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# LIFE HISTORY AND ECOLOGY OF FLAMMULATED OWLS IN A MARGINAL NEW MEXICO POPULATION

D. ARCHIBALD MCCALLUM,[1] FREDERICK R. GEHLBACH,[2] AND
SOPHIE W. WEBB[3]

ABSTRACT.—In 1981–1986, we studied Flammulated Owls (*Otus flammeolus*) nesting in a forest-woodland ecotone at the species' lower elevational limit. Most adults did not renest in the same tree cavity despite previous success. Clutch size was smaller, and eggs were less likely to produce fledglings than in a coniferous forest population studied concurrently by Reynolds and Linkhart (1987b). Additional features of life history and nesting density were similar to other populations, but nesting mass of females and productivity were lower, while density flux was higher. Our study population is marginal ecologically, perhaps limited by food shortage during courtship plus predation and maintained by immigration. *Received 25 April 1994, accepted 15 Feb. 1995.*

The Flammulated Owl (*Otus flammeolus*) nests in tree cavities in mature coniferous forest, largely in ponderosa pine (*Pinus ponderosa*) and mixed conifer associations (McCallum 1994a, b). Its small mass, clutch of two or three eggs, and migratory habits differ from congeners such as the Eastern Screech-Owl (*Otus asio*), a larger permanent resident with a larger clutch (Gehlbach 1994). Here we analyze the life history and ecology of Flammulated Owls in a marginal ecological situation in New Mexico and compare them with other populations and the Eastern Screech-Owl.

## STUDY SITE AND METHODS

Cottonwood Gulch (CWG), our study site 12 km South of Thoreau, McKinley County, New Mexico, was described by McCallum and Gehlbach (1988). The vegetation is mature and ecotonal between ponderosa pine forest and pinyon (*Pinus edulus*)-juniper (*Juniperus* spp.) woodland at 2230–2277 m in the Zuni Mountains. This is the lower elevational limit of Flammulated Owls locally (they nest to at least 2780 m). Because we make detailed comparisons with Flammulated Owls in central Colorado, it is important to note that this population lives at 2550–2855 m in coniferous forest more typical of the species and was studied concurrently by Reynolds and Linkhart (1987a, b).

At CWG, call surveys and searches of all possible tree cavities were made annually during late April-early July, 1981–1986, in a 160 ha plot. Small owl population highs and lows are 3–4 years apart on average (Korpimaki 1981, Gehlbach 1994), so we tried to study the population during at least two cycles. Before recording any nesting data for analysis, we allotted at least a week of owl-human habituation time. At two nests with nestlings and

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[1] Dept. of Biology, College of Charleston, Charleston, South Carolina 29424.
[2] Dept. of Biology, Baylor Univ., Waco, Texas 76798.
[3] Point Reyes Bird Observatory, 4990 Shoreline Highway, Stinson Beach, California 94970.

fledglings in 1982, foraging by both adults was recorded in the first hour after sunset (11 h total). In 1983, we made all-night observations of feeding rates at four nests in incubation and nestling periods (141 h total). Other field techniques are elaborated in Gehlbach (1994), the source of comparative information on other owls, particularly the Eastern Screech-Owl.

We mapped suitable cavities (McCallum and Gehlbach 1988) and nest sites on a 1:8700 aerial photo. Locations, physical features, and habitat boundaries were digitized using ERDAS program Digpol and a GTCO Digi-pad. Data analyses included parametric and nonparametric statistics and transformations appropriate to two-sided tests (SAS Inst. 1988, Wilkinson 1990a). We used the $P = 0.05$ alpha level of significance. Summary statistics are mean ± one standard deviation unless otherwise stated.

## RESULTS

*Habitat and nest sites.*—Flammulated Owls selected 14 nest cavities 260 ± 147 m from nearest-neighbor nest sites in mature (open) vegetation typical of the species (McCallum and Gehlbach 1988, McCallum 1994a, b). Nest sites tended toward regular spacing ($R = 1.4$, Clark and Evans 1954), and most (79%) were within 50 m of grassland. Other than two sites that faced grassy openings at the edges of ponderosa pine thickets, dense saplings were avoided except for roosting.

We found 39 nest cavities and useable alternatives, 7.8 times the number needed to house the maximum density of five breeding pairs. The cavity surplus and lack of inter- or intra-specific disputes over cavities suggests that our birds were not site limited (also the case in Eastern Screech-Owls). For example, Flammulated Owls and Mountain Chickadees (*Parus gambeli*) nested simultaneously in the same pine twice without conflict, once in cavities on opposite sides of the tree at nearly the same height.

Three Flammulated Owl nests housed nesting colonies of *Liometopum occidentale,* an ant that attacked us, producing painful bites and stings when we investigated owl eggs and nestlings. The owls were not bothered and fledged all chicks successfully. A similar potentially protective relationship between tree ants and Eastern Screech-Owls has been described and observed once in Western Screech-Owls (*O. kennicottii*). This may be a unique symbiosis in *Otus,* although it seems to be infrequent.

*Site fidelity.*—None of 13 banded nestlings was recaptured at CWG, nor were nestlings recaptured in Colorado (Reynolds and Linkhart 1987a, 1990). Among 18 nesting adults, only a male and four females (28%) returned to our study plot in subsequent years. By contrast, the return rate was 55% for 20 adults in Colorado, but this is not a significant difference, perhaps because of the small samples (Fisher's Exact $P = 0.27$).

Of the five returnees at CWG, only one female used the same nest cavity more than once (repeated twice). Failure to reuse a cavity followed three nest failures but also 14 successes at CWG, similar to the species in Oregon (Goggans 1986) and British Columbia (Van Woudenberg 1992), unlike the Eastern Screech-Owl which reuses cavities after successes not failures.

Four breeding dispersals averaged 423 ± 126 m, no different than five in Colorado (mean 474 m; $t = 0.8$, ns). The mean is about one territory diameter, based on an average diameter of 424 m in Colorado (Reynolds and Linkhart 1987a) and is 1.6 times the mean distance between neighboring nest cavities, suggesting that our owls moved only about one territory away before nesting again as their counterparts did in Colorado.

*Breeding density.*—Nests per 100 ha averaged 2.9 ± 1.5 (5 yr), a value slightly higher than nests in Colorado (2.1 ± 0.8, 4 yr; Reynolds and Linkhart 1987b) and Oregon (1.4 ± 0.3, 2 yr; Goggans 1986). Mean differences are not significant, however ($F = 1.5$, ns). Density flux, measured by the coefficient of variation, was 0.52 at CWG compared to only 0.38 in Colorado and 0.21 in Oregon.

Because four nest sites were near edges of our study plot, which was smaller than plots in Colorado and Oregon, we calculated minimal spanning distances of trees at all nest sites and used the annual mean distances as area-independent estimates of density (Wilkinson 1990b). These distances were 519 m at CWG (5 yr) and 472 m in Colorado (2 yr, calculated from Linkhart 1984), substantiating the similarity of population densities based on nest counts (Mann-Whitney $U = 7$, ns).

*Productivity.*—Mean clutch size was 2.3 ± 0.5 (N = 11) and brood size 2.2 ± 0.6 (N = 10). Hatchability (mean brood/mean clutch) was 0.96. Fledglings in 10 nests were 1.8 ± 0.8, hence fledgability (mean fledglings/mean nestlings) was 0.82. Ten of 12 nests fledged chicks, a success rate of 0.83, multiplied by the product of hatchability and fledgability (0.79) to give an estimated productivity of 0.65 fledglings per egg or 1.5 per nest. This is significantly lower ($t = 2.4$, $P = 0.04$) than 0.74 fledglings per egg and the mean of 2.3 per nest in Colorado (Reynolds and Linkhart 1987b, McCallum 1994b), partly because clutches at CWG are smaller (mean 2.7 in Colorado; $t = 2.3$, $P = 0.03$).

*Egg and adult mass.*—Mean egg mass was 10.4 ± 0.4 g (N = 9). Eight incubating females weighed 69.9 ± 8.4 g, dropping to 63.1 ± 1.2 g at hatching of the last egg (estimated from regression), and six with nestlings weighed 59.7 ± 5.8 g. The loss was estimated as 0.52 g/day by regressing the masses of seven females, each weighed at least three times, on nestling age with Julian date and female identity as covariates. Controlling for among-individuals variation, nestling age explained a significant 42% of the variance in female mass ($r^2 = 0.90$, $P < 0.001$).

By contrast, incubating and brooding females in Colorado were significantly heavier with means of 78.3 g (incubation) and 63.3 g (nestlings,

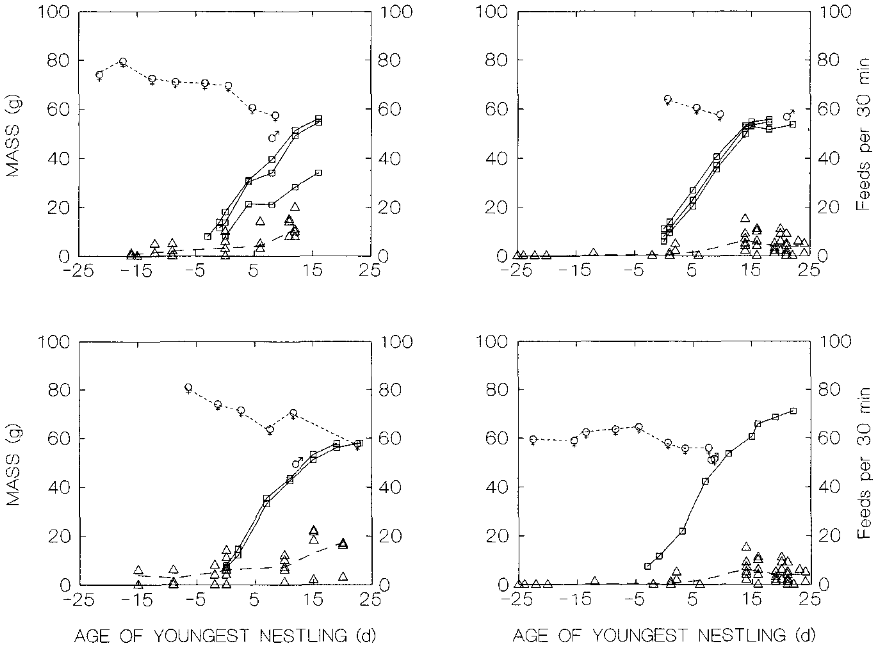

FIG. 1. Mass of adult females (short dashes), males (single symbols), and their nestlings (solid lines) in relation to age of youngest nestling in each of four nests, 1983. Feeding visits between sunset and midnight are triangles (long dashes); trends fitted by robustly weighted regressions.

$t > 1.9$, $P < 0.03$; data from Reynolds and Linkhart 1987b). However, eight males delivering food to nestlings at CWG weighed 52.5 ± 3.3 g, essentially like their counterparts in Colorado (mean 53.2 g).

*Chick growth, fledging, and provisioning.*—Seven hatchlings weighed 6-8 (7.5 ± 0.8) g and grew to 48-71 (56.2 ± 5.9) g at fledging, similar to Colorado owlets. Growth was sigmoid but did not level off at fledging (Fig. 1), as in Colorado, suggesting that chicks vacate their nest cavity a few days before they can fly as do the chicks of Eastern Screech-Owls. Three fledged at 23.7 ± 2.1 d of age, fluttered to the ground, and walked, hopped, and climbed trees with bills, feet, and flapping wings like fledgling Eastern Screech Owls. Their nestling period was the same as in Colorado (mean 23.0 d, $t = 0.5$, ns; data from Reynolds and Linkhart 1987b). The upper left graph in Fig. 1 shows the reduced growth rate of a last-hatched chick found dead in the nest after its siblings fledged, while the lower right graph shows the unusually large mass of a single nestling that fledged at 26 d. These contrasting examples, and two other cases of

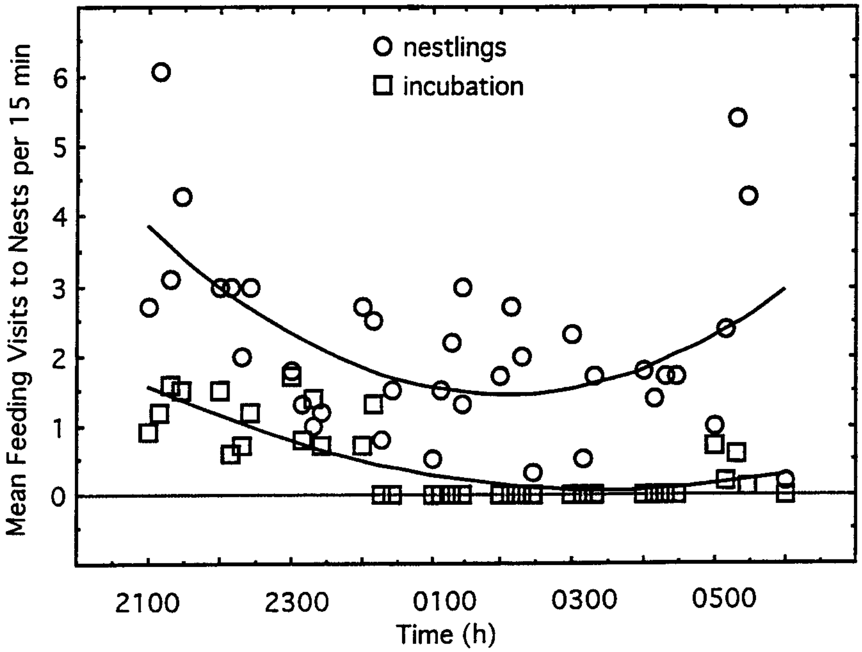

FIG. 2. Average feeding at four nests in 1983 during mid-incubation through the nestling period until the 25th day after hatching of the last egg. Data not collected at 00:30–03:00 h during incubation, when casual observations showed little or no activity (set at 0 for analysis but note actual 0 data). Bimodal patterns verified by 2° polynomial regressions ($r^2 > 0.30$, $P < 0.003$).

brood reduction, suggest that reduced productivity might be influenced by reduced parental feeding. Generally, feeding rates increased 10–15 days after the last chick hatched (Fig. 1).

Dusk and dawn peaks of feeding were evident (Fig. 2). Feeding per 15 min interval averaged 3.6 ± 1.3 at 21:30–23:30 and 05:30–06:30 h compared to only 1.6 ± 1.8 at 24:00–05:00 h ($F = 36.1$, $P < 0.001$). There was a marginally significant difference between the greater dusk and lesser dawn rates ($F = 4.0$, $P = 0.06$) and a pronounced difference between these peaks in the incubation and nestling periods ($F = 20.7$, $P < 0.001$, 2-way ANOVA; Fig. 2).

This bimodal pattern, typical of *Otus* at lower latitudes, also occurred in Flammulated Owls in Idaho (Hayward 1986). We figured an average of 81 (maximum 121) feeding trips per night during the nestling period, similar to Hayward's single-nest average of 73 over eight nights. Reynolds and Linkhart (1987b) did not watch dawn feeding, but their observations per 15 min in the first 4 h after sunset did not differ from ours ($F = 0.2$, ns), suggesting similar prey availability, and showed the same incubation versus nestling-period distinction ($F = 41.0$, $P < 0.001$; 2-way ANOVA).

*Foraging and flying.*—Flammulated Owls at CWG hunted in sit-and-wait fashion 3-50 m from their nests as Eastern Screech-Owls do. Thirty-seven straight-line forays to pine twig-tips (78%) or the ground (22%) resulted in at least 30 captures (81% success), very similar to the Eastern Screech-Owl's 83% success rate on insects. Identifiable prey were seven lepidopteran larvae and three small moths taken from pine foliage and a cricket caught on the ground at the edge of a grassy opening. Most foraging (78% of 81 perches) occurred along the interface between forest or woodland and grassland as in Oregon (Goggans 1986).

Adults arriving at nests with or without food often swooped up to the cavity from a 2–3 m flight path under or in the lower tree canopy and when departing tree cavities dived steeply and again flew low. This flight pattern was not seen in Colorado (R. Reynolds, pers. comm.). However, adults sometimes flew straight to a feeding perch and then to the cavity, as they did in Colorado, and the Eastern Screech-Owl displays both flight patterns.

## DISCUSSION

Our study population at the lower edge of its local elevational range resembled the contemporaneous Colorado population located higher in elevation in conifer forest and also populations in Oregon (Goggans 1986) and British Columbia (Van Woudenberg 1992). Among the life history traits, reuse of nest cavities, foraging style, breeding mass decline, bimodal feeding, brood reduction, early fledging, and degree of hunting success characterize the Eastern Screech-Owl as well. Conversely, habitat type, breeding dispersal distance, nesting density, infrequent reuse of nest cavities, clutch-size, and nestling period are similar only among populations of Flammulated Owls.

Despite similarities, the CWG population exhibited productivity that was 0.8 fledglings per nest lower and a density flux 31–51% higher than in Colorado and Oregon. Also, site fidelity was somewhat lower as might be expected of a marginal locale. These and other differences suggest that the CWG population is cyclic and transient (high density flux, low site fidelity) because it is stressed (low female mass, low productivity) compared to the more stable population in central Colorado.

However, low productivity and high density flux are not unusual in *Otus*. Flammulated Owl productivities are like those of Eastern Screech-Owls in central Texas with 0.2–1.3 fledglings per breeding pair when declining and 1.8–2.5 in the increase phase of population cycles. Also, that species' coefficients of annual density variation are 16–46%, resembling the 21–51% range of values in Flammulated Owls. By contrast, the much larger Tawny Owl (*Strix aluco*) produces 0.5–0.9 fledglings per pair with a density flux of only 5% (calculated from Southern 1970).

Research might have stressed our CWG population, but this seems unlikely in view of individuals renesting in the same cavities after disturbance caused abandonment (two cases). Moreover, the owls have been exposed to human activity for most of this century and are readily habituated. CWG was a lumber camp in the 1920s and, since then, has been used continuously as a children's summer camp. Rather than investigative biases, we believe that the CWG population is a natural sink, possibly supplied by a source population higher in the Zuni Mountains.

Spatial constraints are not evident at CWG, as nest cavities are in excess and territory size plus breeding dispersal are about the same as in Colorado. Also, food availability during incubation and nestling periods may not differ from that in Colorado, based on similar nest-provisioning rates, but could be reduced during courtship (production feeding), since the lighter-weight females at CWG laid fewer eggs per average clutch. While the kind of local stress is problematical, it may be related to food scarcity early in the nesting season.

Predation is a second possible limiting factor, contrastingly absent in the Colorado population (Reynolds and Linkhart 1987b). Known agents of failed nests at CWG were a gopher snake (*Pituophis melanoleucus*) that ate a clutch of eggs and an *Accipiter* sp. that consumed an adult. In addition, Abert's squirrels (*Sciurus aberti*) used at least two tree cavities used by Flammulated Owls and could be nest-site competitors if not predators. Symbiotic ants may be too infrequent to deter significant numbers of intruders.

Low productivity and high density flux also typified a predator-impacted population of Eastern Screech-Owls by contrast to a concurrently stable one in central Texas. There, arboreal snakes and mammals were the major predators in a situation resembling CWG by contrast to Colorado. Besides food supply and nest-site availability as regulatory factors in raptor populations (Newton 1991), predation may limit smaller species such as the *Otus* owls and should not be overlooked in future studies.

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## LITERATURE CITED

CLARK, P. J. AND F. C. EVANS. 1954. Distance to nearest neighbor as a measure of spatial relationships in populations. Ecology 35:445–453.

GEHLBACH, F. R. 1994. The Eastern Screech Owl: life history, ecology, and behavior in the suburbs and countryside. Texas A. and M. Univ. Press, College Station, Texas.

GOGGANS, R. 1986. Habitat use by Flammulated Owls in northeastern Oregon. M.S. thesis, Oregon State Univ., Corvallis, Oregon.

HAYWARD, G. D. 1986. Activity pattern of a pair of nesting Flammulated Owls (*Otus flammeolus*) in Idaho. Northwest Sci. 60:141–144.

KORPIMAKI, E. 1981. On the ecology and biology of Tengmalm's owl (*Aegolius funereus*). Acta Univ. Ouluensis, Ser. A, Biol. 13.

LINKHART, B. D. 1984. Range, activity, and habitat use by nesting Flammulated Owls in a Colorado ponderosa pine forest. M.S. thesis, Colorado State Univ., Fort Collins, Colorado.

MCCALLUM, D. A. 1994a. Flammulated Owl (*Otus flammeolus*). *in* The birds of North America, No. 93 (A. Poole and F. Gill, eds.). Academy of Natural Sciences of Philadelphia; American Ornithologists Union, Washington, D.C.

———. 1994b. Review of technical knowledge: Flammulated Owls. Pp. 14–46 *in* Flammulated, Boreal, and Great Gray owls in the United States: a technical conservation assessment (G. D. Hayward and J. Verner, eds.). USDA Forest Serv. Gen. Tech. Rept. RM-253.

——— AND F. R. GEHLBACH. 1988. Nest-site preferences of Flammulated Owls in western New Mexico. Condor 90:653-661.

NEWTON, I. 1991. Population limitation in birds of prey: a comparative approach. Pp. 3–21 *in* Bird population studies: relevance to conservation and management (C. M. Perrins, J. D. Lebreton, and G. J. M. Hirons, eds.). Oxford Univ. Press, New York, New York.

REYNOLDS, R. T. AND B. D. LINKHART. 1987a. Fidelity to territory and mate in Flammulated Owls. Pp. 234–238 *in* Biology and conservation of northern forest owls (R. W. Nero, R. J. Clark, R. J. Knapton, and R. H. Hamre, eds.). USDA Forest Serv. Gen Tech. Rep. RM-142.

——— AND ———. 1987b. The nesting biology of Flammulated Owls in Colorado. Pp. 239–248 *in* Biology and conservation of northern forest owls (R. W. Nero, R. J. Clark, R. J. Knapton, and R. H. Hamre, eds.). USDA Forest Serv. Gen. Tech. Rep. RM-142.

——— AND ———. 1990. Longevity records for male and female Flammulated Owls. J. Field Ornithol. 61:243–244.

SAS INSTITUTE. 1988. SAS/STAT user's guide, release 6.03. SAS Institute Inc., Cary, North Carolina.

SOUTHERN, H. N. 1970. The annual control of a population of tawny owls (*Strix aluco*). J. Zool. London 162:197–285.

VAN WOUDENBERG, A. M. 1992. Integrated management of Flammulated Owl breeding habitat and timber harvest in British Columbia. M.S. thesis, Univ. British Columbia, Vancouver, British Columbia.

WILKINSON, L. 1990a. Systat: the system for statistics. Systat Inc., Evanston, Illinois.

———. 1990b. Sygraph: the system for graphics. Systat Inc., Evanston, Illinois.