

BOREAL OWL MATING HABITAT IN THE NORTHWESTERN UNITED STATES

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ABSTRACT.—We examined boreal owl (*Aegolius funereus*) mating habitat in the Sierra Madre range of the Medicine Bow National Forest in Wyoming in the northwestern United States during 1992–93. In nocturnal surveys, we found 22 boreal owl singing locations which we compared to 68 random locations in the study area. Owls used stands dominated by Engelmann spruce (*Picea engelmannii*) and subalpine fir (*Abies lasiocarpa*) more often (77%) than stands of lodgepole pine (*Pinus contorta*). Stand size ranged from 0.2–122.8 ha though adjacent stand type (forest or opening) was not investigated. All boreal owls were found in areas with old forest characteristics including high basal areas of trees, tall snags, many large down logs, and a tall overstory canopy. Some boreal owls sang from old forest stands adjacent to clearcuts, one as close as 15 m. Older forests may provide nest holes for boreal owls which are obligate cavity nesters.

KEY WORDS: *boreal owl; Aegolius funereus; mating habitat; old growth; Sierra Madre Forest; clearcut.*

Habitat de apareamiento de *Aegolius funereus* en el noroeste de los Estados Unidos

RESUMEN.—Durante 1992 y 1993, examinamos el hábitat de apareamiento de *Aegolius funereus* en la Cordillera de Sierra Madre del Medicine Bow National Forest en Wyoming, al noroeste de los Estados Unidos. En recorridos nocturnos, encontramos 22 sitios de canto de este búho, los que comparamos con 68 sitios al azar en el área de estudio. Los búhos usaron más a menudo (77%) parches dominados por *Picea engelmannii* y *Abies lasiocarpa* que parches de *Pinus contorta*. El rango del tamaño del parche fue de 0.2 a 122.8 ha. Todos los búhos fueron encontrados en áreas con características de bosque antiguo, incluyendo grandes áreas basales de árboles, ramas espigadas, grandes troncos caídos y grandes sotobosques. Algunos individuos de esta especie se encuentran hasta alrededor de 15 m de claros de bosque. Antiguos bosques pueden proveer de sitios de nidificación para estos búhos que nidifican obligadamente en cavidades.

[Traducción de Ivan Lazo]

Boreal owl (*Aegolius funereus*) mating and nesting habitat is poorly understood in the U.S. because of their nocturnal behavior in remote forests. During their late winter mating season in the western states, boreal owls associate with older high-elevation forests generally composed of Engelmann spruce (*Picea engelmannii*, ES) and subalpine fir (*Abies lasiocarpa*, SA) (Webb 1982, Palmer 1986, Hayward et al. 1993). High elevation patches of ponderosa pine (*Pinus ponderosa*), Douglas fir (*Pseudotsuga menziesii*), and quaking aspen (*Populus tremuloides*) are important when available (Hayward et al. 1993). These forest types also support the owl's primary prey, the southern red-backed vole (*Clethrionomys gapperi*) (Hayward et al. 1993).

During the mating season, male owls sing for a mate with a continuous high-pitched song that can easily be heard from 1.5 km and, on clear, cold nights, up to 3.5 km (Bondrup-Nielsen 1984). This allows an observer to locate owls without excessive intrusion. Owl singing locations indicate habitat use and represent potential breeding sites (Meehan 1980, Bondrup-Nielsen 1984, Hayward et al. 1993). Breeding sites vary by vegetation type but boreal owls are obligate cavity nesters (Mikkola 1983).

In this study, we sought to describe habitat used by boreal owls during the 1992–93 mating seasons. We compared owl singing locations with random habitat locations within the study area. The research also illustrates the distribution of boreal owl singing locations in a mosaic of forest patches comprised mainly of lodgepole pine (*Pinus contorta*,

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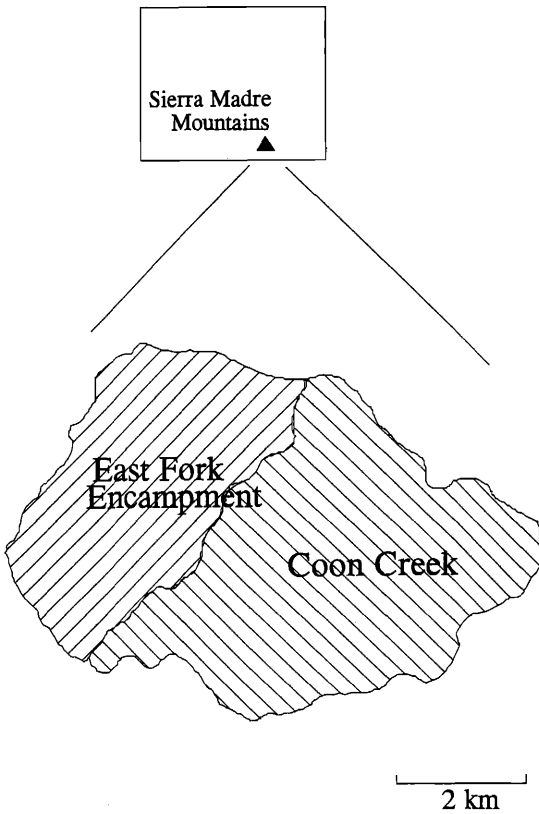


Figure 1. The two watersheds (2526 ha) in the study area located in the Sierra Madre mountains of Wyoming.

LP) and spruce/fir (SF) with interspersed clearcuts. Together with prey and nest hole availability, breeding habitat may be the most critical factor affecting the persistence of owl populations. We specifically describe (1) forest structure at owl singing locations relative to the forested available habitat on the study area, and (2) locations of singing owls relative to clearcuts.

STUDY AREA

The Blackhall Mountain Study Area is located in the Sierra Madre mountains of southcentral Wyoming in the Medicine Bow National Forest (41°N, 107°W). Two contiguous watersheds, Coon Creek (1615 ha) and the Upper East Fork of the Encampment River (911 ha), are contained in the study area and lie near the Colorado border, 38 km south of Riverside, Wyoming (Fig. 1). Both drainages are heavily-forested mosaics of SF and LP patches, with a few small meadows along the creeks and ridgetops. Lodgepole pine covers 58% of Coon Creek, and 67% of the East Fork for 61% overall. The remaining forests are SF. Half of all stands in both watersheds were classified by the U.S. Forest Service (USFS) as older for-

ests [scoring >38 on Marquardt's (1984) Old Growth Scorecard]. Timber on the Coon Creek watershed was harvested with numerous small clearcuts as part of a water augmentation experiment in the early 1990s. The East Fork was left as an undisturbed control.

Elevation on the study area ranges from 2600–3300 m. Current land uses include logging and grazing; small-scale mining while harvesting for railroad ties occurred historically.

The well-drained soils are 50–150 cm deep. Mean annual precipitation measures 86.4 cm (1983–93), 70% of which falls as snow from late September until late June. Snow survey data from 1993 show a maximum snow depth in late March 1993 of 235.2 cm (Gonyer 1994). The mean annual temperature is 0.6°C, with a low of -42.8°C and high of 30.6°C (Gonyer, 1994).

METHODS

Boreal Owl Surveys. We established 24 transects throughout the study area to locate male boreal owls during the mating season. When possible, we surveyed by snowmobile on unplowed roads and on snowmobile routes traveled by other researchers. We surveyed more remote areas by snowshoe on routes following stream courses and ridges. A total of 122 listening stations (61 on each watershed) on the 24 transects allowed us to detect singing males in all areas of the two watersheds. Although audibility of a boreal owl song is 100% within 700 m (Holmberg 1979), the stations in this study were a maximum distance of 500 m apart to increase detection of singing owls over broken topography.

We surveyed for singing owls for approximately 6 hr after dusk from late February through May of 1992–93. To account for temporal and seasonal variations in singing activity, we surveyed each station at least three times over the two mating seasons in different phases of mating season (early season—late February, mid season—March and April, late season—May), at different times of the night (early, mid, late), during different moon phases (¼, ½, ¾, full), and under different cloud cover (clear, partly cloudy, overcast), snowfall (none, light, moderate), and wind (none, light, medium) conditions. We did not survey under conditions of strong winds and heavy snowfall which were the two factors most affecting calling activity in northcentral Colorado (Palmer 1986).

Because of the potential bias of luring an owl from a singing location toward the listening station, tape play back was not used. All owl locations used in this study represent habitat used by spontaneously singing boreal owls. When owl singing was heard, we either moved toward it until the actual singing tree was located or we identified the location by triangulating the site from two stations (providing the singing continued while we traveled between stations). All singing locations were marked on a 1:24000 U.S. Geological Survey topographic map. We combined all locations from both survey years to describe habitat used by boreal owls during their mating season. Locations that were used more than once during the study were counted as a single location.

Microhabitat. The U.S. Department of Agriculture Forest Service Rocky Mountain Forest and Range Experiment Station conducts long-term wildlife research in the study area. A sampling grid of 90 stations in each water-

shed along north-south transects 400 m apart has been established for these wildlife studies. Stations are located 200 m apart, numbered and flagged. We used a subset of those 180 stations to describe available habitat. To achieve a representative subsample, we listed stations from both watersheds by cover type, discarded stations that occurred in clearcuts, and chose every third station on the list until we had at least three times the number of owl singing locations ($N = 22$) and approximately 60% LP stations and 40% SF stations. Each location represented suitable habitat for boreal owls during their mating season.

We determined habitat associations of areas used by boreal owls during their mating season through bird-centered ("singing tree") habitat sampling. We used the James and Shugart (1970) method as modified by Noon (1980) to measure habitat variables at owl singing locations and at available habitat sampling stations. The method employs a 0.04 ha (11.3 m radius) plot. At owl singing locations, the actual "singing tree" was used when it had been found. Otherwise, the closest tree >23 cm diameter breast height (dbh) within 10 m to the triangulated locations was used to represent the "singing tree" and therefore the potential nest tree. The minimum nest tree size used for breeding in Idaho was 23 cm (Hayward et al. 1993).

Within each plot, we classified each tree by species and diameter size class (dbh). We classified each snag >6 m tall into a diameter size class and height, and each downed log >2 m long was placed into a diameter size class and its length measured. We used a I-factor metric Reloskop to measure basal area of the three tree species (m^2/ha) from the center tree and to measure maximum canopy height in the plot. Percent overstory canopy cover was estimated from the average of four measurements in each cardinal direction at the 11.3 m plot edge using a spherical densiometer (Model C). Ground cover was not measured, as the study area was generally dominated by low-growing grouse whortleberry (*Vaccinium scoparium*) and forbs. Aspect was estimated for all plots using the GRASS Geographical Information System (GIS).

Macrohabitat. We derived stand size information from USFS maps made prior to clearcutting. Stands were delineated based on vegetative, topographic, and edaphic features. The size of each of the 401 stands within the two watersheds was estimated using a GIS. Stands with owl singing locations were identified by location and site number.

Distance to Clearcuts. Because there were no clearcuts in the East Fork watershed, we used the Coon Creek watershed singing locations and available habitat sampling stations ($N = 16$ and 29, respectively) to describe the distance to a clearcut. We measured the distance with a metric tape for plots within sight of a clearcut which was a maximum of 51 m. Plots without a clearcut in sight were categorized as >51 m from a clearcut.

Data Analysis. To test if boreal owls used habitats in a nonrandom manner, comparisons of 23 vegetation variables were made at the microhabitat scale. Nonnormal distributions and unequal variances in the data led to the use of nonparametric statistical tests for univariate analysis. Because we used multiple, simultaneous Mann-Whit-

ney U tests, we used Bonferroni-adjusted probability level for $\alpha \geq 0.05$ to $P < 0.0022$.

To examine multivariate patterns in the habitat data, we used an exploratory discriminant function analysis. Eleven variables (basal area, LP >38 cm dbh, ES 15–38 cm dbh, ES >38 cm dbh, SA 0–15 dbh, snags >39 cm dbh, snag height, logs 10–32 cm, logs >32 cm, canopy cover, and canopy height) with low Pearson correlations ($r < 0.55$) were used in three direct discriminant analyses (SPSS, Inc. 1990). Three analyses were done because the two classification groups to separate in the discrimination (owl locations and available sites) were of unequal sample sizes ($N = 22$ and 68, respectively). Three subsamples (S1, S2, and S3) of the available sites were drawn to better balance sample sizes (Williams and Titus 1988). Therefore, each analysis was between all owl locations and one of the three random subsamples (S1, S2, S3) of available sites. Prior probabilities for classification were set for the fraction of cases (habitat plots) in each group. Variables with significant structure coefficients (>0.30) from the three subsamples are reported and biologically interpreted (Williams and Titus 1988).

Forest cover type at owl singing locations was determined through cluster analysis (SPSS, Inc. 1990). We used basal area of LP, basal area of SF, the number/ha of LP in two size classes (15–38 cm dbh and >38 cm dbh), and the number/ha of SF in the same two size classes.

Chi-square analyses were done on three categorical variables: aspect, the distance to a clearcut, and cover type. Aspect, and the two categories of distance to a clearcut (<51 m, >51 m), were tested with the chi-square homogeneity test for differences between the expected and observed frequency of use (Jelinski 1991). A chi-square goodness-of-fit test was used to test if the owls used cover type (as determined by cluster analysis) in different proportions than expected based on available habitat proportions of 60% LP and 40% SF (Jelinski 1991, Neu et al. 1974).

The distance to clearcut tests used only the owl singing locations and systematic habitat sampling points in the Coon Creek watershed with the clearcuts ($N = 16$ and 29, respectively). Distance to a clearcut data analysis had two parts. After the chi-square test, a t -test was used to test for differences in the measured distances (<51 m) to a clearcut.

We compared the central tendency of stand sizes used by boreal owls to sizes of all stands at the study area. We used a t -test to compare the sample stands (owl-use stands) to the population (all stands within the two watersheds).

RESULTS

Twenty-two boreal owl singing locations were found during the two years of surveys. Six were in undisturbed parts of the East Fork watershed and 16 were in areas of the Coon Creek watershed where there were several small clearcuts. Eight locations were actual "singing trees" where owls were seen in the trees. The remaining 14 locations

Table 1. Comparison of habitat variables at boreal owl singing sites with habitat variables at three nonsinging sites (S1, S2, S3) in the study area.

VARIABLE	S1	S2	S3	OWL SITE
Structure Coefficient				
Down logs >32 cm dbh	0.552	0.612	0.581	
Canopy height	0.359	0.457	0.362	
Snag height	0.337	0.373	0.430	
ES >38 cm dbh		0.336	0.323	
SA <15 cm dbh	0.369			
Means				
Down logs >32 cm diam	3.6	7.9	3.1	7.7
Canopy height	22.9	21.9	22.5	26.7
Snag height	10.7	9.0	8.2	16.6
ES >38 cm dbh	37.2	20.0	20.7	64.7
SA <15 cm dbh	441.5	481.5	462.7	869.2
Canonical correlation	.777	.816	.805	
% Correctly classified	92.98	96.49	94.74	
Centroids	1.53	1.75	1.68	
	-.961	1.10	1.05	

were found after hearing owls at two listening stations. All 22 locations were treated equally.

Microhabitat. Four of the 23 variables tested in univariate analysis were significantly different between boreal owl locations and available habitat. The four variables were: basal area of ES (12.4 m²/ha vs 6.6 m²/ha, owl locations vs available habitat, respectively, $P < 0.0001$); basal area of SA (12.4 m²/ha vs 8.7 m²/ha, $P = 0.0005$); canopy height (27 m vs 23 m, $P = 0.0004$); and large, downed logs (7.7 vs 3.7, $P < 0.0001$).

Taller overstory canopy, tall snags, and many large (>32 cm dbh) downed logs were identified as important forest characteristics in the discriminant analyses (Table 1). The three analyses (S1, S2, S3), based on 11 forest structure variables, accounted for 60%, 67%, and 65% of the variance within the groups, respectively. The single canonical function generated for each analysis significantly distinguished between available habitat and sites used by singing boreal owls ($P < 0.001$). The first subsample (S1) added the number/ha of small SA trees to the function while S2 and S3 added the number/ha of large (>38 cm dbh) ES trees to the function. Discriminant function analyses provided 93%, 96.5%, and 95% correct classification, respectively, suggesting substantial differences between available habitat and owl singing sites.

Snag height (somewhat correlated with large diameter snags, $r = 0.45$) was also identified in the

discriminant analysis. At owl singing locations, large diameter snags (>39 cm dbh) were generally taller (21.23 m, range 12–31.8 m) than medium (18–39 cm dbh) diameter snags (15.6 m, range 6–26.8 m, $P < 0.013$). Large diameter snag density at the Blackhall Mountain study area was estimated at 19 ± 21.7 snags/ha at boreal owl singing locations, while the available habitat had an estimated 8 ± 16 snags/ha.

Cluster analysis of basal area and tree density data for owl location plots determined the forest cover type. Five locations were in the LP cover type and 17 in the SF cover type.

The SF cover type was used by boreal owls more frequently than its proportional availability (40%) at the study area ($\chi^2 = 13.54$, $df = 1$, $P < 0.005$). The lodgepole cover type was used less than its proportion of availability (60%).

The aspect at boreal owl singing locations did not differ from aspects at sampled available habitat locations ($\chi^2 = 9.19$, $df = 7$, $P = 0.239$). The chi-square test of homogeneity compared observed and expected frequencies between owl locations and available sites ($N = 22$ and 68, respectively).

Macrohabitat. The 22 owl singing locations occurred in 16 stands. One large (122.8 ha) SF stand had five locations, two LP stands had two singing locations each, and the remaining 13 stands had one singing location per stand. It is quite possible that the same bird used several of these locations.

Boreal owl breeding season home ranges have been reported to vary between 240–352 ha for two birds in Colorado (Palmer 1986) and to average 1451 ± 552 ha in Idaho (Hayward et al. 1993).

At this scale, boreal owl singing locations were almost equally distributed by cover type into SF stands (55%) and LP stands (45%). This differed from plot level cover type designation (from cluster analysis) for three of the 16 stands used by singing boreal owls.

The mean stand size at the study area (6.9 ± 13.7 ha) differed from mean stand size at owl locations (35.5 ± 36.4 ha, $P = 0.0067$). Stands in the available habitat ranged in size from 0.005–122.8 ha; stands used for singing ranged from 0.17–122.8 ha.

Distance to Clearcuts. The 227 small clearcuts in the Coon Creek watershed have left 82% of the forest within 200 m of a clearcut. The maximum possible distance from a clearcut is 270 m (E. O'Doherty pers. comm.). Boreal owl singing locations did not differ in the distance to a clearcut from the random available habitat locations ($\chi^2 = 1.65$, $df = 1$, $P = 0.199$). The chi-square test of homogeneity tested the two categories of distance to a clearcut (<51 m, >51 m) for boreal owl singing locations ($N = 16$ in this watershed) and random available habitat sampling points ($N = 29$ in this watershed). Further, a *t*-test between the measured distances (<51 m) showed no difference ($P = 0.65$) in the mean distance to a clearcut between owl singing locations (29 ± 12.8 m) and the available habitat sampling points (31.7 ± 12.9 m) in the Coon Creek watershed. The closest "singing tree" to a clearcut was 15 m and the average distance was 27 ± 30 m.

DISCUSSION

The majority of owl singing locations at the Blackhall Mountain study area were in the SF cover type with microhabitat structure typical of mature or old-growth forests (large downed logs, a high overstory canopy, tall snags, large ES trees, and small fir trees). Large snag (>39 cm dbh) density at owl singing locations, greater than in either the available habitat or other study areas in Colorado (Palmer 1986, Ryder et al. 1987) or Idaho (Hayward et al. 1993), increases the potential for suitable nest sites for boreal owls. Dense ES forests also offer protection from predators such as pine marten (*Martes martes*) (Korpimäki 1988) and larger birds of prey (Mikkola 1983). The singing locations

in LP cover types had large lodgepole trees instead of ES trees, as did boreal owl singing locations in LP stands on the Beaverhead National Forest in Idaho (Hayward et al. 1993). Hence, some LP stands appear to have adequate forest structure for boreal owls to use as singing sites.

Canopy height and large downed logs were identified as important differences between owl singing sites and random sites in both multivariate and univariate tests. Large downed logs are an important component of old-growth forests (Maser et al. 1979, Meslow et al. 1982) and were correlated with boreal owl mating habitat on our study area. Webb (1982) also described three of his five boreal owl locations in northern Colorado as having "much fallen timber." Although studies on boreal owl foraging sites did not report the log component directly, the highest numbers of foraging sites were in mature or older SF forests that support the owl's primary prey, the red-backed vole (Palmer 1986, Hayward et al. 1993). The old-growth locations used by boreal owls during the mating season at the Blackhall Mountain study area may also be used for foraging.

Microhabitat at owl singing locations indicated that SF cover types were used most often by boreal owls. Similarly, Palmer (1986) found a higher density of boreal owls in Colorado's high elevation SF though four other habitat types were available. Only in years with an abundance of boreal owls at his study area were lower elevation mixed forest habitat types used. He suggested that the SF is optimum habitat in the Cameron Pass area (Palmer 1986) 87 km south of the study area.

Hayward et al. (1993) found from surveys throughout the northern Rockies that a majority of boreal owl locations were in SF habitat types. In Idaho, the owls bred more often in mixed conifer and aspen habitats and, in the wilderness study site, did not nest in boxes hung in LP stands. At Blackhall Mountain, the aspen cover type was not available, and some LP stands were used for singing. Like some of the boreal owl singing sites in Colorado (Palmer 1986, 1987), sites used in Blackhall Mountain during mating season may be suboptimal. Without knowing the density and reproductive success of boreal owls at the Blackhall Mountain study area and in the surrounding habitat, inferences about the use of areas of lesser quality could not be made. Hayward et al. (1993) suggested that suboptimal habitat may still be important at a regional and metapopulation scale.

The discrepancy in cover-type designation between USFS maps and the cluster analysis for three of the 16 stands used by singing boreal owls is probably due to the difference in scale. This situation illustrates the importance of collecting habitat data on the ground rather than from a large-scale map.

The wide range of stand sizes used by singing boreal owls at Coon Creek suggests that even small stands provide forest structure to allow the owls to attempt breeding. However, adjacent stand conditions (clearcut, cover type, stand size, etc.) were not investigated though they may have had a significant influence. Also, the present and future degree of suitability of these small sites was unknown. Rosenberg and Raphael (1986) found that small patches of old-growth support forest-interior species, although their smallest stand measured 5 ha. In the long term, as the amount of habitat available is reduced, owl populations will decline (Hayward et al. 1993).

The choice of habitat made by boreal owls may be of ecological importance to their survival. Microhabitat selection may help avoid predation by larger owls. Food supply may be easier to obtain thereby conserving energy in this very harsh environment.

Boreal owls in the Coon Creek watershed sang in trees near clearcut edges. The "singing tree" and microhabitat data suggested that old-growth conditions are found near the edges of clearcuts. Owls may use edges for several other reasons. If the location was used for nesting prior to the clearcuts, it may continue to be used because of nest site tenacity by male boreal owls when suitable nest sites are scarce as in Sweden (Lundberg 1979) and western Finland (Korpimäki 1988). If clearcutting eliminated more suitable sites and packed owls into remaining forest, suboptimal locations may be used. Korpimäki (1987), for example, found that male boreal owls used nest holes just over 1 km from the edge. We speculate that stand structure is more important than any factor relating to edge. Boreal owl populations are associated with old growth characteristics including large, tall trees. Large downed logs are an indirect indicator of such stands and may also provide foraging sites for boreal owls.

Perhaps the most intriguing finding of this study is that the majority of the singing locations were in the watershed containing clearcuts. Korpimäki (1988) found that Tengmalm's owls in western Fin-

land preferred voles (*Microtus* sp.) that occupied clearcut areas where snow melted earlier than in woodlands. During breeding, which starts as the snow is melting, these owls mainly hunted in fields. He found that agricultural lands interspersed with productive ES forests lowered the variability of food supply which benefitted breeding owls. The mosaic of openings and forests provided several species of small mammals and therefore balanced the seasonal and year-to-year population fluctuations. Foraging boreal owls in Norway avoided clear-fellings that had higher prey densities than old-forest stands because the higher, denser vegetation made prey less accessible (Sonerud et al. 1986). Recent clearcuts in the Coon Creek watershed may provide greater prey availability for boreal owls at forest edges than in the undisturbed East Fork watershed. It is possible the owls have benefitted from some clearcutting in the short-term.

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LITERATURE CITED

- BONDRUP-NIELSEN, S. 1984. Vocalizations of the boreal owl, *Aegolius funereus richardsoni*, in North America. *Can. Field-Nat.* 98:191-197.
- GONYER, L. 1994. Snow survey data. Rep. No. 3. Medicine Bow National Forest, Hayden Ranger District, Encampment, WY U.S.A.
- HAYWARD, G.D., P.H. HAYWARD AND E.O. GARTON. 1993. Ecology of boreal owls in the northern Rocky Mountains, USA. *Wild. Monogr.*, No. 124.
- HOLMBERG, T. 1979. Punktaxing av Parluggia *Aegolius funereus*—en Metodstudie. *Vår Fågelvärld* 38:237-244.
- JAMES, F.C. AND H.H. SHUGART. 1970. A quantitative method of habitat description. *Audubon Field Notes* 24:727-736.
- JELINSKI, D.E. 1991. On the use of chi-square analyses in studies of resource utilization. *Can. J. For. Res.* 21:58-65.
- KORPIMÄKI, E. 1987. Selection for nest hole shift and tactics of breeding dispersal in Tengmalm's owl *Aegolius funereus*. *J. Anim. Ecol.* 56:185-196.

- . 1988. Effects of territory quality on occupancy, breeding performance and breeding dispersal in Tengmalm's owl. *J. Anim. Ecol.* 57:97–108.
- LUNDBERG, A. 1979. Residency, migration and compromise: adaptations to nest site scarcity and food specialization in three Fennoscandian owl species. *Oecologia* 41:273–281.
- MARQUARDT, S. 1984. Old growth scorecard user's guide. Unpubl. rep. USDA Forest Service, Medicine Bow National Forest, Laramie, WY U.S.A.
- MASER, C., R.G. ANDERSON, K. CROMACK, JR., J.T. WILLIAMS AND R.E. MARTIN. 1979. Dead and down woody material. Pages 78–95 in J.W. Thomas [Ed.], *Wildlife habitats in managed forests: the Blue Mountains of Oregon and Washington*. USDA Forest Service, Agriculture Handbook 553, Washington, DC U.S.A.
- MEEHAN, R.H. 1980. Behavioral significance of boreal owl vocalizations during the breeding season. M.S. thesis, Univ. Alaska, Anchorage, AK U.S.A.
- MESLOW, C.E., C. MASER AND J. VERNER. 1982. Old-growth forests as wildlife habitat. *Trans. N. Am. Wildl. Nat. Resour. Conf.* 46:329–335.
- MIKKOLA, H. 1983. *Owls of Europe*. Buteo Books, Vermillion, SD U.S.A.
- NEU, C.W., C.R. BYERS AND J.M. PEEK. 1974. A technique for analysis of utilization-availability data. *J. Wild. Manage.* 38:541–545.
- NOON, B.R. 1980. Techniques for sampling avian habitats. Pages 42–52 in D.E. Capen [Ed.], *The use of multivariate statistics in studies of wildlife habitat: a workshop*, April 23–25. Burlington, VT U.S.A.
- PALMER, D.A. 1986. Habitat selection, movements and activity of boreal and saw-whet owls. M.S. thesis, Colorado State Univ., Fort Collins, CO U.S.A.
- . 1987. Annual, seasonal, and nightly variation in calling activity of boreal and northern saw-whet owls. In R.W. Nero, C.R. Knapton and R.J. Hamre [Eds.], *Biology and conservation of northern forest owls*. USDA For. Serv. Gen. Tech. Rep. RM-142.
- ROSENBERG, K.V. AND M.G. RAPHAEL. 1986. Effects of forest fragmentation on vertebrates in Douglas-fir forests. Pages 263–272 in J. Verner, M. Morrison and C.J. Ralph [Eds.], *Wildlife 2000*. Univ. Wisconsin Press, Madison, WI U.S.A.
- RYDER, R.A., D.A. PALMER AND J.J. RAWINSKI. 1987. Distribution and status of the boreal owl in Colorado. In R.W. Nero, C.R. Knapton and R.J. Hamre [Eds.], *Biology and conservation of northern forest owls*. USDA For. Serv. Gen. Tech. Rep. RM-142.
- SONERUD, G.A., R. SOLHEIM AND B.V. JOCOBSEN. 1986. Home-range used and habitat selection during hunting in a male Tengmalm's Owl *Aegolius funereus*. *Fauna Norv., Ser. C. Cinclus* 9:100–106.
- SPSS, INC. 1990. *SPSS-X User Guide*, release 4.0.1 edition. SPSS Inc. Chicago, IL U.S.A.
- WEBB, B.D. 1982. Distribution and nesting requirements of montane forest owls in Colorado. M.S. thesis, Univ. Colorado, Boulder, CO U.S.A.
- WILLIAMS, B.K. AND K. TITUS. 1988. Assessment of sampling suitability in ecological applications of discriminant analysis. *Ecology* 69:1278–1285.

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