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LIFETIME REPRODUCTION OF FLAMMULATED OWLS IN COLORADO

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ABSTRACT.—We investigated lifetime reproductive success (LRS) of 22 male and 46 female adult Flammulated Owls (*Otus flammeolus*) in Colorado from 1981–2003. Sexual differences in LRS were at least partially attributable to incomplete breeding histories of females, due to females having a higher estimated emigration rate from the study area than males. The mean number of lifetime breeding attempts for males was 3.4 ± 0.6 (SE; range = 1–12), and for females it was 1.9 ± 0.3 (range = 1–8). Adjusted for emigration beyond the study area, the estimated mean number of lifetime breeding attempts was 3.6 for males and 2.5 for females. The mean number of lifetime successful breeding attempts (fledging at least one owlet) was similar to lifetime breeding attempts for each sex, reflecting the fact that 84% (85 of 101) of all breeding attempts were successful. Breeding lifespan was correlated with lifetime reproduction for both sexes. Males tended nests that produced 6.9 ± 1.2 fledglings over 4.3 ± 0.8 yr, while females produced 4.0 ± 0.6 fledglings over 2.0 ± 0.3 yr; adjusted for emigration beyond the study area, males tended nests that produced 7.2 fledglings over 4.5 yr, while females produced 5.2 fledglings over 2.6 yr. Relatively few individuals of each sex produced most of the offspring, as 18% of females and 24% of males produced 50% of total owlets. Our finding that relatively few adults accounted for most offspring appears to be associated with habitat quality in territories. Flammulated Owls tend to have a life-history strategy similar to larger raptors by having a relatively low annual reproductive rate and a relatively long lifespan.

KEY WORDS: *Flammulated Owl*; Otus flammeolus; *lifetime reproductive success*; *LRS*; *reproductive strategy*.

REPRODUCCIÓN DURANTE LA VIDA DEL BÚHO *OTUS FLAMMEOLUS* EN COLORADO

RESUMEN.—Estimamos el éxito reproductivo durante la vida (ERV) de 22 machos adultos y 46 hembras adultas del búho *Otus flammeolus* en Colorado, desde 1981 hasta 2003. Las diferencias en el ERV fueron en parte atribuibles a historias reproductivas incompletas de las hembras, debido a que éstas tienen una mayor tasa estimada de emigración del área de estudio que los machos. El número promedio de intentos reproductivos durante la vida de los machos fue 3.4 ± 0.6 (rango = 1–12) y él de las hembras fue 1.9 ± 0.3 (rango = 1–8). El número promedio de intentos reproductivos exitosos durante la vida, ajustado por la emigración fuera del área de estudio, fue 3.6 para los machos y 2.5 para las hembras. El número promedio de intentos reproductivos exitosos durante la vida (produciendo por lo menos un volantón) fue similar al éxito reproductivo durante la vida para cada sexo, lo cual refleja el hecho de que el 84% (85 de 101) de todos los intentos reproductivos fueron exitosos. La duración de la vida reproductiva se correlacionó con la producción reproductiva durante la vida en ambos sexos. Los machos atendieron nidos que produjeron 6.9 ± 1.2 volantones en 4.3 ± 0.8 años, mientras que las hembras produjeron 4.0 ± 0.6 volantones en 2.0 ± 0.3 años, y ajustando los datos por la migración fuera del área de estudio, los machos atendieron nidos que produjeron 7.2 volantones en 4.5 años, mientras que las hembras produjeron 5.2 volantones en 2.6 años. Relativamente pocos individuos de cada sexo produjeron la mayoría de la progenie, dado que el 18% de las

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hembras y el 24% de los machos produjeron el 50% del total de las lechuzas juveniles. Nuestro resultado de que relativamente pocos adultos dan cuenta de la mayoría de la producción de la progenie, parece estar asociado con la calidad del hábitat de los territorios. Los búhos de la especie *O. flammeolus* tendieron a tener una estrategia de historia de vida similar a la de las aves rapaces de mayor tamaño, al tener una reproducción anual relativamente baja y una vida relativamente larga.

[Traducción del equipo editorial]

Avian studies have long used differences in the breeding performance of individuals to provide insight into the reproductive strategies of species and the factors that affect the evolution of life histories (Lack 1954, Stearns 1976, Marti 1997a, Annett and Pierotti 1999). Variation in reproductive performance, which is known to be quite extensive within and among species (Fitzpatrick and Woolfenden 1989, Owen and Black 1989, Korpimaki 1992), is best assessed in measurements of lifetime reproductive success (LRS), the total offspring raised by individuals over their lifetimes. Compared to cross-sectional studies, which generally track the performance of unknown individuals over relatively few years, LRS studies provide more accurate estimates of inter- and intra-sexual variance in reproductive parameters and are less subject to the effects of stochastic environmental variation (Clutton-Brock 1988, Newton 1989a). Because LRS studies provide information on the relative contribution of particular phenotypes, these data may provide the best estimates of individual fitness and allow identification of traits that most contribute to fitness (Williams 1966, Newton 1989a).

Despite their value, LRS data are limited due to the difficulty of monitoring marked individuals for life, especially in long-lived species. Consequently, LRS has been reported in just eight species of raptors: four falconiforms, Eurasian Sparrowhawk (*Accipiter nisus*; Newton 1989b), Osprey (*Pandion haliaetus*; Postupalsky 1989), Merlin (*Falco columbarius*; Wiklund 1995, Espie et al. 2000), and Common Buzzard (*Buteo buteo*; Kruger and Lindstrom 2001), and four strigiforms, Eastern Screech Owl (*Otus asio*; Gehlbach 1989), Ural Owl (*Strix uralensis*; Saurola 1989, Brommer et al. 1998), Tengmalm's Owl (*Aegolius funereus*; Korpimaki 1992), and Barn Owl (*Tyto alba*; Marti 1997a).

We present 23 yr (1981–2003) of LRS data for a population of Flammulated Owls (*O. flammeolus*) in Colorado. Flammulated Owls are secondary cavity-nesters that breed in montane forests of western North America (Van Woudenberg 1992, McCallum et al. 1995, Marti 1997b, Linkhart et al. 1998, Arsenault 1999). Because the owls are insectivorous, feeding mostly on moths (Reynolds and Linkhart 1987, Powers et al. 1996, Ross 1969; but see Linkhart and Reynolds 1994, Oleyar et al. 2003), northern populations are migratory (McCallum 1994). As with most birds (Greenwood 1980), male Flammulated Owls exhibit greater site fidelity than females (Linkhart 2001). Whereas most males appeared to remain on their original territories for their entire breeding lives, approximately 30% of females changed territories annually in our Colorado study area from 1981–2003 (Linkhart and Reynolds in press). Because rates of breeding dispersal may be underestimated in finite study areas due to individuals emigrating undetected beyond study boundaries (Baker et al. 1995, Koenig et al. 2000), estimates of demographic parameters such as LRS may be biased low, particularly when observed dispersal rates are known to be relatively high, such as with females in our Colorado study area. Consequently, we present LRS data for both sexes that are unadjusted, as well as adjusted, for undetected emigration.

LRS study in Flammulated Owls is interesting because, while their reproductive strategy might be expected to be similar to other raptors (e.g., generally low annual reproductive rate and long lifespan), they are one of the smallest (50–65 g) of the North American strigiforms (Earhart and Johnson 1970). Our objectives were to describe individual variation in LRS, identify life-history attributes that affect LRS, and compare the owl's reproductive strategy to those of other raptors.

METHODS

Study Area. The 511-ha study area was located on the Manitou Experimental Forest in central 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 2550–2855 m.

Data Collection and Analysis. Each breeding season (May–August) during 1981–2003, we searched the entire

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study area for territorial males. We identified territory boundaries by spot-mapping and using radiotelemetry, and we located nests by regularly checking (at least once every 2 wk) all tree cavities with entrance diameters >4 cm from the onset of incubation (late May) to the time the young fledged (mid- to late July; Reynolds and Linkhart 1984, Linkhart et al. 1998). We also regularly checked nest boxes that were placed in territories having relatively few natural tree cavities. We found most nests during incubation (late May to mid-June), and we checked nest contents at least weekly until the young fledged. Adults were captured at nests or on day roosts and banded (Reynolds and Linkhart 1984). Adults could not be aged absolutely unless they were banded as nestlings on the study area.

We determined LRS for all adult males and females captured or recaptured over the study according to the following criteria. First, we included only adults that had at least one breeding attempt (at least one egg laid) in the study area. We rarely captured and banded territorial, unpaired males, and we rarely detected unpaired females. Second, we based LRS calculations solely on breeding attempts that occurred within the study area. No extra breeding years were added for individuals that apparently left the study area for ≥1 yr and then returned to breed on the study area. We also could not verify if individuals bred beyond the study area prior to, or subsequent to, their tenure on the study area. Third, an adult was excluded from LRS calculations if its breeding history included the first or last year of study. However, in order to avoid excluding relatively long-lived adults whose breeding histories were incomplete, adults in the latter category were included in calculations of LRS if their total breeding attempts were the same or greater than the mean for all adults whose entire breeding histories occurred within the study period. Because the mean number of breeding attempts for males whose entire breeding histories occurred within the study period was 3.1 ± 0.6 ($\bar{X}$ ± SE; N = 21), and for females was 1.6 ± 0.2 (N = 42), this criterion added to LRS analyses one male (with eight breeding attempts) and four females (one each with seven, five, four, and three breeding attempts).

For adults meeting the above criteria, we determined the following parameters for both genders: (1) lifetime breeding attempts, defined as the total number of successful (i.e., fledged at least one owlet) and failed breeding attempts; (2) lifetime successful breeding attempts; (3) lifetime production of fledglings, which was identical to lifetime production of banding-age owlets, because no nests failed and no owlets died after we banded owlets at age 14–21 d; (4) relationship between lifetime production of fledglings and breeding lifespan, defined as the total years from banding as an adult (usually when they first bred) to disappearance; and (5) contribution to the total number of offspring produced on the study area by individual adults.

In addition to calculating unadjusted estimates of LRS parameters, we calculated adjusted estimates of LRS to account for adults that dispersed undetected beyond the study area. To do this, we devised an adjustment to estimates of observed breeding dispersal (adults that changed breeding territories within the study area from one year to the next) by constructing a hypothetical landscape surrounding our study area based on the assumptions that the landscape outside the study area (1) consisted of similar forest types and structure and (2) contained a similar density and juxtaposition of owl territories. We believed these assumptions were reasonable, based on our familiarity with the surrounding landscape and based on the fact that each year we detected several territorial males, and occasionally owl nests, in areas adjacent to the study area. We created the hypothetical landscape by producing eight duplicate maps of the study area, constructed in ArcView (ESRI 1995), to prevent spatial distortions, and we attached one map to each side and corner of the original map.

We used the resulting landscape mosaic to estimate, for each of the 12 territories on the study area, the fraction of potential dispersal destinations up to two territories away (the maximum detected dispersal distance) that occurred within the study area (and thus 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 according to:

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

where m_i is the number of banded adults of a given gender in territory i that failed to return from one year to the next, and n_i is the number of those adults found nesting in a new territory within the study area in a subsequent year.

Using this equation, we calculated an adjusted total of 36 dispersal events for females and 8 dispersal events for males, which may be conservative because the number of dispersal events to destinations more than two territories away was not estimated. Based on the observation of 12 female dispersal events within the study area, we estimated that 24 female dispersal events went undetected, or 0.29 of the 82 opportunities to assess whether a banded female returned to her original territory in a subsequent year. Similarly, as we observed three male dispersal events within the study area, we estimated that five male dispersal events went undetected, or 0.05 of the 97 total opportunities to assess whether a banded male returned to his original territory. We then used these proportions to adjust upwards our unadjusted estimates of LRS.

We assumed that the behavioral parents of offspring were the biological parents in our LRS calculations. While we have documented some extra-pair copulations in Flammulated Owls, one of two strigiforms in which they have been reported (Reynolds and Linkhart 1990, Haug et al. 1993), available data suggest that the rate of extra-pair paternity was not likely to be significant. In our study area, microsatellite DNA tests in 2002 revealed no evidence of extra-pair parentage in five owl families (B. Linkhart unpubl. data), and in New Mexico, mini-satellite DNA tests from 1997–99 revealed no evidence of extra-pair paternity in 17 family groups (Arsenault 2002).

We performed statistical analyses using SAS (SAS Institute 1995). We used Wilcoxon's test (PROC NPAR1-

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WAY) to evaluate sex differences in LRS parameters and linear regression (PROC GLM) to examine relationships between variables. We present means ± standard errors (SE). Analyses were considered significant if $P \leq 0.05$.

RESULTS

From 1981 to 2003, we recorded 3–6 breeding attempts per yr on 12 territories on the study area, for a total of 101 breeding attempts. The majority of breeding attempts (94%; 95 of 101) were in natural tree cavities. Six breeding attempts were in nest boxes, all of which occurred in one of the seven territories that contained nest boxes. We documented the reproductive lives of 68 adults, consisting of 46 females and 22 males. Except for five males and five females that bred in 2003, no other individuals were known to be alive in 2003, apart from one female that bred in 2002 and was undetected until she returned to breed in 2004. Four of the 68 individuals (all females) returned to breed on the study area after being absent for one breeding season (one in 1998, 1999, and 2003) or two breeding seasons (one in 2002). Unless otherwise noted, the following data are based on these 68 adults.

Lifetime Breeding Attempts. Lifetime reproduction is the product of mean clutch or brood size and the lifetime total of breeding attempts, and the latter is the product of the mean number of breeding attempts per year and the total years of breeding. For this owl population, the mean clutch size was 2.5 ± 0.1 eggs ($N = 29$, range = 2–3), and the mean brood size in successful nests was 2.5 ± 0.1 owlets ($N = 78$, range = 1–4). Individuals had no more than one breeding attempt per year. We documented no instances of renesting or multiple broods, even in pairs whose nests failed early in the breeding period. The initiation of breeding early in life may affect the total years of breeding in birds, if rates of extrinsic mortality are low and if senescence does not occur, although early reproduction also may have trade-offs, such as lower survival in adults (Tavecchia et al. 2001, Reid et al. 2003). Age of first breeding in Flammulated Owls, which could be estimated only for two males banded as nestlings that returned to breed on the study area, was 5 yr and 6 yr. These males were not detected on the study area between the year they fledged and the year they first bred.

The mean lifetime breeding attempts per breeding adult was 2.4 ± 0.3 (median = 1, range = 1–12). Breeding males had a mean of 3.4 ± 0.6 breeding attempts in their lifetime, compared to a mean of 1.9 ± 0.3 lifetime breeding attempts for females

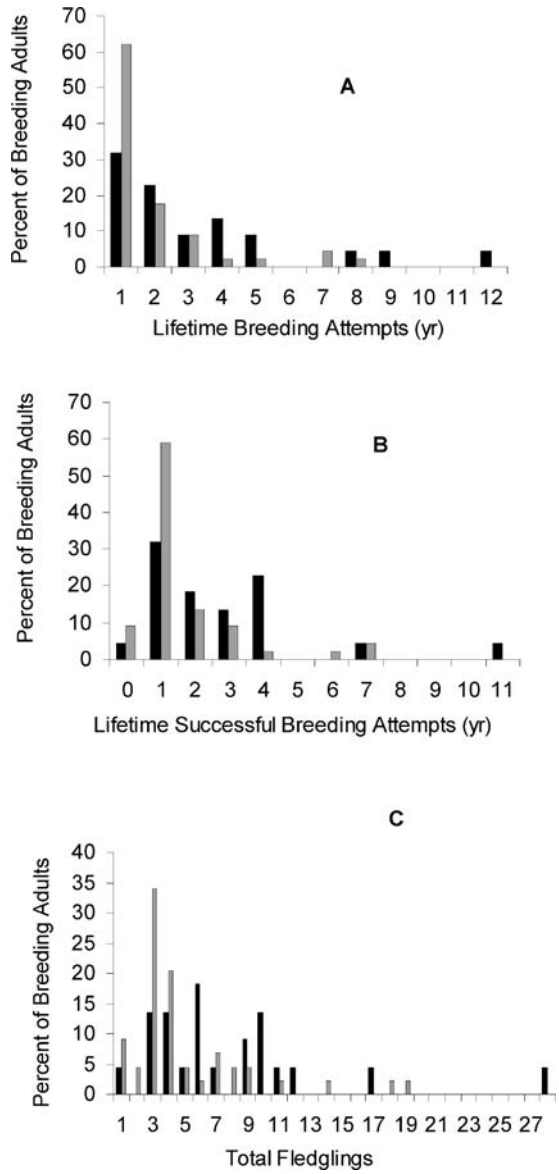


Figure 1. Lifetime number of breeding attempts (A), successful breeding attempts (B), and lifetime production of fledglings (C), by female owls ($N = 44$; light bars) and male owls ($N = 22$; dark bars).

($z = 2.5$, $P = 0.01$; Fig. 1A). Just 20% of females had three or more breeding attempts compared to 46% of males. Adjusted for emigration beyond the study area, the estimated mean lifetime breeding attempts was 3.6 for males and 2.5 for females.

Mean lifetime successful breeding attempts for all owls was 2.1 ± 0.2 (range = 0–11). As with lifetime

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breeding attempts, on average, males bred successfully more years (2.8 ± 0.5 yr) than females (1.7 ± 0.2 yr; $z = 2.5$, $P = 0.01$; Fig. 1B). Just 21% of females bred successfully for ≥3 yr, compared with 48% of males. Adjusted for emigration beyond the study area, the estimated mean lifetime successful breeding attempts was 2.9 for males and 2.2 for females.

The relatively similar values for the mean lifetime breeding attempts and the lifetime successful breeding attempts for each sex reflected the fact that only 16 nests failed during the study — 84% (85 of 101) of all breeding attempts were successful. No females accounted for more than one failed nesting attempt, while two males accounted for 50% (five of 10) of the failed nesting attempts where male identity was known.

Lifetime Reproduction. Overall, owls produced or tended nests that produced 5.0 ± 0.6 fledglings over a breeding lifespan of 2.8 ± 0.3 yr. However, males tended nests that produced 6.9 ± 1.2 fledglings (median = 5) over 4.3 ± 0.8 yr (median = 2.5), while females produced 4.0 ± 0.6 fledglings (median = 3) over 2.0 ± 0.3 yr (median = 1; $z = 2.7$, $P = 0.01$; Fig. 2). Nine percent of females and 5% of males produced no fledglings (their nests failed), while 25% of females and 48% of males produced six or more fledglings. Adjusted for emigration beyond the study area, males tended nests that produced an estimated 7.2 fledglings over 4.5 yr, and females produced an estimated 5.2 fledglings over 2.6 yr.

Lifetime production of fledglings was positively correlated with breeding lifespan in females ($r = 0.91$, $F = 213.2$, $P < 0.001$; Fig. 2A) and males ($r = 0.85$, $F = 53.6$, $P < 0.001$; Fig. 2B), and these high correlations generally reflect high nesting success in the population. The higher correlations among females occurred because each female attempted to breed every year she was known to be present in the study area, whereas among males, some individuals bred nearly annually over their lifetimes, while others remained unpaired on their territories up to 4 yr following a breeding attempt. The most productive female produced 18 fledglings over a breeding lifespan of 8 yr, accounting for 10% of all fledglings produced by all females during the study period. Overall, 18% of females produced 50% of all fledglings (Fig. 3). The most productive male tended nests that produced 27 fledglings over a breeding lifespan of 14 yr, accounting for 18% of all fledglings. Overall, 24% of males produced 50% of all fledglings (Fig. 3). LRS was not correlated with nesting success or brood size for either sex.

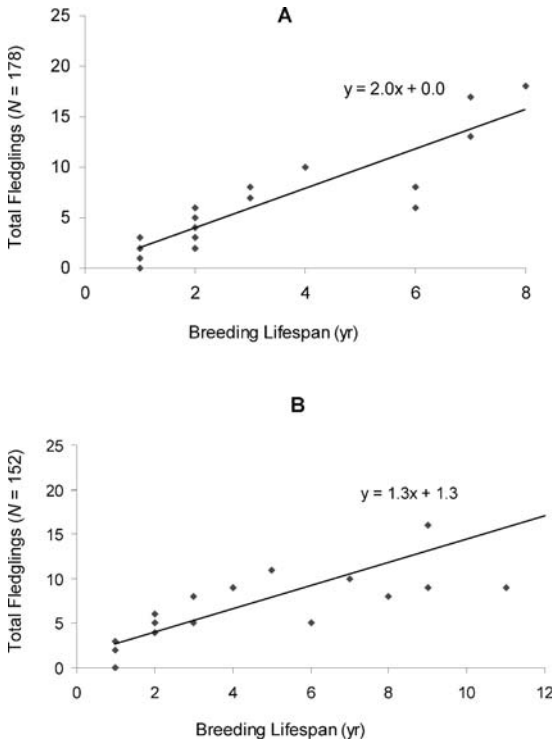


Figure 2. Relationship between breeding lifespan and total fledglings by (A) female and (B) male owls. Duplicate symbols are omitted from the graphs.

DISCUSSION

Sexual Variation in LRS. Apparent LRS differences between males and females were associated with higher emigration rates among females, suggesting that female longevity was underestimated in the study. Based on gender differences in rates of breeding dispersal within the study area, we estimated that approximately 29% of females and 5% of males that left the study area may have emigrated, rather than died (Linkhart and Reynolds in press). The observation that four females returned to breed on the study area after being undetected for one to two years supports the assertion that some proportion of the individuals that disappeared may have emigrated. However, the fact that disparity between male and female LRS and longevity still exceeded 30%, even after adjusting for undetected emigration, suggests that either emigration rates were still underestimated in females, or that there were other contributing factors.

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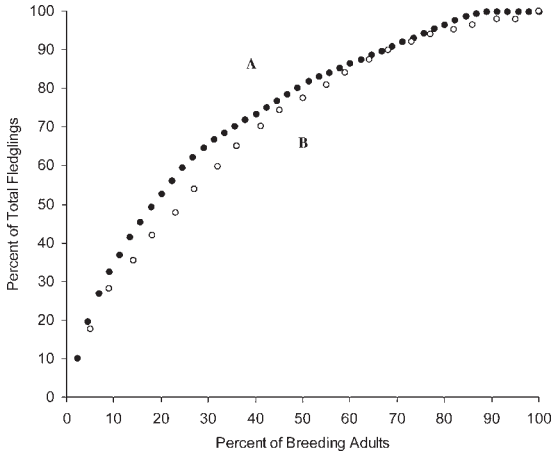


Figure 3. Percent of total fledglings produced by varying percentages of (A) female owls (closed circles; $N = 44$), and (B) male owls (open circles; $N = 22$). Total fledglings produced by known females in (A) was 178 and by known males in (B) was 152. Axes showing percent of males and females were based on ordering individuals from highest to lowest productivity.

Across avian taxa, gender differences in LRS generally are positively correlated with the extent of sexual dimorphism (Newton 1989a). Among raptors, which exhibit varying degrees of reversed sexual size dimorphism (Snyder and Wiley 1976, Mueller 1986), gender differences in LRS has been studied only in Ospreys (Postupalsky 1989) and Barn Owls (Marti 1997a). No gender differences in LRS were found in either of these two species, where females are larger by 11% in Barn Owls (Earhart and Johnson 1970) and 26% in Ospreys (Postupalsky 1989). As female Flammulated Owls were only ca. 15% larger than males in our study population (Linkhart and Reynolds 2004), sex differences in LRS would not be expected.

The possibility that females have shorter lifespans than males is suggested by the presence of unpaired, territorial males, which occupied 26 ± 3% of territories on the study area annually (Linkhart 2001), although unpaired females, if they existed, might have been difficult to detect. While sex-biased mortality is known among adults of many ground-nesting waterfowl (Baldassarre and Bolen 1994), relatively few studies of raptors have found sex-biased survival among adults (see Newton 1986, Kenward et al. 1999).

Individual Variation in LRS. Studies of LRS generally have shown that some proportion of territorial or breeding adults fail to produce any offspring during their lifetimes (Clutton-Brock 1988, Newton 1989a). The estimated percentage of Flammulated Owls that produced no offspring (9% for females, 5% for males) was similar to that in other raptors, which ranges from 3% in Ural Owls (Saurola 1989) to 22% in Osprey (Postupalsky 1989) and Barn Owls (Marti 1997a). The percentage for female Flammulated Owls may have been overestimated if some individuals emigrated from the study area and bred elsewhere. In contrast, the percentage for males may have been underestimated given that our study only included individuals that bred at least once, because unpaired males were difficult to capture. While the proportion of unpaired males that eventually bred over their lifetimes was unknown, the fact that banded males showed high territory fidelity (96%), even when they did not breed for up to 4 consecutive yr, and the fact that breeding typically occurred on the same territories annually, suggests that at least some of the unpaired males never bred (Linkhart and Reynolds in press).

A second pattern shown by LRS studies is that a small percentage of breeders typically account for the majority of offspring produced by the population (Clutton-Brock 1988, Newton 1989a). Among raptors, the percentage of females that accounted for 50% of total fledglings ranges from 16% in Ospreys (Postupalsky 1989) to 23% in Ural Owls (Saurola 1989), while the percentage for males ranged from 17% in Common Buzzards (Kruger and Lindstrom 2001) to 24% in Ospreys (Postupalsky 1989). The percentages for female (18%) and male Flammulated Owls (24%) were similar to these data, but the value for males may have been overestimated because of the possibility that at least some of the unpaired, territorial males may never have bred.

Life History Correlates of LRS. Breeding lifespan has emerged as the major demographic determinant of LRS among birds, including raptors (Newton 1989a). This factor also was correlated with LRS in Flammulated Owls, and it was the only life history parameter that varied among individuals. Among all birds, including raptors, regression analyses have shown that variance in fledgling production that was accounted for by breeding lifespan ranged from 29% in Barnacle Geese (*Branta leucopsis*; Owen and Black 1989) to 86% in Blue Tits (*Parus caeruleus*; Dhondt 1989). Other factors contributing to differences in LRS among birds include offspring survival between the egg and fledgling stages and fecundity (Newton 1989a).

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Importance of Habitat Quality. Despite the fact that habitat quality has been shown to influence short-term demographic parameters in many avian studies (Donovan et al. 1995, Holmes et al. 1996, Hunt 1996), habitat quality has been associated with LRS in studies of only a few species, including Eurasian Sparrowhawks (Newton 1989b), Ural Owls (Saurola 1989), and Tengmalm's Owls (Korpimaki 1992). Our finding that relatively few adults accounted for most offspring appears to be associated with habitat quality in territories. Linkhart (2001) reported that 50% of Flammulated Owl territories produced 83% of all owlets during 1981–99, and that territory productivity was positively correlated with mature, open forests of ponderosa pine/Douglas-fir, and negatively correlated with younger, denser Douglas-fir forests. The most-productive adults were associated with the most productive territories, where the mostly mature, open forests were preferentially used by breeding males for foraging, day-roosting, and singing (Linkhart et al. 1998, Linkhart 2001). Interestingly, the two males that accounted for a majority of the failed nesting attempts were associated with moderately-productive territories, not the least-productive territories, where we documented relatively few breeding pairs. These data suggest that forest structure may affect LRS of individuals and productivity of Flammulated Owl populations in Colorado. Future research efforts need to focus on comparing LRS of populations in different forest types and ages across the species' range to better understand how individual performance is affected by habitat quality.

Reproductive Strategy. Across avian taxa, body mass generally is negatively correlated with reproductive output (Newton 1998). However, Flammulated Owls do not appear to be consistent with this pattern. While the owls have the second-smallest mass among the 19 species of North American strigiforms (Earhart and Johnson 1970), mean clutch size was relatively small and invariable in our study population (2.5 ± 0.1 eggs), as well as in New Mexico (2.3 ± 0.5 [SD] eggs, $N = 11$; McCallum et al. 1995) and in Oregon (2.7 ± 0.8 [SD] eggs, $N = 6$; Goggans 1986). In other North American strigiforms, mean clutch size, which is subject to wide temporal and spatial variation among populations of several species (Murray 1976, Mikkola 1983), varies from 2.2 eggs (range = 2–4) in Spotted Owls (*S. occidentalis*; Forsman et al. 1984) to 7.7 eggs (range = 5–14) in Snowy Owls (*Bubo scandiaca*; data from Finland, Mikkola 1983), with 4–6 eggs per clutch more typical in many species. Given that Flammulated Owls also had just one breeding attempt per year in our study even when nests failed early, in contrast to other small raptors in temperate regions (Newton 1979), these data indicate that the owl has a relatively low annual rate of reproduction.

Another pattern evident across avian taxa is that body mass is positively correlated with lifespan (Newton 1998), which also may hold for North American strigiforms (Linkhart and Reynolds 2004). However, among raptors for which data exist, male Flammulated Owls have a conservative estimate of mean breeding lifespan (4.3 yr; unadjusted for emigration) that exceeds the mean lifespan of Tengmalm's Owls (3.5 yr; Korpimaki 1992), Eurasian Sparrowhawks (3.3 yr; Newton 1989b), Merlins (3.2 yr; Wiklund 1995), Eastern Screech Owls (3.2 yr; Gehlbach 1989), and Barn Owls (1.7 yr; Keran 1981), whose respective masses range from approximately 200% to 900% of Flammulated Owls. Only Ospreys (7.6 yr; Postupalsky 1989) and Ural Owls (7.9 yr; Saurola 1989) have a mean lifespan that exceeds the mean breeding lifespan of Flammulated Owls, and their masses are approximately 15 times and 29 times that of Flammulated Owls. Moreover, based on the estimated age of first breeding in two males (5 yr and 6 yr), who were unlikely to have bred prior to arriving on the study area given the high territory fidelity in males (96%; Linkhart and Reynolds in press), the mean lifespan of breeding males was almost certainly greater than the mean breeding lifespan that we calculated. Elsewhere, we reported that the maximum lifespan of male Flammulated Owls (14+ yr) is similar to, or exceeds that, reported for several larger species (Linkhart and Reynolds 2004).

By having a relatively low annual reproductive rate and longer lifespan, in addition to high annual survival in adult males (83 ± 4%; B. Linkhart and R. Reynolds unpubl. data), these data support the view that Flammulated Owls have a life-history strategy similar to many larger raptors (McCallum 1994). This strategy contrasts with Barn Owls, whose high annual reproductive rate and short lifespans resemble many passerine species (Marti 1997a).

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