

Flammulated Owls in Ponderosa Pine: Evidence of Preference for Old Growth¹

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Abstract.—In Colorado, nesting flammulated owls (*Otus flammeolus*) showed a preference for old trees and stands of ponderosa pine and Douglas-fir. Owls more often settled in areas dominated by older forests than young forests when they returned in the spring to nest. Flammulated owls used old trees and forest stands more often for foraging and for defending territories. Individual owls returned more often to territories that were in old stands of ponderosa pine mixed with Douglas-fir compared to territories composed of mosaics of stands of other tree species and ages.

INTRODUCTION

The flammulated owl is a little known migratory owl that occurs in dry, montane coniferous forests in Central and western North America (Bent 1938, Sutton and Burleigh 1940, Johnsgard 1988). The owl is an obligate cavity-nester (Earhart and Johnson 19701, and breeds from the Rocky Mountains to the Pacific Coast Mountains and from southern British Columbia south to Vera Cruz, Mexico (Sutton and Burleigh 1940, Winter 1974, Cannings et al. 1978, Reynolds and Linkhart 1984 1987b, and others). The winter range is thought to be from Guatemala and El Salvador north to Jalisco, Mexico (Phillips 1942). It is possible that some individuals winter in the extreme southern portion of the United States (Phillips et al. 1964, Winter 1979).

Throughout their range flammulated owls are found in the yellow pine belt – from lower elevations where the pine is mixed with oak (*Quercus* spp.) or pinyon pine (*Pinus monophylla*) to the higher elevations where the pine is mixed with firs (*Abies* spp.), Douglas-fir (*Pseudotsuga menziesii*), incense-cedar (*Calocedrus decurrens*), or quaking aspen (*Populus tremuloides*) (Huey 1932, Marshall 1939, Marshall 1957, Johnson and Russell 1962, Phillips et al. 1964, Bull and Anderson 1978, Marcot and Hill 1980, Webb 1982, Reynolds and Linkhart 1984 1987b, McCallum and Ghelback 1988). With the exception of one nest in a pinyon pine stand in the Argus Mountains in California (Huey 19321, all reported nests of the flammulated owl were in forest stands containing at least some yellow pines (subsec. Ponderosae; Critchfield and Little 1966) mixed with one or more of the above tree species. In reports where forests surrounding nests were described or photographed, all nests were in, or adjacent to, mature or old-

growth stands (Hanna 1941, Bull and Anderson 1978, Canning et al. 1978, Hasenyager et al. 1979, Cannings 1982, Bloom 1983, Reynolds and Linkhart 1984 1987b, Fix 1986, Goggans 1985, Hayward 1986, Howie and Ritcey 1987, McCallum and Ghelback 1988). However, Hasenyager et al. (1979) and Bloom (1983) reported nests in forests that had been partially cut but contained large, residual trees, and Winter (1974) found the owl in second-growth forests, although he did not report nesting in this age-class.

Flammulated owls are entirely insectivorous (Ross 1969, Goggans 1985, Hayward 1986, Reynolds and Linkhart 1987b). During cold spring and early summer nights, the owls feed almost entirely on the only insects available – nocturnal adult lepidoptera (Reynolds and Linkhart 1987b). As summer progresses and other arthropods become available, lepidopteran larvae, grasshoppers, spiders, crickets, and beetles are added to the diet (Goggans 1985, Reynolds and Linkhart 1987b).

Habitat selection by birds occurs in an hierarchically ordered series of choices: first, a geographic location must be chosen, then a habitat in which to settle, and finally, specific microhabitats for nesting, foraging, and other activities must be selected (Hilden 1965, Johnson 1980, Hutto 1985). Because movements of a nesting bird are energetically limited to a finite area around its nest, the kinds of microhabitats available are constrained by the first two choices. To determine more clearly the habitat associations of flammulated owls, we began a long-term study (1980-present) of (1) the types of forests into which flammulated owls settled in the spring, (2) the species and age of trees used for territorial defense, foraging, and nesting, (3) the species composition and age of forests in which they forage, (4) their diets and foraging behavior (5) and differences in fidelity to territories in forests of different tree species and ages. The following is a compilation of evidence of preference for older forests in flammulated owls presented originally in Linkhart (1984) and Reynolds and Linkhart (1987a, 1987b, 1990) and in our yet unpublished work.

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STUDY AREA AND METHODS

The study was conducted on 452 ha of the Manitou Experimental Forest in central Colorado. Terrain was moderately steep (20-80% slopes) and elevations ranged from 2,500 to 2,800 m. Forests on the area formed a mosaic of types and ages, the most abundant (75% of area) of which was old-growth (> 200 yrs) ponderosa pine (*Pinus ponderosa*) and Douglas-fir. These mixed ponderosa pine and Douglas-fir stands, which contained scattered limber pine (*P. flexilis*), were mainly on ridge tops and east-, south-, and west-facing slopes. Small (< 3 ha) stands of young (< 100 yr-old) Douglas-fir mixed with blue spruce (*Picea pungens*) (8% of area) as well as mixed stands of mature (100-200 yr-old) quaking aspen and blue spruce (9% of area) were scattered throughout on north- and east-facing slopes. Mature stands of pure quaking aspen (7% of area) were scattered within these three types of forests, but occurred primarily in moist creek bottoms (Linkhart 1984, Reynolds and Linkhart 1987b). Forests surrounding the study area formed a similar mosaic of stand compositions and ages. The study area was located and established as follows: after confirming the presence of some territorial owls, boundaries were drawn to include sufficient area for 10-20 territories based on Marshall's (1939) estimate of territory size (274 m diameter), and nest searches and census for owls were then expanded to the boundaries.

Intensive broadcast censuses and nest searches were conducted in and around the study area each year (May through July) to determine densities and locations of flammulated owls. Territorial fidelity was determined by capturing (and recapturing) all owls and banding them with Fish and Wildlife Service aluminum leg bands (Reynolds and Linkhart 1984). The foraging behavior and habitat use of 7 nesting males (7 of the 9 males that nested on the study area; 1 nest failed, 1 male could not be captured) were intensively studied with radio-telemetry (Reynolds and Linkhart 1984, Linkhart 1984, Reynolds and Linkhart 1987, Linkhart et al. MS.). Each of the 4 forest types within 1) the study area and 2) each of the 7 males' territories was mapped and the amount and proportion of each type in these areas was measured with a planimeter (Linkhart 1984). Locations of foraging and territorial song trees were mapped and the associated forest type, tree species and age (determined with increment borers) were recorded. Species and age of trees used by the owls were compared to 615 trees at random points within the study area. Size of territories and foraging areas were estimated using the minimum convex polygon method (Mohr 1947).

The choice of habitat by owls settling in the spring was examined by comparing the proportion of forest types within territories to the proportion of types available within the study area. The owl's preference of forest type for foraging was determined by comparing the proportional use of forest type by owls to the availability of types within territories.

RESULTS AND DISCUSSION

Study Area vs Territories. A comparison of the proportions of forest types and ages within the study area and within territories showed that the owls settled into areas having greater proportions of old-growth ponderosa pine/Douglas-fir, lesser proportions of young Douglas-fir/blue spruce, and about the same proportions of mature blue spruce/quaking aspen and mature quaking aspen (Table 1) (Linkhart et al. MS).

Table 1. Percent of area of 4 forest types and ages in the study area (452 ha) and in 7 flammulated owl territories (x=14.7 ha) in central Colorado.

Forest Type ¹	Study	
	Area(%) ²	Territories(%)
old-growth PIPO/PSME	58	78
young PSME/PIPU	27	7
mature PIPU/POTR	11	8
mature POTR	3	6

¹ PIPO/PSME = ponderosa pine/Douglas-fir, PSME/PIPU = Douglas-fir/blue spruce, PIPU/POTR = blue spruce/aspen, POTR = aspen.

Habitats Used Within Territories. As in most other raptors, male flammulated owls are the principal food providers for the family. Males mainly gleaned arthropods from needle bunches and the bark of limbs and trunks of large conifers. Occasionally the owls hawked flying insects between tree crowns, or dropped from the lower crown branches to arthropods on the ground (Reynolds and Linkhart 1987b). Mean territories of the 7 males was 14.7 ha (range, 8.5 - 24.0 ha) (Linkhart et al. MS.).

A Bonferroni simultaneous comparison of the frequency of 221 total observations of foraging males in each of the forest types to the availability of the types within territories showed a significant selection for old-growth ponderosa pine/Douglas-fir (190 foraging bouts observed vs. 169 expected), and a significant avoidance of young Douglas-fir/blue spruce (1 observed, 17 expected) and mature quaking aspen (7 observed, 15 expected). Mature blue spruce/quaking aspen was used in about the same proportion as its availability (23 observed, 20 expected) (Linkhart et al. MS.).

Foraging Trees. Of 167 trees in which an arthropod was known to have been captured (excluding cases of hawking and ground foraging), 80 percent were ponderosa pine and Douglas-fir (Table 2). A random sample of 77 of the 167 foraging trees had a mean age of 199 years (range, 72 - 395 yrs), considerably older than the mean of 111 years for 615 trees randomly chosen in the study area.

Song Trees. During territorial-song bouts (periods when males defended territories by singing) males sang from 1 to 10 trees. Males sang from hidden positions next to tree trunks or in dense clumps of foliage. Ponderosa pine and Douglas-fir were the only species used as song trees, and the mean age of 22 of

Table 2. Percent by tree species in which foraging and territorial singing were observed and the percent by species of 615 randomly chosen trees on the study area.

<i>Tree species</i>	<i>Foraging</i>	<i>Song</i>	<i>Available</i>
Douglas-fir	61	50	39
ponderosa pine	19	50	29
quaking aspen	9		17
limber pine	6		10
blue spruce	5		5
total trees (n)	167	22	615

these trees (exact tree unknown in 76 cases) was 289 years (range, 94 - 419 yrs) (Linkhart et al. MS.) (Table 2).

Intensive Foraging Areas. Radio-telemetry data showed that male flammulated owls had favored areas within their territories where they foraged repeatedly (Linkhart et al. MS). Eighty-one percent of 221 total observed foraging attempts occurred in 15 intensive foraging areas (IFAs). IFAs were distributed among the 7 territories as follows: 3 territories contained 2 IFAs, 2 contained 1 IFA, 1 contained 3 IFAs, and 1 contained 4 IFAs. Mean size of the 15 IFAs was 0.5 ha (SD = 0.4, range = 0.1-1.4 ha) and mean total area contained in IFAs in the 7 territories was 1.0 ha (SD = 0.3, range = 0.7-1.5 ha).

The composition of forests within IFAs suggests the importance of old ponderosa pine/Douglas-fir in the foraging of the owl. Thirteen of the 15 IFAs were composed of old-growth ponderosa pine/Douglas-fir (1 of these contained some quaking aspen trees), and 2 IFAs were composed of mature quaking aspen/blue spruce.

Territorial Fidelity. Strong annual fidelity to territory is more common in longer-lived birds that occupy stable habitats (Harvey et al. 1979). Flammulated owls show strong fidelity to their territories. Once they establish a nesting territory, males return every year for what appears to be the remainder of their lives, only rarely moving to an adjacent, unoccupied territory. Females also return to their territories and to their previous year's mate. However, when a female's mate did not return in the spring, it moved to an adjacent territory and paired with an experienced male whose prior mate did not return (Reynolds and Linkhart 1987a, Reynolds and Linkhart 1990). In our 12-year study, all territories that contained contiguous old-growth ponderosa pine/Douglas-fir forest were occupied every year of the study. If an established male did not return in the spring, a new male quickly claimed the territory. In contrast, territories that contained less than 75 percent old-growth ponderosa pine/Douglas-fir, were occupied only as long as the original male returned to nest (1 to 3 years) (Linkhart et al. MS.).

Why Old-growth Ponderosa Pine Forests? The association of flammulated owls and old ponderosa pine/Douglas-fir forests likely involves both habitat composition and structure, and food. The owl is an

obligate secondary cavity nester, and older forests typically contain an abundance of snags and lightning-damaged trees with cavities. Old yellow-pine forests (whether pure or mixed with other species) typically form open stands with well-developed grass or shrub understories. These understories support arthropods in a forest layer that is used extensively by fledged owlets and molting adults in late summer. Although the abundances of lepidoptera and other arthropods in, and the extent to which the species are limited to, ponderosa pine and associated tree species are unknown, many are host-plant specific (Munroe 1979). However, there are up to 4 times as many lepidopteran species associated with Douglas-fir and ponderosa pine than other common western conifers (Furniss and Carolin 1977).

In addition, two common foraging tactics, hawk-glean, hover-glean, are used inside of the crown of trees by the owl (Reynolds and Linkhart 1987b). The interior of large, old ponderosa pine and associated species (e.g., Douglas-fir) are open, exposing large limbs and trunks that provide the owls with perches and access to areas where arthropods feed and rest. The openness of these stands also provides space for hawking flying insects between crowns, and for hover-gleaning them from outer needle bunches (Reynolds and Linkhart 1987b).

Finally, the unique structure of older forests in the northern portion of the owl's range also occurs in pine forests in their winter range (Central America and Mexico). If, in fact, flammulated owls winter in these forests, then the owl may have "fine-tuned" its foraging repertoire to the structure of trees, stands, and foods in these forests through evolutionary time and may have given up the behavioral plasticity required to live in other forests.

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LITERATURE CITED

- Bent, A.C. 1938. Life histories of North American birds of prey, part 2. *U.S. Nat. Mus. Bull.* 167.
- Bloom, P.H. 1983. Notes on the distribution and biology of the flammulated owl. *Western Birds* 14: 49-52.
- Bull, E.L.; and Anderson, R.G. 1978. Notes on flammulated owls in northeastern Oregon. *The Murrelet* 59: 26-27.
- Cannings, R.J. 1982. A flammulated owl nests in a nest box. *Murrelet* 63:66-68.
- Cannings, R.J.; Cannings, S.R.; Cannings, J.M.; Sirk, G.P. 1978. Successful breeding of the flammulated owl in British Columbia. *The Murrelet* 59: 74-75.
- Critchfield, W.B.; Little, E.L. 1966. Geographic distribution of the pines of the world. *Misc. Publ.*

991. Washington, DC: U.S. Department of Agriculture, Forest Service. 97 p.
- Earhart, C.M.**; Johnson, **N.K.** 1970. Size dimorphism and food habits of North American owls. *The Condor* 72: 251-264.
- Furniss, R.L.; **Carolin, V.M.** 1977. Western forest insects. *Misc. Publ.* 1339. U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station. 654 p.
- Fix, D. 1986. Flammulated owls in the western Oregon Cascades. *Oregon Birds* 13: 38-40.
- Goggans, R.** 1985. Habitat use by flammulated owls in northeastern Oregon. Corvallis, OR: Oregon State University. 54 p. M.S. thesis.
- Hanna, W. C. 1941. Nesting of the flammulated screech owl in California. *The Condor* 43: 290-291.
- Harvey, P.H.; Greenwood, P.J.; Perrins, C.M. 1979. Breeding area fidelity of great tits (*Parus major*). *Journal of Animal Ecology* 48: 305-313.
- Hasenyager, R.N.; Pederson, J.C.; Haggen, A.W. Haggen. 1979. Flammulated owl nesting in a squirrel box. *Western Birds* 10: 224.
- Hayward, G.** 1986. Activity pattern of a pair of nesting flammulated owls (*Otus flammeolus*) in Idaho. *Northwest Science*. 60: 141-1444.
- Hildén, O.** 1965. Habitat selection in birds: a review. *Annales Zoologici Fennici*. 2: 53-75.
- Howie, R.R.; Ritcey, R. 1987. Distribution, habitat selection, and densities of flammulated owls in British Columbia. In: *Biology and Conservation of northern forest owls: proceedings of the symposium; 1987 February 3-7; Winnipeg, Manitoba*. Gen. Tech. Rep. RM-142. U.S. Department of Agriculture, Forest Service: 249-254.
- Huey, L.M. 1932. Two noteworthy records for California. *Auk* 49: 107.
- Hutto, R.L.** 1985. Habitat selection by nonbreeding, migratory land birds. In: M.L. Cody, ed. *Habitat selection in birds*. Orlando, FL.: Academic Press, Inc.: 455-476.
- Johnsgard, P.A. 1988. North American owls. Smithsonian Institution Press, Washington, D.C. 304 p.
- Johnson, D.H. 1980. The comparison of usage and availability measurements for evaluating resource preference. *Ecology* 61: 65-71.
- Johnson, **N.K.**; Russell, W.C. 1962. Distribution data on certain owls in the western Great Basin. *The Condor* 64: 513-514.
- Linkhart, B.D. 1984. Range, activity and habitat use by nesting flammulated owls in a Colorado ponderosa pine forest. Fort Collins, CO: Colorado State University. 45 p. M.S. thesis.
- Linkhart, B.D.; Reynolds, R.T. 1987. Brood division and postnesting behavior of flammulated owls. *Wilson Bulletin*. 99: 240-243.
- Linkhart, B.D.; Reynolds, R.T.; Ryder, R.A. Home ranges and habitat use by flammulated owls in Colorado. Unpublished manuscript.
- Marcot, B.G.**, Hill, R. 1980. Flammulated owls in northwestern California. *Western Birds*. 11: 141-149.
- Marshall, J.T., Jr. 1939. Territorial behavior of the flammulated screech owl. *The Condor*. 41: 71-78.
- Marshall, J.T., Jr. 1957. Birds of pine-oak woodland in southern Arizona and adjacent Mexico. *Pacific Coast Avifauna*. 32: 1-125.
- McCallum, D.A.**; Gehlach, F.R. 1988. Nest-site preferences of flammulated owls in western New Mexico. *The Condor*. 90: 653-661.
- Mohr, C.O. 1947. Table of equivalent populations of north American small mammals. *American Midland Naturalist*. 37: 233-249.
- Munroe, E. 1979. Lepidoptera. In: H.V. Danks, ed. *Canada and its insect fauna*. Ottawa, Canada: Entomological Society of Canada, No. 108: 427-481.
- Philips, A.** 1942. Notes on the migrations of the elf and flammulated screech owls. *Wilson Bulletin*. 54: 132-137.
- Phillips, A; Marshall, J.T.; Monson, G. 1964. The birds of Arizona. **Tucson, AZ**: University of Arizona Press. 212 p.
- Reynolds, R.T.; Linkhart, B.D. 1984. Methods and materials for capturing and monitoring flammulated owls. *Great Basin Naturalist*. 44: 49-51.
- Reynolds, R.T.; Linkhart, B.D. 1987a. Fidelity to territory and mate in flammulated owls. In: *Biology and Conservation of northern forest owls: proceedings of the symposium; 1987 February 3-7; Winnipeg, Manitoba*. Gen. Tech. Rep. RM-142. U.S. Department of Agriculture, Forest Service: 234-238.
- Reynolds, R.T.; Linkhart, B.D. 1987b. The nesting biology of flammulated owls in Colorado. In: *Biology and conservation of northern forest owls: proceedings of the symposium; 1987 February 3-7; Winnipeg, Manitoba*. Gen. Tech. Rep. RM-142. U.S. Department of Agriculture, Forest Service: 239-248.
- Reynolds, R.T.; Linkhart, B.D. 1990. Extra-pair copulation and extra-range movements in flammulated owls. *Ornis Scandinavica*. 21: 74-77.
- Ross, A. 1969. Ecological aspects of the food habits of insectivorous screech owls. *Proceedings Western Foundation Vertebrate Zoology*. 1: 301-344.
- Sutton, G.M.; Burleigh, T. D. 1940. Birds of Las **Vigas, Vera Cruz**. *The Auk* 57: 234-243.
- Webb, B. 1982. Distribution and nesting requirements of montane forest owls in Colorado. *Pat. III: flammulated owl (Otus flammeolus)*. *Colorado Field Ornithology Journal*. 16: 76-81.
- Winter, J. 1974. The distribution of the flammulated owl in California. *Western Birds*. 5: 25-44.