



Territories of Flammulated Owls (*Otus flammeolus*):
Is Occupancy a Measure of Habitat Quality?

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Abstract.—Annual territory occupancy by Flammulated Owls (*Otus flammeolus*) in Colorado was evaluated from 1981-1996. Fourteen territories occurred within a 452 ha study area. Each year, three to six territories were occupied by breeding pairs and three to seven were occupied by unpaired males. Territories were occupied by breeding pairs a mean of 5.1 years (not necessarily consecutive) and by unpaired males a mean of 3.9 years (not necessarily consecutive). Territories most consistently occupied by breeding pairs contained the highest percentage of old (200-400 years) ponderosa pine / Douglas-fir, whereas territories least occupied by breeding pairs contained the least amount of this vegetation type.

Little is known about habitat selection in the Flammulated Owl (*Otus flammeolus*), an insectivorous and migratory species (Balda et al. 1975, Phillips 1942, Ross 1969). The owl is an obligate cavity-nester (Linkhart and Johnson 1970) and commonly breeds in ponderosa pine (*Pinus ponderosa*), Jeffrey pine (*P. jeffreyi*), and mixed-conifer forests of western North America (Cannings et al. 1978; Reynolds and Linkhart 1984, 1987; Sutton and Burleigh 1940; Winter 1974).

A model proposed by Fretwell and Lucas (1970) suggested that in stable, heterogeneous environments, birds first settle into high-quality habitats (i.e., habitats in which birds have the highest reproductive success) until these habitats are saturated, then settle into habitats of poorer quality where reproduction may be lower. We examined this model of habitat selection by associating habitat conditions in territories with the extent to which territories were occupied by Flammulated Owls. Our hypothesis is that territories occupied by breeding pairs every year are the highest quality, and the poorer-quality territories are occupied only occasionally by breeding adults. We have assumed that over the study the relative quality of territories changed little, and territory boundaries remained relatively stable.

Here we rank 14 territories on the number of years each was occupied by breeding owls, and describe differences in forest overstories within territories according to the ranking.

STUDY AREA

The 452 ha study area was located in central Colorado on the Manitou Experimental Forest, Teller County. Boundaries of the study area were established during initial surveys in 1980 to include approximately 15 to 20 territorial Flammulated Owls. Forests within the study area consisted of (1) ponderosa pine mixed with Douglas-fir (*Pseudotsuga menziesii*), generally on ridgetops and south- and west-facing slopes; (2) quaking aspen (*Populus tremuloides*) stands, on the bottoms and lower slopes of moist drainages; (3) quaking aspen stands mixed with blue spruce (*Picea pungens*), in bottoms, lower slopes, and benches in moist areas; and (4) Douglas-fir mixed with blue spruce, at higher elevations and on north-facing slopes. Tree cutting on the study area had not occurred since the 1880's, when a light harvest for railroad ties occurred. There were a mean of 1.3 snags and live trees with cavities per hectare in the study area (Reynolds et al. 1985). The study area was surrounded by forests composed of a similar mix of forest types and ages.

METHODS

The study was conducted from May to September, 1981-1996. Each spring and summer, we searched the entire study area for territorial

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males (Marshall 1939). Territories were identified by marking territorial song-tr ees of males (Reynolds and Linkhart 1984), and by using radio-telemetry during 1982-1983 (Linkhart 1984). Once territory boundaries were delineated, we located all suitable nesting cavities (tree cavities with entrance diameters >4 cm) within territories and checked each for nesting owls (Reynolds and Linkhart 1984). Adults were captured at nests (occasionally on perches or day roosts) and banded with U.S. Fish and Wildlife Service leg bands (Reynolds and Linkhart 1984). Non-nesting owls were not usually captured. Each year, we determined the breeding status of all territorial males by searching for nests and monitoring the owls' behavior. Unpaired males typically sang throughout the breeding season, whereas singing in breeding males dramatically declined after the pairs' eggs hatched (Reynolds and Linkhart 1987). A total of 69 adults (32 males and 37 females) were banded on the study area in the 16 years.

Four forest types, distinguished by plurality of tree species and age (determined with increment borer) of overstory, occurred in the study area: old (200-400 years) ponderosa pine/Douglas-fir; mature (100-200 years) quaking aspen/blue spruce; mature (75-125 years) quaking aspen; and young (<100 years) Douglas-fir/blue spruce. A meadow (grass/forbs) vegetation type was also identified on the study area. Areas of each type greater than 0.1 ha were delineated on aerial photographs (scale 1:1,000) of the study area. A circle with radius of 212 m (mean radius for territories of Flammulated Owls delineated by radio-telemetry (Linkhart 1984) was inscribed on aerial photographs corresponding to the area defended by each territorial male. The percent area occupied by vegetation types in each "habitat circle" was determined by overlaying an acetate grid (2 x 2 mm = 10 x 10 m ground-equivalent, 660 total grid squares) on the inscribed circle and counting the number of squares fully occupied by each vegetation type. Portions (20-50 percent) of habitat circles for four territories (A2, A7, A13, and A20) extended beyond the bounds of the study area; for these habitat circles, we calculated percentages of vegetation types that occurred only within the study area (vegetation types were not delineated outside of the study area). One territory (A40) was excluded from analysis because its occupancy status was only determined in 1995 and 1996.

We determined the occupancy status (breeding pair, unpaired male, or unoccupied) of all territories each year from 1981-1996. Frequency of occupancy status was compared among territories using a contingency table. We used Spearman rank correlation (Snedecor and Cochran 1967) to determine if the number of years territories were occupied by breeding pairs was correlated with the percent of vegetation types within habitat circles. The null hypothesis was no correlation of occupancy with vegetation types. For all tests, results were significant if $P < 0.05$.

RESULTS

Fourteen territories occurred on the study area from 1981-1996 and each was occupied by breeding pairs and unpaired males a mean of 8.9 years (SD = 4.6, range = 3-16 years) (years not necessarily consecutive) (table 1). Each year three to six territories were occupied by breeding pairs and three to seven territories were occupied by unpaired males. Most territories remained relatively fixed in space over the 16 year study, with two notable exceptions. The A24 territory was only occupied from 1981-1983. In 1984, the male in an adjacent territory (A29) expanded his movements and activities into much of the area formerly in A24 territory. A portion of A15 territory, only occupied from 1981-1984, was incorporated in the same manner in 1985 by the A8 male.

Territories were occupied by breeding pairs a mean of 5.1 years (SD = 4.1, range = 0-14 years) (years not necessarily consecutive) (table 1). Rate and type of occupancy differed among territories ($\chi^2 = 95.6$, d.f. = 22, $P < 0.001$). Two territories (A4 and A29) were occupied by breeding pairs for 12 or more years, while eight territories (A12, A7, A15, A24, A18, A27, A20, and A2) were occupied by breeding pairs for 4 or fewer years (table 1). Territories were occupied by unpaired males a mean 3.9 years (SD = 3.0, range = 0-10 years) (years not necessarily consecutive) (table 1). Two territories (A12 and A18) were occupied by unpaired males 9 or more years and two (A15 and A24) were never occupied by unpaired males (table 1). Six territories (A12, A7, A18, A27, A20, and A2) were occupied more often by unpaired males than breeding pairs (table 1).

Territories occurred throughout the study area and the mean percent vegetation composition



Table 1.—Number of years territories were occupied by Flammulated Owls (*Otus flammeolus*) in Colorado, 1981-1996.

Territory	Number of years occupied by		Total years occupied
	Breeding pairs	Unpaired males	
A4	14	1	15
A29	12	4	16
A8	7	6	13
A11	7	4	11
A13	7	2	9
A10	6	3	9
A12	4	9	13
A7	3	5	8
A15 ¹	3	0	3
A24 ²	3	0	3
A18	2	10	12
A27	2	5	7
A20	1	2	3
A2	0	3	3
MEAN	5.1	3.9	8.9
SD	4.1	3.0	4.6

¹ Not occupied after 1984 when A8 male expanded his territory into portions of A15.

² Not occupied after 1983 when A29 male expanded his territory into most of A24.

within habitat circles was similar to the per cent vegetation composition of the entire study area (table 2). Thus, Flammulated Owls appeared to use all available habitats within the study area (sensu Fretwell and Lucas 1970). However, individual habitat circles contained from 27 to 94 percent old ponderosa pine/Douglas-fir. Four habitat circles (A4, A15, A24, and A29) contained more than 75 percent old ponderosa pine/Douglas-fir, while five habitat circles (A12, A18, A27, A20, and A2) contained less than 50 percent of this type (table 2). Habitat circles also contained from 0 to 65 percent young Douglas-fir/blue spruce, and four habitat circles (A12, A18, A20, and A2) contained more than 45 percent of this type, while eight habitat circles (A4, A29, A8, A11, A10, A7, A15, and A24) contained less than 10 percent (table 2).

Occupancy of territories by breeding pairs was positively correlated with the amount of old ponderosa pine/Douglas-fir in habitat circles ($r_s = 0.75$, $P < 0.01$, $n = 12$), and was negatively correlated with the amount of young Douglas-fir/blue spruce in habitat circles ($r_s = -0.72$, $P <$

0.01 , $n = 12$) (A15 and A24 were omitted from the rank correlation, since these territories were subsumed by males in adjacent territories). Thus, territories most frequently occupied by breeding pairs had habitat circles containing the highest percentages of old ponderosa pine/Douglas-fir and the least percentages of young Douglas-fir/blue spruce. Occupancy of territories by breeding pairs was not correlated with mature blue spruce/quaking aspen ($r_s = -0.04$, $P = 0.90$, $n = 12$), mature quaking aspen ($r_s = 0.49$, $P = 0.11$, $n = 12$), or meadow ($r_s = 0.45$, $P = 0.20$, $n = 12$), in habitat circles.

DISCUSSION

We distinguished three categories of years that breeding pairs occupied territories: (1) 12 or more years, (2) 6 and 7 years, and (3) 4 or fewer years. Territories occupied 12 or more years (A4 and A29) had habitat circles containing more than 75 percent old ponderosa pine/Douglas-fir, with less than 13 percent of any other vegetation type. Territories occupied for 6 and 7 years (A8, A11, A13, and A10) had habitat circles containing 54-74 percent old ponderosa pine/Douglas-fir, with up to 35 percent of the other vegetation types. Territories most often occupied by unpaired males and rarely by breeding pairs (A12, A7, A18, A27, A20, and A2) had habitat circles containing 27 to 68 percent old ponderosa pine/Douglas-fir, with up to 65 percent of the other vegetation types. Two territories, A15 and A24, were occupied for only 3 years by breeding pairs and had habitat circles containing more than 78 percent old ponderosa pine/Douglas-fir. However, portions of these territories were taken over by adjacent territorial males (A8 and A29, respectively) in 1984 (A24) and 1985 (A15).

Territories that were occupied by breeding pairs most of the 16 years also produced the most owlets (> 16 total young, unpubl. data) over the study. These territories likely confer the greatest fitness to individuals and may act as sources of owls to occupy other habitats (sensu Pulliam 1988). Territories that were most often occupied by non-breeding owls produced the fewest owlets (< 8, unpubl. data), and may act as sinks for the population (sensu Pulliam 1988).

Our long-term data suggests that territory occupancy may be an indicator of habitat quality for Flammulated Owls. Old ponderosa

Table 2.—Percent vegetation composition in Flammulated Owl (*Otus flammeolus*) habitat circles in Colorado, ranked by number of years territories were occupied by breeding pairs, 1981-1996.

Territory	Old (200-400 yr) ponderosa pine/ Douglas-fir	Young (<100 yr) Douglas-fir/ blue spruce	Mature (100-200 yr) blue spruce/ quaking aspen	Mature (75-125 yr) quaking aspen	Meadow
A4	94	0	0	6	0
A29	76	3	12	6	3
A8	72	7	0	16	5
A11	55	6	33	6	0
A13 ¹	54	35	11	0	0
A10	74	5	21	0	0
A12	32	46	18	4	0
A7 ¹	68	0	0	32	0
A15 ²	87	7	0	6	0
A24 ³	79	2	8	11	0
A18	27	65	8	0	0
A27	42	41	17	0	0
A20 ¹	36	51	12	1	0
A2 ¹	49	47	4	0	0
Mean	60	23	10	6	1
SD	21	23	10	9	2
Study Area	58	27	11	3	1

¹ Percent overstory in habitat circles (see text) presented only for the proportion of circles occurring within the study area.

² Not occupied after 1984 when A8 male expanded his territory into portions of A15.

³ Not occupied after 1983 when A29 male expanded his territory into most of A24.

pine/Douglas-fir appears to be the best breeding habitat for the owls; territories most consistently occupied by breeding pairs had habitat circles containing the highest percentage of this vegetation type, while territories least occupied by breeding pairs had habitat circles containing the least amount of this vegetation type. Breeding by owls occurred less often in territories where habitat circles contained higher percentages of young Douglas-fir/blue spruce. Other vegetation types (mature blue spruce/quaking aspen, mature quaking aspen, and meadow) occurring in habitat circles were not correlated with the number of years territories were occupied by breeding pairs. The extent to which territory occupancy is an indicator of habitat quality in Flammulated Owls requires corroboration by correlating habitat structure and floristics with other demographic parameters, such as reproduction, survival, tenure, and fidelity of owls on territories.

A correlation between territory occupancy and territory quality was found in other birds. Territories most often occupied by breeding pairs contained the highest-quality habitats in black-billed Magpies (*Pica pica*) (Baeyens 1981), Bobolinks (*Dolichonyx oryzivorus*) (Bollinger and Gavin 1989), Tengmalm's Owl (*Aegolius funereus*) (Korpimäki 1988), and European Sparrow-hawks (*Accipiter nisus*) (Newton and Marquiss 1976, 1982).

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