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HOME RANGE AND HABITAT OF BREEDING FLAMMULATED OWLS IN COLORADO

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ABSTRACT.—We used radiotelemetry to determine habitat use by Flammulated Owls (*Otus flammeolus*) during the breeding season on 452 ha of montane conifer forest in central Colorado in 1982–1983. Mean size and SD of home ranges was 11.1 ± 1.9 ha (range = 8.5–12.5 ha, n = 4) in 1982 and 18.3 ± 5.1 ha (range = 14.0–24.0 ha, n = 3) in 1983. Habitat use by nesting males was affected by distribution of old forests of ponderosa pine (*Pinus ponderosa*) mixed with Douglas-fir (*Pseudotsuga menziesii*), by topography, and by juxtaposition of home ranges of conspecifics. In spring, both new and returning owls settled into areas containing more old ponderosa pine/Douglas-fir than in other overstory types available in the study area. After settling, males foraged significantly more often in old ponderosa pine/Douglas-fir than in other overstory types available within home ranges. Eighty-one percent of foraging locations by males occurred in one to four intensive foraging areas within each home range. Mean size of intensive foraging areas was 0.5 ± 0.4 ha (range = 0.1–1.4 ha). Eighty percent of intensive foraging areas consisted entirely of old ponderosa pine/Douglas-fir. Use of this overstory type by Flammulated Owls is probably related to its composition and structure, and prey availability.

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When settling into landscapes birds must distinguish among available habitats, each of which may differ in quantity and quality of requisite resources (Fretwell and Lucas 1970). Habitat selection during settling likely involves an hierarchically-ordered series of choices during which a bird selects a geographic area (first-order), types of habitat in which the territory is established (second-order), and specific microhabitats for activities such as nesting, foraging, and roosting (third-order; Johnson 1980). At each order of selection a species may use different criteria for discriminating among available habitats. Western Kingbirds (*Tyrannus verticalis*), for example, may select territories on the basis of maximum canopy height, and nest-sites (microhabitats) on the basis of tree characteristics (Bergin 1992). Habitats selected at each order are limited by the preceding choice because movements of breeding birds are energetically limited to some finite area around nests. Descriptions of habitat are therefore scale-dependent (Wiens 1986, Kotliar and Wiens 1990) and focusing on a single order may preclude discerning patterns at other orders (Maurer 1985). Understanding a species' habitat selection requires the consideration of choices at each scale.

The breeding range of Flammulated Owls (*Otus flammeolus*) is from the Rocky Mountains to the Pacific Coast Mountains (except Oregon and Washington) and from south-central British Columbia to Veracruz, Mexico (McCallum 1994). Flammulated Owls are migratory and may winter from the southern United States to as far south as El Salvador (Phillips et al. 1964, American Ornithologists' Union 1983). Habitats within home ranges of Flammulated Owls have not been compared to habitats available within landscapes. Nesting Flammulated Owls have been reported in yellow pine [subsect. *Ponderosae* (Critchfield and Little 1966)] and mixed-conifer forests. These forests were often mixed with oak (*Quercus* sp.) or pinyon (*Pinus edulis*) at lower elevations, and fir (*Abies* sp.), Douglas-fir (*Pseudotsuga menziesii*), or quaking aspen (*Populus tremuloides*) at higher elevations (e.g., Marshall 1957, Bull and Anderson 1978, Richmond et al. 1980, Goggans 1986, Reynolds and Linkhart 1987, McCallum and Gehlbach 1988). Nesting Flammulated Owls were occasionally found in pinyon (Huey 1932) and Douglas-fir forests (Howie and Ritcey 1987, Powers et al. 1996).

We determined habitat selection by Flammulated Owls at multiple scales by comparing forests within owl home ranges to forests

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available in a landscape, and by comparing the owls' use of forest types and ages to availability of these within owl home ranges. We also describe the size, shape, and juxtaposition of nesting home ranges, and the species and age of trees used by the owls during foraging, territorial singing, day-roosting, and resting.

STUDY AREA AND METHODS

We established boundaries of the 452 ha study area on the Manitou Experimental Forest, Teller Co., Colorado during initial surveys (1980) for territorial Flammulated Owls. After we confirmed the presence of owls, boundaries were arbitrarily drawn around an area large enough to contain approximately 20 territorial males, based on an estimate of territory size for this species (274 m in diameter; Marshall 1939). We then conducted searches for territorial males and their nests (Reynolds and Linkhart 1984) within the boundaries from 1981–1983. Forests within the study area consisted of (1) ponderosa pine (*Pinus ponderosa*) mixed with Douglas-fir, generally on ridgetops and south and west facing slopes, (2) quaking aspen stands on lower slopes and bottoms 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, on higher slopes in drainages and on north facing slopes. Tree cutting on the study area had not occurred since the 1880s, when cuts were made for railroad ties. Snags and trees with cavities were relatively abundant throughout the study area (Reynolds et al. 1985). The forest understory, consisting of over 100 species of grasses, forbs, and shrubs, was poorly developed in all but the moist creek bottoms (Reynolds et al. 1985). Terrain was moderately steep (20–80% slope) and elevations ranged from 2550–2855 m. Annual precipitation was 40–45 cm. Daily high temperatures from June to September averaged 19° C and low temperatures averaged 5° C (Reynolds and Linkhart, unpubl. data). The study area was imbedded within forests composed of a similar mix of overstory types and ages.

We conducted the study from mid-May (pair formation) to late July (fledging of young) in 1982 and 1983. Movements and behaviors of owls after fledging of young were reported by Linkhart and Reynolds (1987). Male owls were captured at nests, banded with U.S. Fish and Wildlife Service leg bands, and equipped with tail-mounted or backpack-mounted radio transmitters (Reynolds and Linkhart 1984). Transmitter mass was 2.3–2.6 g, 4–5% of adult mass (male $\bar{x}$ = 55 g, n = 27; Reynolds and Linkhart 1987), and we detected transmitter signals up to 800 m. During the two study years, nine males nested on the study area and we studied seven of these with telemetry. One male (A4-82) was not radio-tagged because his nest was inaccessible, and another male (A24-83) abandoned his nest before he could be captured. Portions of the home ranges of five additional males occurred on the periphery of the study area; behavior of these males indicated they were not nesting (Reynolds and Linkhart 1987) and none was radio-tagged.

TABLE 1. Number of locations associated with four activities of seven radio-tagged Flammulated Owls in Colorado, 1982–1983.

	Activity				
Home range	Foraging	Day-roosting	Territorial singing	Resting	Total locations
A10-82	25	9	8	0	42
A15-82	27	9	9	2	47
A24-82	35	12	3	8	58
A29-82	35	5	10	5	55
A4-83	36	31	39	0	106
A11-83	42	20	9	5	76
A29-83	21	26	23	4	74
Total	221	112	101	24	458

We radio-tagged males after egg-laying (early June). Prior to using telemetry, we recorded locations of males observed in territorial song. We monitored the movements and behaviors of radio-tagged males by following them with a handheld radio-receiver and yagi antenna. When we first visually located a radio-tagged male, we assigned his behavior to one of the following activities: foraging, territorial singing, day-roosting, or resting. We defined foraging as an observed attempt by an owl to capture prey. Foraging attempts were nearly always followed by prey deliveries to nests (see below). We observed each owl's behavior for 1–3 h at a time, aided by flashlight or by silhouetting the owl against the sky. A stationary observer equipped with a two-way radio at the nest of the focal owl reported arrival, departure, and flight direction of the departing owl to a similarly-equipped mobile observer (always Linkhart).

In 1982, we monitored the movements of four nesting males during 52 h of observation (36% between 20:00–21:59 MST; 44% between 22:00–23:59; 20% between 24:00–01:59). In 1983, we monitored the movements of three nesting males during 45 h (40% between 20:00–21:59; 47% between 22:00–23:59; 13% between 24:00–01:59). During the two years, we recorded a total of 458 locations—202 locations in 1982 and 256 locations in 1983 (Table 1).

We mapped and plotted all foraging, territorial singing, day-roosting, and resting locations of males on aerial photographs (scale 1:1000) of the study area. Home ranges of owls were determined with the minimum convex polygon (MCP; Mohr 1947) and the area within home ranges was determined with a planimeter. On occasion, radio-tagged males intruded into the home ranges, often to the nests, of neighboring pairs (Reynolds and Linkhart 1990). We excluded these extra-range movements from the MCP determination of home ranges. To determine the sufficiency of our radio-telemetry sampling, we plotted the cumulative MCP area, using five sequential locations at a time, against the number of locations for each radio-tagged

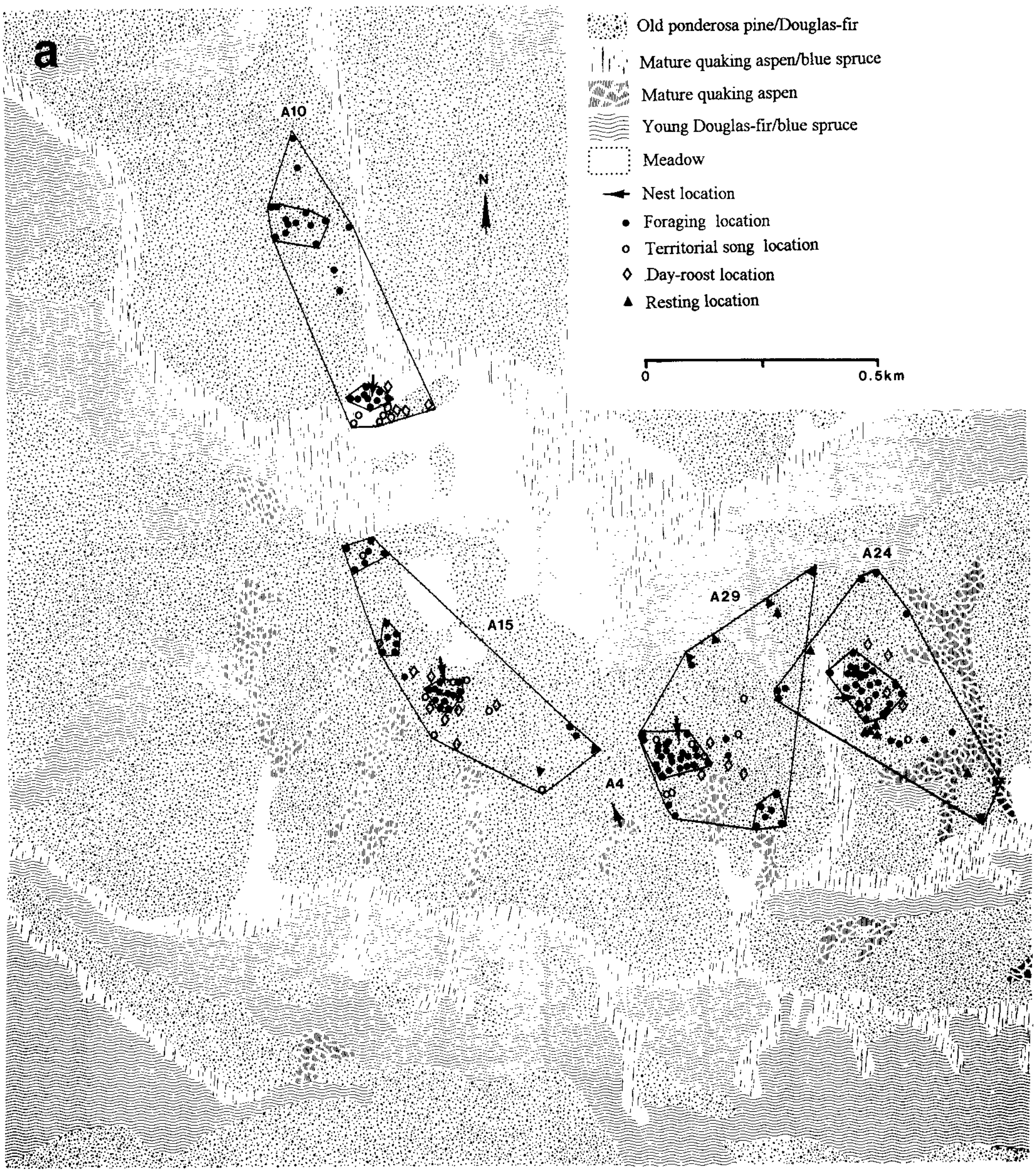

FIG. 1. Home ranges, intensive foraging areas (enclosed areas within home ranges), nests, and radio-telemetry locations of Flammulated Owls with respect to overstory types in (a) 1982 and (b) 1983. The study area is the entire area shown.

male. Asymptotes in these plots were attained in 30–80 locations (Linkhart 1984).

Five vegetation types, distinguished by overstory species, 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; young (<100 years) Douglas-fir/blue spruce; and meadow. We estimated age of overstory trees by aging (with increment borer) 130 representative overstory trees, selected approximately proportional to the area of each overstory type on the study area. We delineated areas of an overstory type greater than 0.1 ha on the aerial photographs of plotted locations, and determined total area of each type with a planimeter. We then summed foraging locations in each overstory type.

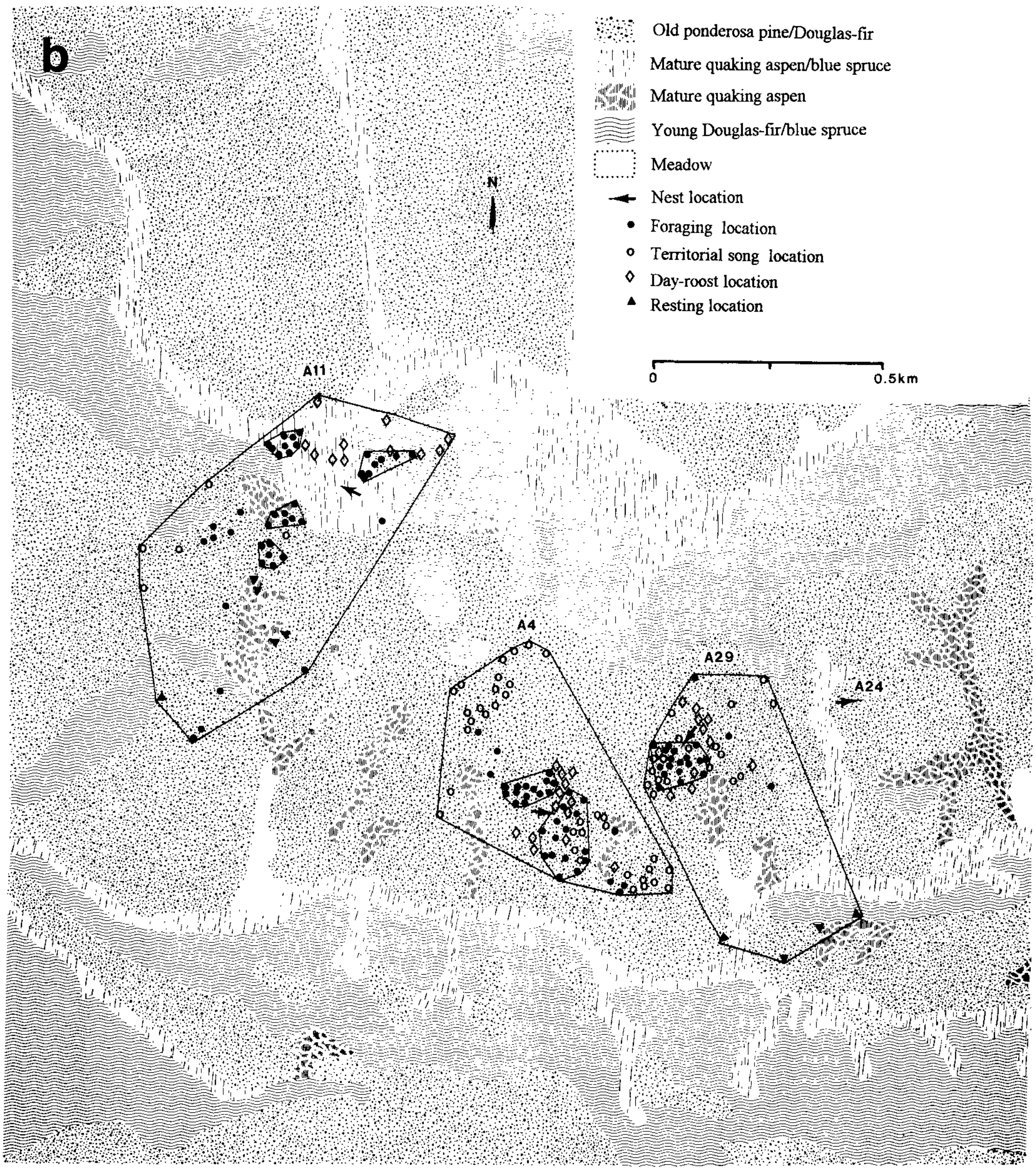

FIG. 1. Continued.

We examined the owls' choices of habitat at the second-order of selection (establishment of home range) by comparing the proportional area of overstory types within home range boundaries to the proportional area of types available within the study area. For this comparison, we established 95% confidence intervals on the mean proportions of each overstory type within the seven home ranges. Our investigation of the owls' third-order habitat selection focused on habitats used for foraging. We determined choice of overstory type for foraging by comparing the proportional use of overstory types by owls to the availability of types within home ranges. Selection for overstory types was determined with a χ^2 goodness-of-fit test and Bonferroni simultaneous intervals (Neu et al. 1974). We lumped locations for all males (n = 7) for the preference analysis because number of locations of each male was insufficient for individual analyses. An attempt to use compositional analysis (Aebischer et al. 1993) failed because signs of log-ratio differences were not the same and too few males were studied. In addition, we describe trees used for foraging, territorial singing, day-roosting, and resting.

The evaluation of habitat use requires sample periods that are long enough to allow an animal to visit available habitats and enough time between successive locations for the animal to depart a habitat. That is, successive locations should be independent (Swihart et al. 1988). We examined independence among an owl's successive foraging locations with Schoener's t^2/r^2 ratio (where t = time between locations and r = variance; Schoener 1981, Swihart and Slade 1985).

Finally, because foraging locations of Flammulated Owls tended to be aggregated, we used a cluster analysis (Ball and Hall 1967) to help quantify and delineate areas used repeatedly. We gridded (10 m × 10 m) the study area on the aerial photographs of plotted locations and referenced foraging locations to their nearest grid corners. The cluster program ISODATA, which locates nearest neighbors (Euclidian distance) by progressively subdividing a single large cluster (all home ranges in a year) into smaller clusters, was used in separate runs for the 1982 and 1983 foraging locations. For each prospective cluster, we ceased iterations when the next iteration subdivided the cluster that was obvious on aerial photos and on the ground. The within-cluster mean squared errors at this iteration ranged from 3.4 to 26.7 ($\bar{x}$ = 14.9 ± 7.0 SD) for 15 clusters in seven home ranges. Because we defined repeated foraging as six or more locations, clusters identified in the final iteration that had fewer than six foraging locations were rejected. We delineated clusters with the MCP method and measured areas with a planimeter; we refer to these areas as intensive foraging areas (IFAs). We calculated distances from IFAs to respective nests from IFA centroids.

RESULTS

The effects of radio-transmitters on Flammulated Owls appeared to be negligible. Owls returned to normal activity within 30 min of release and there was no evidence that nesting was impaired. For example, 5 broods (excluding 2 nests where brood size could not be determined) whose adult males were radio-tagged had a mean 2.6 ± 0.6 nestlings of bandable age, whereas 59 broods whose adult males were not radio-tagged (same study area, 1981–1997) had a mean 2.1 ± 1.0 nestlings (Linkhart and Reynolds, unpubl. data).

Home range.—While some home ranges shared common boundaries, especially along ridgetops, there was little overlap of MCP home ranges (Fig. 1). In the single case where the same male's home range was determined in both years (A29), the shapes of the home ranges differed because the male used different areas for resting (same nest used in both years; Fig. 1). Excluding extra-range movements (16 cases; Reynolds and Linkhart 1990), the maximum distance we observed any owl from its nest was 636 m (A11-83, foraging).

We recorded fewer total locations for males in 1982 ($\bar{x}$ = 50 ± 7 locations/home range) than in 1983 ($\bar{x}$ = 85 ± 18 locations/home range) as a result of differences in the timing and focus of sampling between years and seasonal changes in male behavior (Table 1). We monitored singing males a total of 10 h (54%) less in the period prior to egg-hatching in 1982 than in 1983. Because of this, and because breeding males sang more frequently prior to egg-hatching (Reynolds and Linkhart 1987), we recorded fewer territorial song locations per home range in 1982 (excepting A11-83; Table 1). We also recorded fewer day-roosting locations per home range in 1982 because telemetry began 9 days later (5 days prior to egg-hatching) in this year, and only radio-tagged males could be located on day roosts. Number of foraging and resting locations per home range changed little between years because most were determined after egg-hatching, a period similarly sampled in both years.

Measured home range sizes (Table 2) were significantly smaller in 1982 ($\bar{x}$ = 11.1 ± 1.9 ha) than in 1983 ($\bar{x}$ = 18.3 ± 5.1 ha; $t = 2.65$, df = 5, $P = 0.04$), probably because of less sampling effort in 1982. Proximity of some territorial song locations to home range boundaries, especially in 1983 (Fig. 1), suggests that Flammulated Owls defended type A territories (Hinde 1956).

Second-order habitat selection.—Of the five overstory types on the study area, old ponderosa pine/Douglas-fir was the most common (58% of total area), followed by young Douglas-fir/blue spruce (27%), mature quaking aspen/blue spruce (11%), mature quaking aspen (3%), and meadow (1%) (Table 2, Fig. 1).

Nests in five of the seven home ranges (A15-82, A24-82, A29-82, A4-83, and A29-83) were on the south facing slope of a main ridge in the study area. Overstories within these five home ranges were primarily old ponderosa pine/Douglas-fir ($\bar{x}$ = 84 ± 7% of home ranges, range = 74–92%; Table 2, Fig. 1). Nests in two home ranges (A10-82 and

TABLE 2. Overstory composition of study area (452 ha) and home ranges of Flammulated Owls in Colorado, 1982–1983.

	Home range size	Old[a] ponderosa pine/Douglas fir		Young[b] Douglas-fir/ blue spruce		Mature[c] quaking aspen/ blue spruce		Mature[d] quaking aspen		Meadow	
	ha	ha	%	ha	%	ha	%	ha	%	ha	%
Study Area		264	58	122	27	47	11	14	3	5	1
A10-82	8.5	6.2	73	0.4	5	1.9	22	—	—	—	—
A15-82	11.0	9.8	89	1.2	11	—	—	—	—	—	—
A24-82	12.5	10.1	81	0.1	1	0.8	6	1.5	12	—	—
A29-82	12.5	10.7	85	1.2	10	—	—	0.6	5	—	—
A4-83	14.0	12.9	92	—	—	—	—	1.1	8	—	—
A11-83	24.0	13.2	55	3.5	14	5.0	21	2.3	10	—	—
A29-83	17.0	12.5	74	1.2	7	1.3	8	1.3	7	0.7	4
$\bar{x}$ within home ranges	14.2	10.8	78	1.1	7	1.3	8	1.0	6	0.1	<1
SD within home ranges	5.0	2.4	13	1.2	5	1.8	10	0.8	5	0.3	2

[a] 200–400 years.
[b] <100 years.
[c] 100–200 years.
[d] 75–125 years.

A11-83) were in creek bottoms in mature quaking aspen/blue spruce. The home ranges of the latter males were comprised of 73% and 55% old ponderosa pine/Douglas-fir, respectively. Compared to the proportion of each overstory type within the study area (Table 2), the seven home ranges contained a mean 20% (95% confidence interval ± 12%) more old ponderosa pine/Douglas-fir, 20% (±5%) less young Douglas-fir/blue spruce, and similar amounts of mature quaking aspen/blue spruce (8 ± 9%), mature quaking aspen (5 ± 4%), and meadow (1 ± 1%).

Third-order habitat selection.—Males were the principal food providers at nests throughout the breeding season, including the period after egg-hatching when rates of prey delivery to nests were highest. Females foraged little from early courtship until several nights before the young fledged (Reynolds and Linkhart 1987). Foraging males gleaned insects (mostly lepidopterans) from the needles, limbs, and trunks of large conifers, and occasionally hawked flying insects between tree crowns or dropped from the lower crown branches to capture arthropods on the ground (Reynolds and Linkhart 1987).

Flammulated Owls are single-prey loaders, delivering one prey item per trip to nests (Reynolds and Linkhart 1987). Single-prey loading requires males to make successive decisions to either return to where they previously foraged or to enter new areas following each prey delivery. Autocorrelation (t^2/r^2 ratios) among successive foraging locations of the seven radio-tagged males ranged from 0.55–1.97. Only one male (A29-83) exceeded the critical value (ratio = 1.97, critical value = 1.51); thus, with the exception of this male, successive foraging locations of males were autocorrelated. The autocorrelation in our sample reflected the tendency of owls to revisit favored foraging areas (see below). For Flammulated Owls the time to independence (Swihart and Slade 1985) was the elapsed time between a prey capture (and subsequent delivery of prey to the nest) and the next foraging attempt. Depending on the stage of nesting and time of night, the time between successive prey deliveries at nests varied from 1–60 min (Reynolds and Linkhart 1987). We used all foraging locations rather than an independent subset (see Swihart et al. 1988) in the preference analysis of foraging habitat because foraging locations were behaviorally independent.

Preference analyses (males combined, n = 7) of four overstory types used for foraging ("meadow" not included because of its negligible area) indicated that use of types differed significantly from availability (χ^2 = 18.70, df = 3, P = 0.001; Table 3, Fig. 2).

TABLE 3. Use and availability of four overstory types within seven home ranges by foraging male Flammulated Owls in Colorado, 1982–1983.

Overstory type	Total area (ha) in home ranges	Expected[a] proportion of locations	Expected[b] number of locations	Observed proportion of locations	Observed number of locations	Bonferroni confidence interval on proportion of occurrence
Old ponderosa pine/Douglas-fir	75.4	0.76	169	0.86	190	$0.799 \leq P_1 \leq 0.921$*
Young Douglas-fir/blue spruce	7.6	0.08	17	0.00	1	$-0.009 \leq P_2 \leq 0.017$*
Mature quaking aspen/blue spruce	9.0	0.09	20	0.10	23	$0.050 \leq P_3 \leq 0.158$
Mature quaking aspen	6.8	0.07	15	0.03	7	$0.001 \leq P_4 \leq 0.604$*
Total	98.8	1.00	221	0.99	221	

[a] Proportion of each overstory type available within the home ranges.

[b] Calculated by multiplying the expected proportion and the total number of locations (e.g., 0.76 × 221 = 169).

Bonferroni simultaneous confidence intervals indicated that old ponderosa pine/Douglas-fir was significantly over-selected while young Douglas-fir/blue spruce and mature quaking aspen overstories were significantly under-selected. Mature quaking aspen/blue spruce was used in about the same proportion as available.

Intensive foraging areas.—A mean 81 ± 8% (range = 71–93%, n = 7 males) of 221 total foraging locations occurred in 15 IFAs. Two home ranges contained one IFA, three ranges contained two IFAs, one contained three, and one range contained four (Fig. 1). There was a mean 12 ± 6 foraging locations (range = 6–25 locations) per IFA and each male was observed foraging in a particular IFA on two to four different nights. Mean size of IFAs was 0.5 ± 0.4 ha (range = 0.1–1.4 ha), and mean total area in IFAs per home range was 1.0 ± 0.3 ha (range = 0.6–1.5 ha). Mean distance of IFAs from nests was 126 ± 123 m (range = 10–401 m). Except for the A11-83 nest, each nest occurred within an IFA. When males foraged in nest IFAs or in IFAs nearest the nest, which occurred frequently in the early evening (20:00–21:30) and at infrequent intervals later in the night, prey delivery rate to nests was one prey every 1–10 min. Later in the night, the delivery rate fell to one every 10–20 min (Reynolds and Linkhart 1987); some males (A10-82, A15-82, and A29-82) foraged in IFAs farther from nests (>250 m) at this time. The two males whose ranges contained only a nest IFA (A4-83 and A29-82) foraged in the nest IFA regardless of the time of night. The nest IFA of A29 (same male in both years) was nearly identical in location and shape in both years. However, in 1983 this male also foraged in a new IFA on the edge of his home range. Twelve of the 15 IFAs (80%) consisted entirely of old ponderosa pine/Douglas-fir, two (13%; one each in A10-82 and A11-83) con-

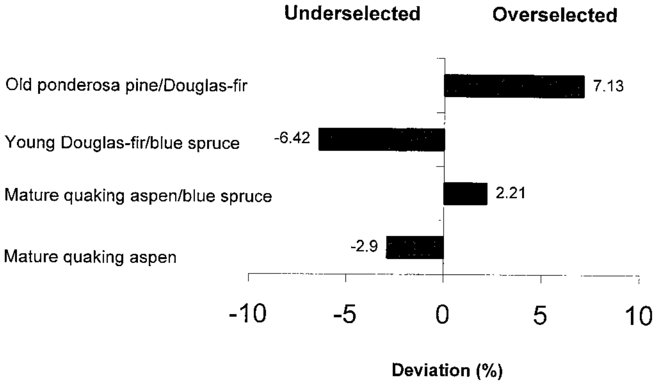

FIG. 2. Percent deviation (Neu et al. 1974) from expected use of four overstory types by foraging Flammulated Owls.

TABLE 4. Percent of telemetry locations by tree species and the percentages of trees available on the study area in Colorado, 1982–1983.

Tree species	Percent of trees available (615)[a]	Activity			
		Foraging (167)[b]	Territorial singing (22)[b]	Day-roosting (112)[b]	Resting (19)[b]
Douglas-fir	39	61	50	58	58
Ponderosa pine	29	19	50	26	35
Quaking aspen	17	9	—	1	1
Limber pine[c]	10	6	—	9	6
Blue spruce	5	5	—	6	—
Total	100	100	100	100	100

[a] Number of trees randomly sampled across study area.
[b] Total number of trees.
[c] *Pinus flexilis.*

sisted entirely of mature quaking aspen/blue spruce, and one (7%; A11-83) consisted of old ponderosa pine/Douglas-fir mixed with quaking aspen.

Foraging trees.—Of 167 trees in which a prey was known to have been captured (excluding cases of hawking, ground foraging, and uncertain sites of capture), 61% were Douglas-fir and 19% were ponderosa pine (Table 4). Mean age of 77 trees randomly selected from these foraging trees was 199 ± 85 years (range = 72–395 years).

Song trees.—Males sang from one to eight trees during an episode of territorial song, and song trees were mostly on mid-slopes and ridgetops. Males frequently sang from within the lower tree crown next to the trunk. Mean age of 22 song trees (exact tree unknown in 76 cases) was 289 ± 96 years (range = 94–419 years); 50% were Douglas-fir and 50% were ponderosa pine (Table 4).

Day-roost trees.—Of 112 day-roost trees of males, 58% were Douglas-fir and 26% were ponderosa pine (Table 4). Perches used by males in day-roost trees typically had a dense, overhead cover of horizontal limbs and/or foliage. During the nesting season males repeatedly roosted in selected trees; 19% of roost trees were used 2–20 times, and these trees accounted for 75% of all day-roost trees. Mean age of day-roost trees was 207 ± 106 years (range = 88–508 years, n = 55). Mean distance between male day-roosts and nest trees was 90 ± 58 m (range = 10–255 m, n = 112 roosts). However, all males day-roosted within 20 m of their nests during the four days before fledging (Linkhart 1984).

Resting trees.—At night, males occasionally rested or perched quietly up to one hour in trees at scattered locations in their ranges. Before eggs hatched males rested occasionally at any hour of night, while after eggs hatched males rested occasionally in the late evening after broods had been fed. During rainy periods, males ceased foraging and rested in protected areas in large trees with dense crowns. The majority of resting trees were Douglas-fir (58%) and ponderosa pine (35%) (Table 4).

DISCUSSION

Radio-telemetry showed that Flammulated Owls established home ranges in areas that contained more old ponderosa pine/Douglas-fir than other overstory types available within the study area. Males also foraged most often in old ponderosa pine/Douglas-fir, and most intensive foraging areas (IFAs) consisted entirely of this overstory type. Most nests of Flammulated Owls were within an IFA, which probably resulted from the owls' need to minimize travel time between nests and foraging sites during periods of high feeding rates. After eggs hatched, males foraged for their broods in the vicinity of nests in the early evening, making as many as 16 trips per hour to nests (Reynolds and Linkhart 1987). Reducing travel time is important because only one small (<0.3 g) prey is delivered per trip (Reynolds and Linkhart 1987). Thus, use of microhabitats depends on their availability and juxtaposition, both of which are affected by choices of habitats made at higher orders of selection.

Male Flammulated Owls used Douglas-fir trees more often than ponderosa pine for foraging, day-roosting, and resting. Old Douglas-fir trees typically appeared to have greater crown volume than old ponderosa pine trees, providing more crown and trunk surface area for foraging, and greater cover for day-roosting and resting. In Idaho (Powers et al. 1996) and southern British Columbia (Howie and Ritcey 1987), Flammulated Owls nested in Douglas-fir forests where little or no ponderosa pine was present.

The use of older stands of ponderosa pine/Douglas-fir by Flammulated Owls on our study area is probably related to habitat structure and prey availability. Older forests typically contain an abundance of snags and lightning-damaged trees with cavities (Reynolds et al. 1985), and Flammulated Owls may have a higher probability of finding nest cavities there. Second, open stands of large, old ponderosa pine/Douglas-fir forest with grass or shrub understories suit the foraging behaviors used by Flammulated Owls within and between crowns, on crown surfaces, and in understories (Reynolds and Linkhart 1987). Third, ponderosa pine and Douglas-fir trees contain up to four times as many lepidopteran species as other western conifers (Furniss and Carolin 1977). Lepidopterans are important prey of Flammulated Owls during the breeding season (Reynolds and Linkhart 1987, Powers et al. 1996). Finally, ponderosa pine/Douglas-fir forests contain an abundance of the large, old trees used by Flammulated Owls for foraging, territorial singing, and day-roosting.

The importance of old ponderosa pine/Douglas-fir to the owl is underscored by data on occupancy and habitat composition of territories on the study area from 1981–1996. Occupancy of territories by breeding pairs was positively correlated with the amount of old ponderosa pine/Douglas-fir, and negatively correlated with the amount of young Douglas-fir/blue spruce, in 14 ha circles centered in territories (Linkhart and Reynolds 1997). Territories most often occupied by unpaired males contained relatively small percentages of old ponderosa pine/Douglas-fir in 14 ha circles (Linkhart and Reynolds 1997).

The structure and species composition of old ponderosa pine/Douglas-fir forests used by Flammulated Owls were historically maintained by frequent, low-intensity ground fires (Cooper 1960). Fire suppression has resulted in increased tree densities in ponderosa pine and mixed-conifer forests, has converted many pine forests to fir forests, and has changed fire type from low-intensity to catastrophic, habitat-destroying, crown fire (Barrett et al. 1980, Gordon 1980). In addition, many old ponderosa pine and mixed-conifer forests within the range of the Flammulated Owl have been harvested. These habitat changes have resulted in declines of Flammulated Owls in some areas (Marshall 1957, 1988; Phillips et al. 1964; Franzreb and Ohmart 1978). Forest management prescriptions that restore the species composition and structure of these forests are needed.

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