates (Black 1996). Studies showing that individual fitness increased following breeding dispersal (Matthysen 1990, Forero et al. 1999) suggest that individuals disperse when costs of fidelity exceed benefits.

Although fidelity and breeding dispersal have been much studied in the past two decades, gaps remain in understanding the process of breeding dispersal, partly because of difficulty distinguishing emigration from

mortality for individuals failing to return. This problem is exacerbated in finite study sites, where failing to detect dispersal beyond study boundaries compromises estimates of dispersal rate and distance (Baker et al. 1995, Koenig et al. 2000). In addition, entire lifetimes might need monitoring to observe dispersal events, which is logistically difficult in long-lived birds and a primary reason that breeding dispersal is not well studied in raptors (but see Korpimäki 1988, Forero et al. 1999, Marti 1999, Forsman et al. 2002, Byholm et al. 2003). Because emigration fundamentally affects population structure and dynamics (Freemark et al. 1995), understanding the ecological bases of dispersal is important for avian conservation (Fahrig and Merriam 1994).

We describe fidelity and dispersal in a Colorado population of Flammulated Owls (*Otus flammeolus*), which are obligate cavity-nesters that breed in montane forests of western North America (McCallum and Gelbach 1988, Marti 1997, Linkhart et al. 1998, Arsenault 1999). Flammulated Owls are insectivorous, feeding mostly on small lepidopterans (Reynolds and Linkhart 1987a). The species is listed as sensitive in the United States (Verner 1994) because it is a Neotropical migrant and is associated with mature forests (McCallum 1994, Linkhart et al. 1998). Despite being one of the smallest North American strigiforms (Earhart and Johnson 1970), Flammulated Owls have a life history similar to that of larger raptors, in that they produce no more than one small clutch (mean $\pm$ SE: 2.5 ± 0.1 eggs) annually, have high nesting success (84%), and are relatively long-lived (Linkhart and Reynolds 2004, 2006).

Here, we expand on a five-year study by Reynolds and Linkhart (1987b) to include 23 years of data (1981–2003) on the same population. Specifically, we (1) describe sex differences in annual return rates; (2) describe sex differences in territory fidelity, defined as reoccupancy of the same territory by an adult for consecutive years; (3) assess effects of nesting failure on fidelity; (4) describe patterns in mate fidelity, defined as the pairing of the same male and female for consecutive years; (5) assess benefits of maintaining pair bonds; (6) describe sex differences in breeding dispersal, defined as movement between breeding territories; and (7) assess a possible cause and possible benefits of breeding dispersal. To account for individuals that annually did not return to the study area but may not have died, we include estimates of fidelity and dispersal adjusted for undetected emigration.

METHODS

Study area.—The 511-ha study area was located on the Manitou Experimental Forest, Teller County, Colorado. Forests consisted primarily of (1) ponderosa pine (*Pinus ponderosa*) mixed with Douglas-fir (*Pseudotsuga menziesii*), generally on ridgetops and south-facing slopes (53% of the study area); (2) Douglas-fir on east- and west-facing slopes (23%); (3) Douglas-fir mixed with blue spruce (*Picea pungens*), on north-facing slopes (8%); and (4) quaking aspen (*Populus tremuloides*) mixed with blue spruce, on lower slopes and drainage bottoms (8%) (Linkhart 2001). Elevation ranged from 2,550 to 2,855 m.

Locating and capturing Flammulated Owls.—Each spring and summer from 1981 to 2003, we searched the study area for territorial males. We identified territory boundaries by spot-mapping and radiotelemetry, and we located nests by regularly checking (at least once every two weeks) all known tree cavities with entrance diameters >4 cm, from the onset of incubation (late May) until the young fledged (mid-July) (Reynolds and Linkhart 1984, Linkhart et al. 1998). We also regularly checked nest boxes placed in territories that had relatively few natural tree cavities, though 94% of nests (95 of 101) were in natural cavities (Linkhart and Reynolds 2006). We found most nests during incubation and we checked nest contents at least weekly until the

young fledged. Most adults were captured and banded at nests (Reynolds and Linkhart 1984). Because unpaired males were difficult to capture, all but one of the banded males were individuals that bred at least once. We banded 91 adults (39 males, 52 females). Unless otherwise noted, we calculated the following parameters from annual capture–recapture data of these adults.

Return rate and fidelity to territory and mate.—We determined annual return rates by calculating the proportion of banded adults in year t that were known to have returned in year $t + 1$. To assess the quality of data on return rates, we calculated recapture rates (p) of banded males and females using the Cormack-Jolly-Seber model in MARK (White and Burnham 1999). We defined territory tenure as the total consecutive years that an adult occupied the same territory. To calculate annual turnover, we divided the number of occasions in which a banded adult was known to have been replaced on a territory by the total number of occasions (opportunities) for which adult identity on a territory was known in consecutive years. We calculated territory fidelity by dividing total years that banded adults returned to original territories by total owl-years, a sum of years for which we could ascertain whether banded males or females returned to original territories or dispersed to new territories. We assumed that a banded male in year t was present on the same territory in year $t + 1$, despite not recapturing him in year $t + 1$, if (1) a male was heard singing in the territory in year $t + 1$ and (2) the original male was recaptured in a subsequent year on the same territory. This assumption, accounting for 21 of 76 male-years, was based on our having never documented any male that left a territory and returned to the same territory in a subsequent year. We assumed that a banded female that nested on a territory in year t did not return to the same territory in year $t + 1$ if she was not seen or if no nest was found, because we never documented a female skipping a year of nesting.

We defined a successful nest as one that fledged ≥ 1 owlets. To determine whether failed nests affected territory fidelity, we compared return rates of adults to original territories in the year following a successful nest with return rates of adults to original territories in the year following a failed nest. We considered two

possible outcomes for each sex: an individual returned to the same territory, or the individual dispersed to a different territory or disappeared. For individuals that disappeared, we could not distinguish between mortality and dispersal beyond the study area.

Mate fidelity was calculated by dividing the total consecutive years in which the same male and female remained paired by pair-years, the total years in which both pair members were known to be alive. We presumed that divorce occurred when pair members from a particular year were known to be alive in a subsequent year but at least one had a different mate, though we could not determine the social causes of divorce (Ens et al. 1996). We assessed the effect of pair duration on two measures of reproductive success, date of incubation onset and brood size, which were associated with pair duration in other birds, including raptors (Newton and Marquiss 1982, Korpimäki 1988), by comparing these measures for mates breeding together for the first time to mates that had bred together in ≥ 2 years. Date of incubation onset was determined by observing nest contents and female behavior, or by backdating from the date that hatching commenced (mean duration of incubation = 22 days; Reynolds and Linkhart 1987a) if we discovered nests after females began incubating. We used raw dates as dependent variables, because of the small annual range in incubation onset (typically 7 to 10 days), and we never detected renesting or multiple broods (Linkhart and Reynolds 2006).

We based our estimates of territory tenure on adults whose entire histories on the study area occurred from 1982 to 2002. However, to avoid excluding relatively long-lived adults whose histories included 1981 or 2003, individuals were included if their longevity on the study area was greater than the median for all adults whose histories were complete. Because the median breeding life span (first breeding to disappearance) for Flammulated Owls with complete histories was two years (mean $\pm$ SE: 3.5 ± 0.7 years; $n = 28$) for males and one year (1.8 ± 0.3 years; $n = 41$) for females, this criterion resulted in the inclusion of two males (one each with longevity of eight years and three years) and four females (one each with longevity of seven years, six years, four years, and three years). Similarly, we included pairs whose

histories included 1981 or 2003 in estimates of pair duration if their duration exceeded the median for all pairs whose histories were complete (median = 1 year; mean 1.3 ± 0.1 years; $n = 59$). This criterion resulted in the inclusion of two pairs (pair duration of three years and two years). We could not verify whether any adults bred beyond the study area before or after their tenure.

Breeding dispersal.—We calculated breeding dispersal for each sex by subtracting rates of territory fidelity from 1. We evaluated one possible cause and three possible benefits of breeding dispersal, which we assessed on the basis of observed dispersal events. To test a “non-return of mate” hypothesis, we assessed whether dispersal occurred when original mates did not return to their territories. To test a “mate quality” hypothesis, we assumed that quality of mates was reflected by their lifetime reproductive success (LRS), a measure of individual fitness (Newton 1989), and we compared LRS of new mates of dispersers with LRS of original mates. To test a “territory quality” hypothesis, we assumed that the total number of owlets produced on a territory during the study reflected territory quality, and we compared total owlets produced on original territories of dispersers to total owlets produced on new territories. To test a “productivity-enhancement” hypothesis, we compared mean brood size of dispersers on original territories to mean brood size on new territories.

Adjusted estimates of fidelity and dispersal.—In addition to calculating unadjusted rates of territory and mate fidelity and breeding dispersal, we calculated adjusted estimates of these parameters to account for adults that dispersed, undetected, beyond the study area. We did this by constructing a hypothetical landscape surrounding our study area, assuming that the landscape (1) consisted of similar forest types and structure and (2) contained a similar density and juxtaposition of owl territories. We believed that these assumptions were reasonable, judging by our familiarity with the surrounding landscape and the fact that each year we detected several territorial males (and occasionally their nests) in areas adjacent to the study area. We created the hypothetical landscape by producing duplicate maps of the study area, constructed in ARCVIEW (Environmental Systems Research Institute, Redlands,

California), and attaching one duplicate map on each side and corner of the original map.

We used the resulting landscape mosaic to estimate, for each territory (i) on the study area (Fig. 1), the fraction of potential dispersal destinations up to two territories away (the maximum detected dispersal distance) that occurred within the study area (and thus were observed):

$$\frac{n_i^{ob}}{n_i^{ob} + n_i^{unob}}$$

where n_i^{ob} is the number of territories one or two territories from territory i within the study area (i.e., observed) and n_i^{unob} is the number of territories one or two territories from territory i outside the study area (i.e., unobserved). The reciprocal of this fraction was used to calculate an adjusted number of breeding dispersal events (D_i) for each sex as

$$D_i = \min \left[m_i, \frac{n_i(n_i^{ob} + n_i^{unob})}{n_i^{ob}} \right]$$

where m_i is the number of banded adults of a given sex in territory i that failed to return from one year to the next and n_i is the number of adults found nesting in a new territory within the study area in a subsequent year. An overall adjusted breeding dispersal rate for each sex, defined as the fraction of adults estimated to change territories from one year to the next, is

$$\frac{\sum_i D_i}{\sum_i N_i}$$

where N_i is the number of years that territory i was occupied by an adult of the specified sex. The difference from 1 is the adjusted rate of territory fidelity.

We calculated the adjusted number of divorces as

$$\sum_i d_i^{adj} = \sum_i d_i^{ob} \left[\frac{\sum_i D_i}{\sum_i n_i} \right]$$

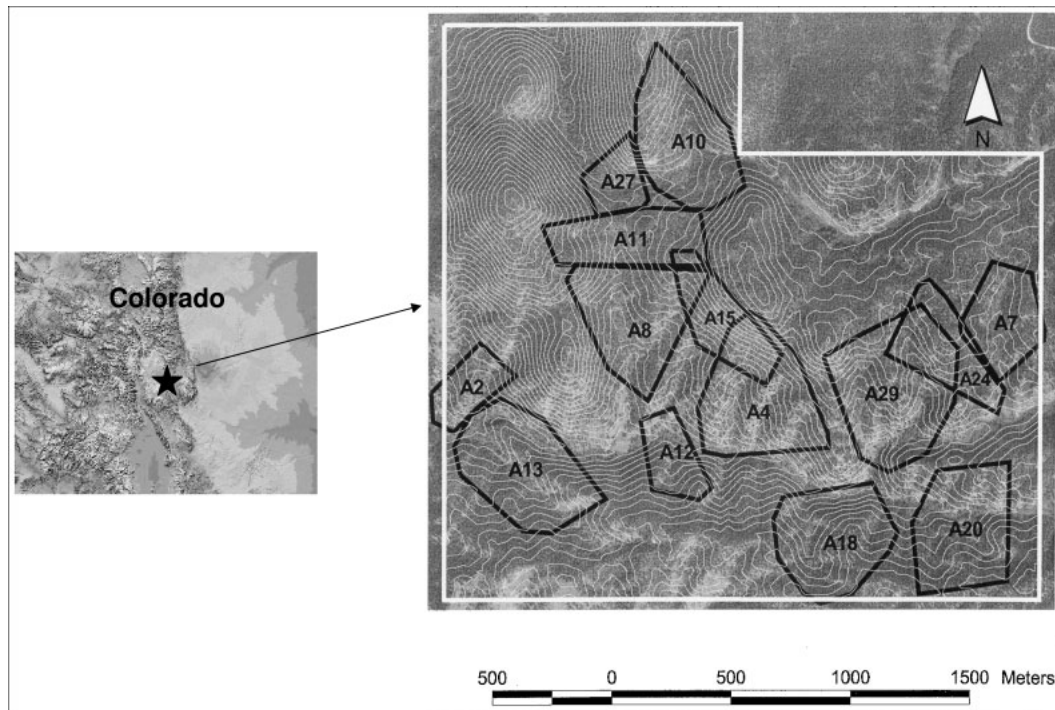


FIG. 1. Location of Flammulated Owl territories (black polygons) on the Manitou Experimental Forest study area (white polygon), in Teller County, Colorado.

where d^{obs} is the number of observed divorces and d^{adj} is the adjusted number of divorces. An overall adjusted divorce rate, then, is

$$\frac{\sum_i d_i^{adj}}{\sum_i N_i^{pair}}$$

where N_i^{pair} is the number of years that territory i was reoccupied by at least one member of the original pair. The difference from 1 is the adjusted rate of mate fidelity.

Statistical analyses.—Statistical analyses were performed using SAS (SAS Institute, Cary, North Carolina). We used Wilcoxon's test (PROC NPAR1WAY) to evaluate sex differences in territory tenure, and Fisher's exact test (PROC FREQ) to evaluate sex differences in return rates, territory fidelity, and effect of nesting failure on territory fidelity. We used Wilcoxon and unpaired t -tests assuming unequal variances (PROC TTEST) to evaluate differences between sexes for fidelity and dispersal parameters, and paired t -tests to evaluate dispersal hypotheses; all tests were two-tailed. We report means $\pm$ SE, and we considered results significant when $P \leq 0.05$.

RESULTS

We determined fidelity and dispersal parameters of owls on 14 territories from 1981 to 2003 (Fig. 1). Each year, Flammulated Owls occupied a mean of 7.9 ± 0.5 territories, including a mean of 4.5 ± 0.2 territories with breeding pairs and 3.4 ± 0.4 territories with unpaired males. Although two territories (A15 and A24) were not occupied after 1984, most territories remained fixed over time, and boundaries of territories shifted little despite turnover of Flammulated Owls. Annual return of adults from spring migration appeared to be sex-biased, as it is in many migratory species (Greenwood 1980, Ens et al. 1996). Males were first detected on territories from 1 to 15 May, and females from 10 to 20 May, though in some years females appeared on territories as late as mid-June.

Annual return rate.—Annual return rate for all adults was 0.66 (118 of 179), but it was higher for males (0.84; 81 of 97) than for females (0.45; 37 of 82; Fisher's exact test, $P < 0.001$). The annual recapture probability was higher for females

(0.79 ± 0.08 ; 95% CI = 0.59 to 0.91) than for males (0.63 ± 0.06 ; 95% CI = 0.51 to 0.74), because breeders are easier to capture than nonbreeders and females always attempted to nest, whereas some males were unpaired for up to four years. Five females returned to breed after they were undetected for one ($n = 4$) or two ($n = 1$) breeding seasons.

Territory fidelity.—Mean tenure on territories for all adults was 2.2 ± 0.3 years ($n = 90$) but varied by sex. Mean tenure of males (3.3 ± 0.6 years, median = 2 years, $n = 33$) was more than twice the mean tenure of females (1.5 ± 0.2 years, median = 1 year, $n = 57$; $z = 3.0$, $P = 0.003$). Eight of 33 males (24%) occupied the same territory for five or more years, compared with just 1 of 57 females (2%).

As data on tenure suggest, turnover on territories was female-biased. The annual turnover rate for females was 0.44 (23 of 52 opportunities) compared with 0.11 (9 of 81 opportunities) for males (Fisher's exact test, $P < 0.001$). Annually, there were one to six opportunities to assess turnover of each sex on breeding territories. At least one female was replaced on breeding territories in 18 of 22 years, but no more than one male was replaced in any year, and just two males were replaced during the last 13 years of the study (1991–2003).

Territory fidelity by all adults was 87% (102 of 117 owl-years), but males were more faithful to territories than females. Fidelity by males was 96% (73 of 76 male-years), whereas fidelity by females was 71% (29 of 41 female-years; Fisher's exact test, $P < 0.001$). Adjusting for undetected emigration beyond the study area, we estimated that male fidelity was 92% (88 of 96 male-years) and that female fidelity was 56% (46 of 82 female-years). Male fidelity was not affected by breeding status (paired vs. unpaired). Fifteen males continued to reoccupy their original territories despite being unpaired for four consecutive years (1 male), three consecutive years (2 males), two consecutive years (2 males), and one year (10 males).

Nesting failure affected territory fidelity in females, but not in males (Fisher's exact test, $P < 0.001$). In females, 41% (27 of 66) returned to their original territories the year following a successful nest and 13% (2 of 15) returned following a failed nest. In males, 79% (45 of 57) returned following a successful nest and 89% (8 of 9) returned following a failed nest. Of the

39 females that did not return to their original territories following a successful nest, 77% (30) were not seen again and 23% (9) dispersed to another territory. Of the 13 females that did not return to their original territories after a failed nest, 77% (10) were not seen again and 23% (3) dispersed to another territory. Of the 12 males that did not return to their original territory following a successful nest, 75% (9) were not seen again and 25% (3) dispersed to another territory. The only male that did not return following a failed nest was not seen again.

Mate fidelity.—Mean pair duration was 1.4 ± 0.1 years (range: 1–4 years). Of 61 pair bonds, 75% (46) endured one year only, 15% (9) endured two years, 8% (5) endured three years, and 2% (1) endured four years. Eighty-one percent of pairs (21 of 26 pair-years) kept the same mate in consecutive nesting attempts and, after adjusting for undetected emigration beyond the study area, we estimated that mate faithfulness was 74% (42 of 57 pair-years). We documented five apparent divorces by four females, four of which followed successful nests. None of the females nested in the study area the year following divorce, but they all returned to nest in the study area after being undetected for one or two years. Two females divorced the same male in the same territory two years apart, and then returned to nest with this same male in consecutive years. This male bred with a new female the year that both females were undetected.

Onset of incubation did not differ between mates that bred together for the first time (4 June $\pm$ 1 day, range: 27 May–20 June, $n = 32$), and mates that bred together for two or more years (1 June $\pm$ 2 days, range: 20 May–13 June, $n = 18$; $t = 1.00$, $df = 39$, $P = 0.31$). Mean brood size also did not differ between first-year pairs (2.3 ± 0.1 owlets, range: 0–3, $n = 42$) and pairs that bred together for two or more years (2.4 ± 0.2 owlets, range: 0–4, $n = 22$; $t = -0.4$, $df = 37$, $P = 0.69$).

Breeding dispersal.—We documented 15 cases of breeding dispersal within the study area, including one pair, in 117 owl-years where status of owls was confirmed, for a minimum dispersal rate of 13%. Females moved to new territories on 12 occasions (in 41 female-years) for a dispersal rate of 29%, whereas males moved to new territories on just three occasions (in 76 male-years) for a dispersal rate of 4%. Adjusting for undetected emigration beyond the study area, we estimated that the dispersal

rate was 44% (36 estimated dispersals in 82 female-years) for females, and 8% (8 estimated dispersals in 96 male-years) for males. Mean distance for all documented dispersals (551 ± 46 m, median = 505 m, range: 320–845 m, $n = 13$) was 1.3 $\times$ the mean diameter of territories (428 ± 29 m; Linkhart 2001). Thirteen percent of documented dispersals (2 of 15) were return dispersals in which females returned to original territories (see above), whereas 54% (8 of 15, including the pair) of individuals dispersed to adjacent territories, and 33% (5 of 15) dispersed two territories away from their original territories.

Other than the five cases of divorce (and excluding the female that dispersed with her original mate), none of the original mates of dispersing females returned (“non-return of mate” hypothesis). However, non-return of mate did not always result in dispersal by females, given that six females returned to their original territories and bred with new males.

In females, LRS of new mates on new territories was higher than LRS of original mates on original territories (“mate quality” hypothesis). Excluding the female that dispersed with her mate and the two instances of return dispersal, LRS of original mates was 5.6 ± 1.0 owlets, whereas LRS of new mates after dispersal was 8.7 ± 1.4 owlets ($t = -3.4$, $df = 8$, $P = 0.01$).

Females dispersed to territories with higher long-term productivity (“territory quality” hypothesis). Excluding the two instances of return dispersal, territories where females originally nested produced 10.3 ± 2.1 owlets over the study, whereas territories to which females dispersed produced 23.1 ± 3.7 owlets ($t = -3.3$, $df = 9$, $P = 0.01$). Territories where males originally nested produced 11.0 ± 6.1 owlets over the study, whereas territories to which males dispersed produced 35.3 ± 7.7 owlets.

Brood size of females was not affected by dispersal (“productivity-enhancement” hypothesis). Excluding the two instances of return dispersal, brood size of females was 2.1 ± 0.2 owlets before dispersal and 2.2 ± 0.3 owlets after dispersal ($t = -0.2$, $df = 8$, $P = 0.82$). For the three males, brood size was 1.8 ± 0.9 owlets before dispersal and 2.7 ± 0.3 owlets after dispersal.

DISCUSSION

Territory fidelity.—Flammulated Owls fit the general pattern found across avian taxa—site or

territory fidelity is male-biased. It is believed this occurs because males have more to benefit from increased familiarity with territory resources in species that have a resource-defense mating system (Emlen and Oring 1977, Greenwood 1980). Territory fidelity may be particularly beneficial to male Flammulated Owls, not only because females and broods rely exclusively on males for prey until late in the nestling period (Reynolds and Linkhart 1987a), as is true in most raptors (Snyder and Wiley 1976), but also because males primarily forage, sing, and roost in older forests of ponderosa pine–Douglas-fir, which are patchily distributed in territories (Linkhart et al. 1998). Learning the locations of these forest patches, whose distributions are temporally and spatially stable, should benefit males over multiple years.

High territory fidelity by male Flammulated Owls in our study, which was somewhat higher than in New Mexico (80%; $n = 20$; Arsenault et al. 2005), led to most individuals occupying one territory for their entire known reproductive lives. This resulted in significant disparity in LRS among males (Linkhart and Reynolds 2006), because females occupied only about half of all territories annually and because nesting occurred most often in the same territories (Linkhart and Reynolds 1997, Linkhart 2001). The fact that males rarely changed territories, even in years when productive territories were vacant, suggested that many newly arriving males settled for life in territories where breeding rarely occurred. Such high territory fidelity counters habitat-selection models that predict that individuals should improve their fitness by moving to higher-quality habitats when they become available (Fretwell and Lucas 1969) and may represent a suboptimal form of habitat selection (Switzer 1993). Males of other species also remained in original territories when higher-quality territories became available (Woelfenden and Fitzpatrick 1984, Lanyon and Thompson 1986, Korpimäki 1988).

Territory fidelity in female Flammulated Owls, which was similar to that found in New Mexico (54%; $n = 13$; Arsenault et al. 2005), was much lower than in males. This occurred in part because return rates were much lower following nesting failure, which is consistent with the pattern across avian taxa (Gavin and Bollinger 1988, Doligez et al. 1999, Forero et al. 1999). Although the extent to which

female Flammulated Owls whose nests failed dispersed beyond the study area (“decision rule” hypothesis; Haas 1998), rather than died because of poor health (“low-quality” hypothesis; Pugesek and Diem 1990), was unknown, the “decision rule” hypothesis may be more plausible, given studies of passerines that show that females dispersed more frequently following nesting failure (Winkler et al. 2004) and that females returned to original territories at lower rates following experimentally induced nesting failure (Haas 1998, Hoover 2003).

Breeding dispersal.—Breeding dispersal of female Flammulated Owls was associated with non-return of mates on original territories, but the fact that females did not always disperse when original mates failed to return suggests that other factors were involved. Dispersal by females when mates do not return is likely adaptive, because the opportunity to breed might be lost while waiting for a breeding partner (Black 1996), especially given that most females return from spring migration after males. Individuals of other species, including raptors, also dispersed when mates did not return (Warkentin et al. 1991, Montalvo and Potti 1992, Forero et al. 1999, Forsman et al. 2002).

The hypothesis that breeding dispersal increases individual fitness is supported by relatively few data, though some studies have found that individuals dispersed to territories with higher-quality nest sites (Beletsky and Orians 1991, Montalvo and Potti 1992), greater reproductive success (Danchin et al. 1998), history of more frequent breeding (Matthysen 1990), lower predation risk (Forero et al. 1999), and higher-quality mates (Daniels and Walters 2000a). We found that females moved to territories where productivity over the study was significantly greater than on their previous territories, which indicates that dispersal was associated with habitat composition, because higher rates of occupancy by breeding pairs and higher productivity were positively correlated with territory area in old ponderosa pine–Douglas-fir forests, and negatively correlated with area in young Douglas-fir forests (Linkhart and Reynolds 1997, Linkhart 2001).

Although females also dispersed to territories where LRS of new mates was higher than LRS of mates on original territories, observations suggest that territory quality was more important. Territories where productivity was highest over

the study were occupied by three to six different males, and although each of these males may have been of high quality, the fact that so few males changed territories suggests that usurping of territories rarely occurred, which might be expected if lower-quality males occasionally gained high-quality territories. Habitat quality was shown to be of greater importance than mate quality in other studies (Alatalo et al. 1986, Slagsvold and Lifjeld 1990, Krebs and Davies 1991). That mean brood size of females did not differ before and after dispersal suggests that our ability to detect reproductive consequences of dispersal, particularly for species with small clutches, may require data over the lifetimes of individuals.

Mate fidelity.—The relatively high mate fidelity in Flammulated Owls in this study contrasts with the pattern of lower mate fidelity in many other migratory birds (10–50%; Beletsky and Orians 1991, Payne and Payne 1993, Clarke et al. 2003; but see Beheler et al. 2003), including Flammulated Owls in New Mexico (40%; $n = 20$; Arsenault et al. 2005), which presumably occurs in part because of difficulty synchronizing arrival times on breeding grounds (Wickler and Seibt 1983, Murphy 1996). Although many studies found that mate fidelity was associated with higher productivity, greater nesting success, or earlier nesting (Korpimäki 1988, Orell et al. 1994, Murphy 1996), our study joins others in finding no apparent benefits (Freed 1987, Warkentin et al. 1991). An alternative explanation is that Flammulated Owls maintain pair bonds because they are constrained from other options (Freed 1987). Male choice may be restricted by available females, whereas female choice may often be limited to males available in neighboring territories, with whose previous breeding experience females are familiar. High mate fidelity may also be facilitated by high territory fidelity by males (Murphy 1996). Indeed, mean territory tenure of males was more than twice that of females, which suggests that returning females were likely to find original males on territories. That mean pair duration was similar to mean territory tenure by females indicates that pair duration was limited by female tenure.

Adjusting for undetected migration.—Relatively few studies have attempted to adjust estimates of dispersal to account for undetected emigration beyond areas of study (but see Daniels and

Walters 2000b, Koenig et al. 2000, Cilimburg et al. 2002). Our attempts to adjust territory-fidelity and breeding-dispersal rates for undetected emigration resulted in estimates that differed most from unadjusted estimates in females (15%), reflecting their higher rate of detected dispersal within the study area. Our adjusted rates may still be conservative, given that we could not account for dispersal to destinations more than two territories away and that some individuals of other species, including raptors, dispersed >10 territory diameters away from original territories (Forero et al. 1999, Cilimburg et al. 2002, Forsman et al. 2002).

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