

Chapter 9

Review of Technical Knowledge: Boreal Owls

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INTRODUCTION

The boreal owl (*Aegolius funereus*), known as Tengmalm's owl in Eurasia, occurs throughout the holarctic in boreal climatic zones. This medium-size owl (100-170 g) occupies boreal and subalpine forests in an almost continuous circumboreal distribution that extends from Scandinavia eastward across the northern forests of Siberia and from Alaska across Canada to the Atlantic (Dement'ev and Gladkov 1954). On each continent, disjunct populations occur in mountains south of the broad transcontinental boreal forest populations (Cramp 1977, Voous 1988). Boreal owls in the mountain regions of Europe and Asia have long been recognized as isolated resident breeding populations, whereas in North America, breeding status was only recently documented in the mountains of the western United States (Hayward and Garton 1983, Palmer and Ryder 1984, Hayward *et al.* 1987a, Whelton 1989).

In-depth study of boreal owl biology and ecology in North America is limited to four, short-term investigations (Bondrup-Nielsen 1978, Meehan 1980, Palmer 1986, and Hayward *et al.* 1993). As an example of the lack of attention paid this species, prior to 1979 the USDI Fish and Wildlife Service had no records for banded boreal owls west of the Mississippi (W. Martin, pers. comm.). Knowledge of the species' biology and ecology comes mostly from Fennoscandia where *Aegolius funereus* may be the most studied owl. Many investigations in Europe are long-term efforts. Franz *et al.* (1984), Sonerud (1989), Schelper (1989), and Korpimaki (1992) each report studies lasting over 15 years. Korpimaki, who initiated investigations in 1966, continues work on the same sites today. Ecologists in Fennoscandia and eastern Europe have emphasized study of breeding biology, productivity, movements, food habits, and relationship with prey populations. These studies stem largely from examination of populations that breed almost exclusively in nest boxes. Results from studies in the Old World indicate that the biology and ecology of boreal owls vary geographically and

are strongly related to local forest conditions and prey populations.

In contrast with studies in Europe, habitat use has been emphasized in the few investigations in North America. Studies on the two continents have generated few data with which to contrast the biology of the species between continents. Therefore, the basis for inferring North American biology and ecology based on European results is unclear. The variability witnessed in Europe suggests caution. However, to the degree that variation in Europe follows geographic, climatic, or habitat gradients, a more sound basis upon which to build inferences for North America is possible.

The paucity of scientific knowledge from North America necessitates reliance on the extensive knowledge accumulated in Europe for portions of the assessment. Ignoring that knowledge would be careless. However, we cannot directly infer ecological patterns in North America based on the European knowledge. Therefore, I have been careful to point out the geographical source of knowledge, and where appropriate, describe ecological patterns for Europe that have been related to environmental gradients. By doing so, I seek to describe patterns recognized in Europe that may relate to populations in North America.

Note: Throughout this paper, measures of variation are 95% bounds on estimates unless otherwise indicated.

SYSTEMATICS

Ford (1967) associated the genus *Aegolius* with *Surnia* and *Ninox* (northern and southern hawk owl genera) based on osteology of 75 owl species. Aside from the boreal owl, the genus *Aegolius* includes three species: the northern saw-whet owl (*A. acadicus*), unspotted saw-whet owl (*A. ridgwayi*), and buff-fronted owl (*A. harrisi*), which all occur only in the New World. The largest species of the genus, *A. funereus* occurs north of the others and is more widely distributed. Norberg (1987) speculates that

the genus originated in the New World and only the boreal owl expanded its range beyond the Americas. The more northern distribution and larger size of *A. funereus* likely facilitated range expansion via the Bering Strait.

Boreal owls in North America represent a homogeneous taxonomic group and are recognized as a single subspecies, *A. funereus richardsoni*. Six subspecies are recognized in Eurasia. Abrupt distinctions are apparent in only *A. f. beickianus* and *caucasicus*, which are southern, more isolated populations. Otherwise, *A. f. funereus* — north and central Europe; *A. f. sibiricus* — north and central Asia; *A. f. magnus* — northeast Siberia; and *A. f. pallens* — west and central Siberia vary as a cline across Eurasia (Dement'ev and Gladkov 1954). Generally the largest and lightest forms are found in northeast Siberia, with a size reduction and darkening westward and southward (Dement'ev and Gladkov 1954). *A. f. richardsoni* is among the darkest forms.

DISTRIBUTION

Species Range

Boreal owls occupy boreal forests throughout the northern hemisphere forming an almost continuous band across North America and Eurasia. In Europe, scattered populations extend south of the circumboreal range in the Pyrenees, Alps, and Caucasus mountains and in Asia along Tarbagatai, Tien Shan, and Zervshan ranges (see maps in Dement'ev and Gladkov 1954:436 and Cramp 1977:607, 608 for worldwide distribution). Similar southern populations occur in North America as described below.

Recently the species' documented range has expanded in Europe like in North America. Most new records are from mountainous locales (see Cramp 1977:607 and Hayward *et al.* 1987a). Rather than a recent range expansion, these records likely represent increased interest in owls and increased human recreation in mountain areas during winter.

North America

Within North America, boreal owls occur in a continuous band concurrent with the boreal forests of Alaska and Canada (see Johnsgard 1988 for continental distribution). The breeding range extends from northern treeline southward in forested regions of Canada to the extreme northern United States in Minnesota (Eckert and Savaloja 1979, Lane 1988) and likely Wisconsin (Erdman 1979), Michigan, and

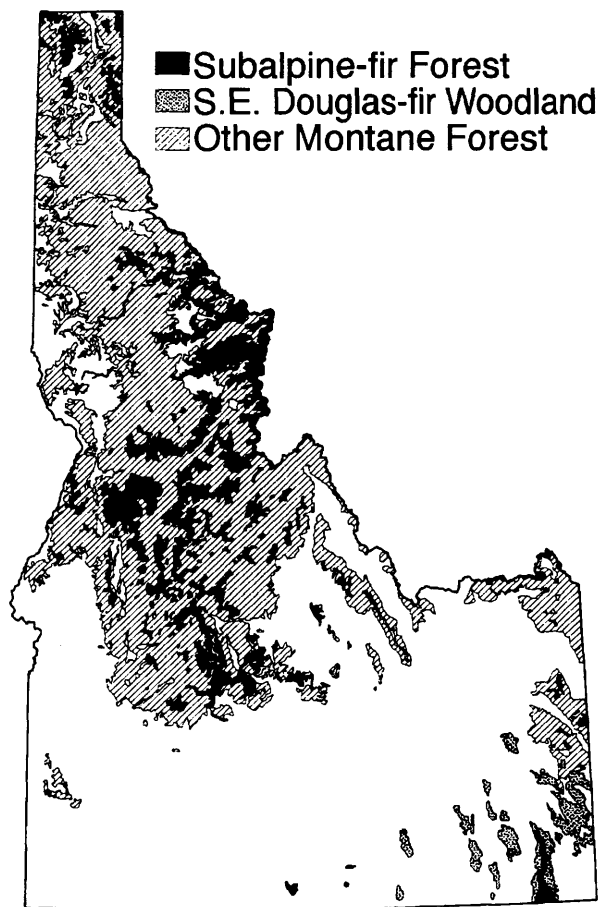


Figure 1.—Example of the patchy nature of boreal owl distribution in the western United States based on the species' estimated distribution in Idaho. Owl distribution inferred from distribution of forest vegetation types. Potential habitat is defined as forested sites in the subalpine-fir zone throughout the state and Douglas-fir woodland in southeastern Idaho. Other montane forests are not considered potential habitat. Data taken from Idaho gap analysis project (adapted from Hayward *et al.* 1993).

Maine (Catling 1972). East of the Rocky Mountains, breeding has been confirmed only in Minnesota. In western North America the species' range extends southward beyond 38° N latitude (Map 2). South of the continuous transcontinental band, populations are restricted to subalpine forests in the Rocky Mountains, Blue Mountains, and Cascade Ranges (Palmer and Ryder 1984, Hayward *et al.* 1987a, Whelton 1989). The southernmost records occur in mountains of northwestern New Mexico (Stahlecker and Rawinski 1990).

Due to the species' association with high elevation forests in the western United States (discussed in-depth under Habitat Use), populations may occur as geographic isolates dispersed throughout the western mountains (for an example see figure 1). As a result of the naturally fragmented nature of boreal owl habitat in the western mountains, the species is distributed in North America in two contrasting patterns. In the north, populations of interacting in-

dividuals may extend for hundreds of miles, while in the south, numerous breeding populations occur as islands of habitat linked only through long-distance dispersal through extensive areas without breeding habitat.

Although boreal owls are thought to breed in much of the forested portion of Alaska, surveys have been conducted in few portions of the state (see Gabrielson and Lincoln 1959, Armstrong 1980). Literature documentation for boreal owls in Alaska extends from the Brooks Range (Campbell 1969), to the Pribilof Islands (Evermann 1913), and to the north Gulf Coast (Isleib and Kessel 1973). Recent surveys document singing boreal owls in southeast Alaska on the mainland and a number of islands (draft agency report, Suring 1993; see Map 2 in sleeve of this book).

The recognized distribution of boreal owls has changed yearly since 1979 as interest in the owl developed and efforts to locate breeding populations increased. Prior to 1979, breeding populations of boreal owls were not thought to occur south of Canada. The 1983 American Ornithological Union checklist of North American birds described the southern extent of western boreal owl populations as south-central Canada, although it also recorded breeding populations in Colorado and northwestern Wyoming. In 1985, Idaho, Washington, and Montana were added (data reported in Hayward *et al.* 1987a) but populations were recognized in only isolated locales in each state. By 1987, biologists realized that populations occurred throughout the northern Rockies in high elevation conifer forests south to northern New Mexico. I expect the documented range to continue to expand as previously unsurveyed regions receive attention. In Idaho and Montana, where surveys have been conducted for over a decade, our understanding of boreal owl distribution will become more refined. In regions where few surveys were conducted in the past, such as Utah, Alaska, northern Wisconsin, northern Michigan, and northern New England, I expect significant changes in the recognized distribution.

Map 2 depicts the estimated breeding range of the species based on reports from the literature and recent surveys conducted largely by state and federal agencies. Reports from the technical literature are acknowledged separately from agency surveys, because these records have undergone greater scrutiny. I recognize that individual records may be suspect.

Some surveys were conducted by inexperienced persons and the level of training and experience of personnel conducting surveys varied. Because the majority of survey personnel received some training and discussed their observations with owl experts, however, I believe the estimated distribution to be reliable.

Species Status and Trend

Direct measures of population status or trend are not available for populations in North America. In contrast with Europe, investigations of boreal owls in North America have been short term and have not emphasized study of productivity or demography. Due to the paucity of historical information, direct estimates of status and trend will be difficult in the near future. Currently, I am aware of only one effort, begun in 1988, to intensively monitor population trend in North America (Hayward *et al.* 1992).

The boreal owl's range in North America is extensive. In northern Canada, it occurs in many areas where land management currently does not alter natural vegetation patterns. Recent surveys indicate the species also occupies an extensive geographic range south of Canada. Populations in this region occur on lands where human impact is greater. The potential influence of land management on owls across these lands will be discussed later in this document. Since direct measures of trend are not available, and the species occupies a large geographic area, any inferences to population trend must be inferred indirectly by linking the species' ecology and observed patterns of landscape change.

In Fennoscandian forests, boreal owls are considered the most abundant Strigiform (Merikallio 1958, cited by Korpimäki 1984). Despite long-term investigation of the species, however, reliable indication of long-term trends are unavailable due to the difficulty in surveying and censusing nocturnal owls (Lundberg 1978). Short-term fluctuations in breeding populations are evident from nest box surveys (e.g. Franz *et al.* 1984, Lofgren *et al.* 1986, Schelper 1989, Sonnerud 1989, and Korpimäki 1992), but status and long-term trends have not been reported. Significant reduction in natural breeding cavities in Scandinavia resulting from removal of old forest (Korpimäki 1981 and others) would imply reduced populations and potentially restricted distribution.

MOVEMENTS: ANNUAL, SEASONAL, AND DAILY

Annual Movements and Site Tenacity of Adults

Annual movement patterns of boreal owls are poorly understood in North America but have received considerable attention in Fennoscandia and Germany. Trapping stations at Whitefish Point, Michigan, and Hawk Ridge Research Station, Minnesota, and records of owl sightings by birders represent the majority of data on boreal owl movements in North America (Kelley and Roberts 1971, Catling 1972, Evans and Rosenfield 1977 and references therein). Trapping observations are difficult to interpret, and conclusions drawn from these observations must be regarded as hypotheses.

Based on the periodic sightings of boreal owls (1922, 1954, 1962, 1965, 1968) south of the species' range in eastern North America, winter irruptions have been hypothesized by Catling (1972) and Evans and Rosenfield (1977). Reported irruptions extend from Maine through Michigan and Minnesota (Catling 1972). Periodic observations of boreal owls have been documented in Illinois (Coale 1914, Wyman 1915), Minnesota (Evans and Rosenfield 1977), Wisconsin (Erdman 1979), and New York (Yunick 1979) and frequently coincide with increased observations of northern saw-whet, great gray (*Strix nebulosa*), and northern hawk owls (*Surnia ulula*). Sightings and captures are concentrated in autumn (late October-mid November) and late winter (February-April). The age and sex composition of the irruptive populations are poorly understood. Furthermore, whether individuals observed during these irruptions attempt to breed in southern areas, return to breeding areas in the north, or represent a population sink, is unknown. Catling (1972:223) suggests that a return flight occurs in April and May. Speculation concerning direction of movements appears to be based on little empirical evidence.

In Idaho, during a single week in February 1986, two radio-marked males left home ranges occupied for more than a year (a third male died during the same period). One male was relocated in May 80 km away. Three radio-marked females in Idaho left their former home ranges within 2 weeks of ceasing brooding young in July. One moved ~17 km while the others moved greater distances and could not be relocated (Hayward *et al.* 1987b). Although these owls were documented making nomadic-like movements, other radio-marked owls in the study re-

mained sedentary. These observations are very limited but suggest nomadic behavior.

In contrast with limited information in North America, extensive European studies suggest a complex pattern of nomadism and site tenacity that varies geographically and differs among sex and age classes. In general, the species is characterized as nomadic, at times exhibiting year-round residence within a stable home range but dispersing in years of poor prey populations (Mysterud 1970, Wallin and Andersson 1981, Lofgren *et al.* 1986, Korpimaki *et al.* 1987, Sonerud *et al.* 1988, Schelper 1989). Korpimaki (1986b) recognized a trend of increased population fluctuations in more northern populations associated with a greater degree of nomadism. He related the pattern to winter snow depth and range of prey available to the owls in winter.

In Scandinavia where year-to-year movements were studied using band recoveries from long-term site specific studies employing nest boxes, a unique pattern of residency and nomadism was first recognized by Mysterud (1970). Mysterud (1970) suggested that nomadic behavior in the Fennoscandian population is adapted to the 3-4 year microtine cycle and regional variability in microtine abundance. Lundberg (1979) refined the model and hypothesized that the conflicting pressures of food stress favoring nomadism and nest site scarcity favoring site tenacity result in different movement patterns in males and females; females exhibit nomadism while males exhibit greater site tenacity. Lofgren *et al.* (1986), Korpimaki *et al.* (1987), and Sonerud *et al.* (1988) confirmed the mixed pattern of male residency and irregular female dispersal in adult Tengmalm's owls. Korpimaki's review (1986b) further refined the understanding of nomadism in the species, suggesting that sexual differences in residency vary geographically. In central Europe both sexes appear to be largely site tenacious, but young owls are nomadic (Franz *et al.* 1984). In southern Fennoscandia males are resident and females and juveniles nomadic. In northern Sweden, both adults and juveniles exhibit nomadism (Korpimaki 1986b).

In addition to the influence of snow conditions, geographic setting, and prey conditions mentioned above, nest predation and nesting success have been shown to influence dispersal in adult female boreal owls (Sonerud *et al.* 1988). Adult females whose nests are unsuccessful have an increased probability of dispersing long distances. Predation of nestlings further increases the probability of long dispersal (figure 2).

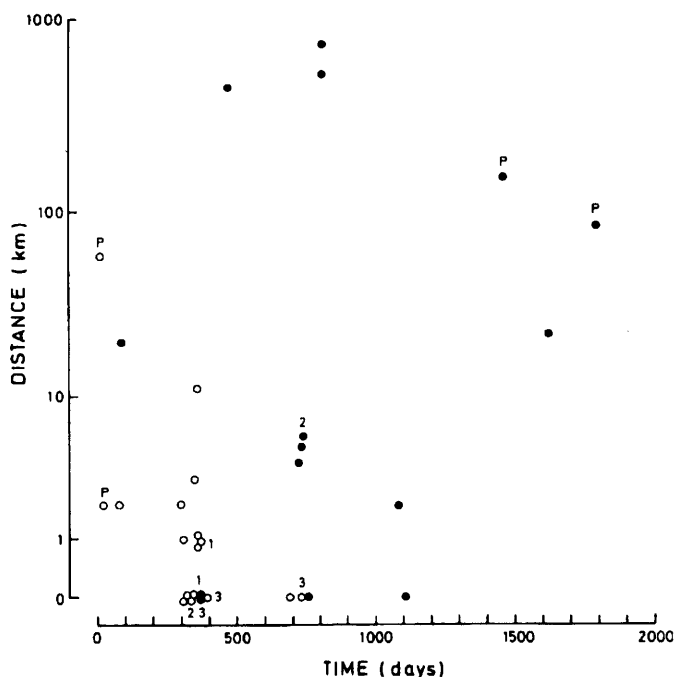


Figure 2.—Distance moved and time elapsed between ringing and recovery of female Tengmalm's owls ringed in Norway while breeding. Open circles denote dispersals occurring within a microtine peak (high prey availability), and filled circles denote dispersals involving a microtine decline (low prey availability). Dispersals following nest predation are indicated by a P. Dispersals made by the same female are indicated by numbers (from Sonerud *et al.* 1988).

Dispersal Frequency

Interpopulation movements are extremely important in metapopulation (population of populations) dynamics. Therefore it is important to determine rates of immigration and emigration among component populations. Estimating the portion of a population involved in nomadic or dispersal movements is difficult, however. For instance, most recoveries of banded birds are from nesting birds re-trapped by the original bander. Therefore, estimates of dispersal will be biased toward documenting site tenacity or short-distance movements.

Despite these shortcomings, studies of boreal owls in Fennoscandia and Germany have estimated emigration rates that follow the north-south geographic gradient described earlier (more nomadic movements in northern populations). After successfully nesting, 0% and 8% of adult females dispersed farther than 20 km from two populations in Germany (central Europe) (Franz *et al.* 1984 and Schwerdtfeger 1984, both according to Sonerud *et al.* 1988). Corresponding proportions for central Norway, Finland, and northern Sweden were 14%, 31%, and 33%, respectively (Lofgren *et al.* 1986, Korpimaki *et al.* 1987, and Sonerud *et al.* 1988). The proportion of adult females dispersing farther than 100 km in central Norway, Finland, and northern Sweden were 13%, 17%,

and 17%. In all cases dispersal over 100 km took place between microtine peaks.

Proportions of males dispersing is more poorly documented because of the greater difficulty in trapping nesting males. In one Finnish study (Korpimaki *et al.* 1987), all re-trapped males ($n = 23$) were caught within 5 km of the original banding site. Of 170 males recovered in Finland, only two have been recovered far from their original breeding site (97 and 180 km).

Based on these patterns, I suggest that boreal owls in the United States likely occur in a metapopulation structure. The nomadic nature of the species, frequent movements by adults and young, and the ability of individuals to disperse long distances indicate the species' behavior facilitates a metapopulation distribution. Furthermore, suitable habitat in the United States occurs in numerous patches separated by tens to hundreds of km (figure 1, also see *Movements as Related to Demography and Metapopulation Structure* later in this chapter). The habitat distribution, then, provides a landscape that will support small populations each separated by distances greater than the normal daily movement and normal yearly movement distances of individual owls. Linkage among populations, then, results from the nomadic movement of adults or exceptional long-distance dispersal of some young owls.

Dispersal Distances

Adults who disperse over 20 km from a breeding site may frequently move long distances as nomads. Documenting long movements is difficult, however. Lofgren *et al.* (1986) reported females breeding 550, 308, 289, 220, 70, and 70 km from their original breeding site in northern Sweden. In the same study, Lofgren *et al.* (1986) reported males breeding 21 and 115 km from their original breeding site. Sonerud *et al.* (1988) reported dispersal distances for breeding adult females first banded in southeastern or central Norway (figure 2) while Korpimaki *et al.* (1987) summarized dispersal distances for Finland (figure 3). In Germany, based on owls banded at nest boxes, Franz *et al.* (1984) found 5% of females nesting in the same box as the previous year and that the shortest 93% (left side of the distribution) of all dispersal movements averaged 9.3 km. Of the 2% of females who dispersed long distances, the maximum was 194 km. Other maximum distances include 728 km for Norway (Sonerud *et al.* 1988), 550 km for Sweden (Lofgren *et al.* 1986), and 550 km for Finland (Korpimaki *et al.* 1987).

Annual Movements and Site Tenacity of Juveniles

Young boreal owls frequently disperse long distances from natal sites but have been recorded breeding within 0.5 km of their natal site (Hayward, G. D. and P. H. Hayward unpublished data from Idaho). Korpimäki *et al.* (1987) reported median distances of 88 and 21 km between juvenile male and juvenile female banding sites and later at two breeding sites in Finland (figures 3 and 4). In Norway, 3 males banded as juveniles were recaptured breeding 5-11 km from the natal site while 9 females had moved 2-239 km (Sonerud *et al.* 1988). Twenty percent of recoveries for owls marked as nestlings exceed 100 km in West Germany (Franz *et al.* 1984) and 51% in Finland (Korpimäki *et al.* 1987).

Seasonal Movements

Patterns of movements associated with seasonal cycles have been studied in only one locale (Hayward *et al.* 1993). Patterns observed during this study in the wilderness of central Idaho may be unique to the geographic characteristics of the study area. Winter and summer home ranges of individual owls overlapped extensively but centers of activity for 12 radio-marked owls shifted. Average elevation of roosts used by the owls was 186 (± 105) m lower in winter than summer. Despite this shift, areas used in winter had complete snow cover exceeding 0.5 m each winter and the owls frequently used areas with 1.5-2.0 m of snow accumulation. Snow-free slopes occurred within 2 km of most owls' ranges during most winters, but owls were not observed using these areas.

Movements Within the Home Range

Burt (1943:351) defined home range as the area traversed by an individual in its normal activities of food gathering, mating, and caring for young. For boreal owls, these movements define how individuals use space during periods when they are not nomadic or dispersing. Except during periods of nomadism, boreal owls are resident within and between years.

Boreal owls studied in the western United States use large home ranges. In Colorado, home ranges of two males located on daytime roosts (>8 locations for each owl spanning 252 and 173 days) encompassed 1,395 and 1,576 ha and overlapped one another by >90% (Palmer 1986). In central Idaho, nest sites occurred in lower portions of home ranges (few

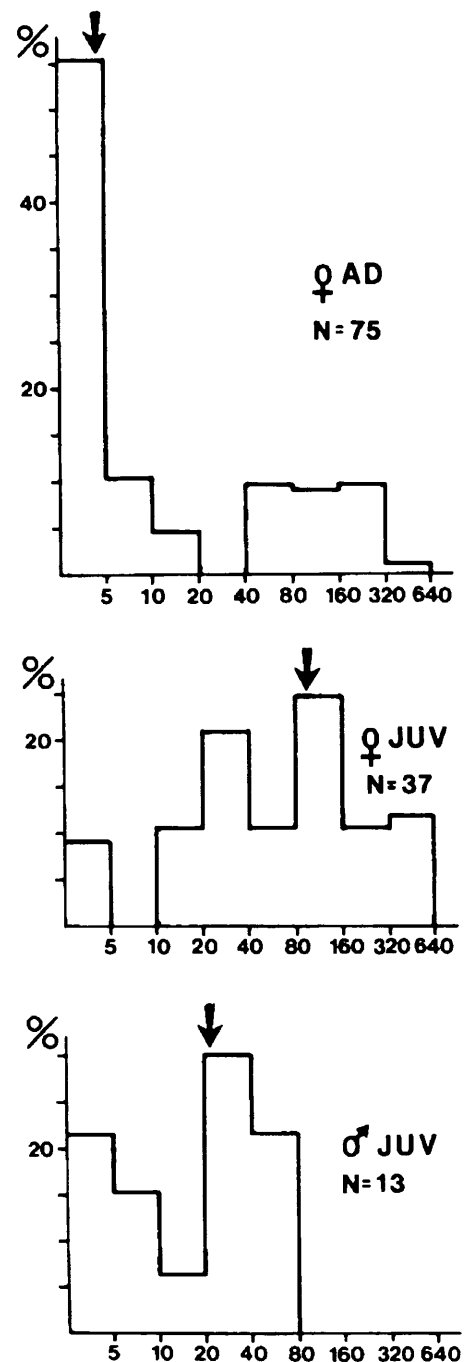


Figure 3.—Dispersal distances (km, log scale) between ringing and recovery sites of Tengmalm's owls ringed as breeding females (upper chart) or nestlings (lower charts) and retrapped in later years when breeding. Medians (4 km, 88 km, and 21 km) are indicated by arrows. N = number of recoveries (from Korpimäki *et al.* 1987).

cavities were found at higher elevations) while roosting and foraging occurred throughout the range. Winter ranges covered 1,451 ha (± 522 ; n = 13, range 320-3390 ha), and summer ranges covered 1,182 ha (± 334 ; n = 15, range 229-2386 ha). These estimates of home range size are based on modest sample sizes and therefore should be considered minimum use areas. Harmonic mean estimates (which were used in this case) tend to be biased low with small sample

size (E. O. Garton; pers. comm.).

Boreal owls are very mobile predators; the owls frequently traverse much of their home range in the course of 2-3 days or weeks (Hayward *et al.* 1987b). In spruce-fir forests of Colorado, roosts used on consecutive days averaged 708 m apart ($n = 113$) (Palmer 1986). In Idaho, distance between consecutive roosts of 14 owls (150 locations of consecutive roosts) averaged 1,540 m (± 446) in winter and 934 m (± 348) in summer (Hayward *et al.* 1993).

Daily Movements

Diurnal Period

Boreal owls move little during the day; they generally remain within the same forest stand during daylight. These owls frequently change roost trees but rarely fly over 40 m when changing roosts (Hayward *et al.* 1993). Based on studies in Idaho (Hayward *et al.* 1993), during daylight boreal owls perch quietly with eyes closed a majority of the time (77% based on 46 hours of observation on 16 days). Periods of sleep rarely exceed 40 minutes and are broken by 2-5 minute periods of preening (6% of time) and looking about (10% of time). Eating (4%), daytime hunting (1%), and moving among roost perches (<1%) are other important daily activities. I observed owls hunt during daylight in winter at 2.9% of roost locations ($n = 448$) and in summer at 7.4% ($n = 446$) of roost locations (Hayward 1989).

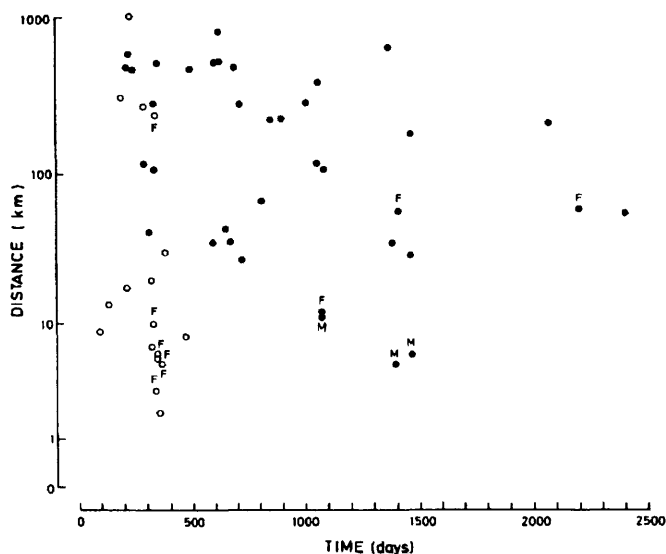


Figure 4.—Distance moved and time elapsed between ringing and recovery of female Tengmalm's owls ringed as nestlings in Norway. Open circles denote dispersals occurring within a microtine peak (high prey availability), while filled circles denote dispersals involving a microtine decline (low prey availability). Males recaptured while breeding are indicated by M, females recaptured while breeding by F (from Sonerud *et al.* 1988).

Nocturnal Period

Nocturnal activity is poorly studied, especially outside the breeding season. Boreal owl foraging activity is concentrated after dark except in northern latitudes during summer. During periods of 24-hour light, foraging is concentrated between sunset and sunrise.

Event recorders have been employed at nest cavities to infer foraging activity patterns of male owls provisioning nests. In Finland, during the incubation period, prey deliveries generally began 1 hour 14 minutes after sunset and ended 49 minutes before sunrise based on records for 6 years (Korpimäki 1981). Depending upon latitude and phase of nesting cycle, night-time activity follows a bimodal pattern with peaks in nest deliveries during the first hours after sunset and again prior to sunrise (Klaus *et al.* 1975, Korpimäki 1981, Hayward 1983). This pattern is most apparent in southern latitudes (i.e., East Germany, Idaho) and early in nesting. In northern Scandinavia, a bimodal pattern appears early in incubation but the two peaks fuse as daylength increases and night-time foraging period decreases (Korpimäki 1981). The foraging activity period also varies depending on phase of the vole cycle. In peak vole years, activity lasted longer each night, the peaks in activity were more pronounced, and prey deliveries after sunrise were more frequent (Korpimäki 1981).

Night-time foraging can be very intense, especially when nestlings near fledging. In Idaho, records from four nests suggest that females leave the nest once each night during incubation (for evacuation) and usually twice after the young hatch (Hayward, G. D. and P. H. Hayward, unpubl. data). Assuming that all records other than for the female's evacuation were prey deliveries, deliveries averaged 3.5 (± 0.33 SD, $n = 84$, range = 0-9) during incubation and 5.0 (± 0.61 SD, $n = 6$, range = 0-12) during brooding. Clutches at the four nests were 2, 2, 3, and 3; each fledged two young. In Finland, Korpimäki (1981) estimated 9.8 deliveries/night during brooding period and 8.0 after the female left the nest.

Norberg (1970), Bye *et al.* (1992), and Hayward *et al.* (1993) documented hunting movements of boreal owls. Based on these observations, the owls can be classified as sit-and-wait predators or searchers (as opposed to pursuers) but are very active while hunting. During a foraging bout, the birds move through the forest in an irregular or zigzag pattern, flying short distances between perches (Hayward 1987). They spend a majority of time perched; little time is spent actively pursuing prey. While perched, the owl constantly looks about with rapid head movements,

apparently responding to forest sounds.

When foraging, owls usually fly 10 to 30 m between hunting perches (Norberg 1970, Hayward 1987). In Idaho, over 75% of all flights were 25 m or less. Although the pattern of flights varied, owls observed foraging in Idaho doubled back frequently and, thus, covered a relatively small area within several forest stands rather than a long narrow path. While searching for prey, boreal owls perch on low branches. Perches used during foraging observations in Idaho averaged 4 ± 0.6 m high ($n = 114$). Similarly, average perch height for 17 owls monitored in Norway ranged from 1.7 to 8.7 m (Bye *et al.* 1992).

Boreal owls may traverse several km during a nocturnal foraging bout. Because daytime roosts appear to represent the end of nighttime foraging bouts, locations of consecutive daytime roosts suggest the magnitude of minimum travel distances (Hayward *et al.* 1987b). Distances between consecutive day roosts of 14 owls (7 females and 7 males) on 150 occasions over 4 years in Idaho ranged from 0-6935 m. Mean distances did not differ significantly between winter and summer (winter 1540 [± 446] m, summer 934 [± 348] m). During nesting, five males roosted over 1000 m from their nests 85% of the time (average 1729 [± 831] 200-5600 m) (Hayward *et al.* 1993).

HABITAT USE

Broad Habitat Use Patterns

As year-round residents, boreal owls use similar habitats during all seasons. They occur only in forested landscapes where they nest exclusively in tree cavities or artificial nest structures (Mikkola 1983). The few studies documenting nesting habitat indicate the species uses a range of vegetation types depending on geographic region (e.g., Bondrup-Nielsen 1978, Eckert and Savaloja 1979, Palmer 1986, Korpimäki 1988a, Hayward *et al.* 1993). In northern portions of their range in North America (Alaska and Canada) the owls breed in boreal forest characterized by black and white spruce (*Picea mariana*, *P. glauca*), aspen (*Populus tremuloides*), poplar (*P. balsamea*), birch (*Betula papyrifera*), and balsam fir (*Abies balsamea*) (Bondrup-Nielsen 1978, Meehan and Ritchie 1982). In northern Minnesota and Michigan, singing sites and nests have been documented in old aspen and mixed-forest sites (Eckert and Savaloja 1979, Lane 1988). In the southern portions of their range in North America (Rocky Mountains, Blue Mountains, and Cascades) published research documents boreal owls in subalpine forest habitats characterized largely by subalpine fir (*Abies lasiocarpa*)

and Engelmann spruce (*Picea engelmannii*) and transition forests within 100 m of this elevation (Palmer 1986, Hayward *et al.* 1987a). Because of changes in life zones with latitude, an elevation range cannot be specified for the entire western region of the United States. However, extensive surveys in Idaho and Montana in 1984 and 1985 found no owls below 1,292 m elevation, and 75% of the locations were above 1,584 m (Hayward *et al.* 1987a). Less extensive surveys in northern Colorado found most locations above 3050 m (Palmer 1986).

In USDA Forest Service Regions 1, 2, 4, 6, 9, and 10, biologists have documented boreal owls occurring (but not confirmed breeding) on 26 National Forests and confirmed breeding on 11 other Forests (Chapter 8, table 2). We asked these biologists for an indication of the forest types where boreal owls have occurred. Spruce-fir forest was reported more than any other type (45% of forests with documented breeding). Other forest types in decreasing order of frequency were lodgepole pine (*Pinus contorta*), mixed-conifer, Douglas-fir (*Pseudotsuga menziesii*), aspen (*Populus tremuloides*), black spruce (*Picea mariana*), red-fir (*Abies magnifica*), and western hemlock (*Tsuga heterophylla*).

In Europe, descriptions of breeding habitats have included conifer and deciduous forest types. In Scandinavia, studies report nests in artificial structures hung in pine (*Pinus* spp.), spruce (*Picea* spp.), and birch (*Betula* spp.) forest (Norberg 1964, Korpimäki 1981, Solheim 1983a). In France, "mountain pine" (*Pinus uncinata* and *P. sylvestris*) forest and old forest stands with beech (*Fagus* spp.) were used by owls located by Dejaifve *et al.* (1990:267) and Joneniaux and Durand (1987), respectively. In Germany, conifer forest with old trees were used for nesting (Konig 1969, Jorlitschka 1988).

Landscape Scale Habitat Use

Published accounts of boreal owl habitat use from North America do not directly address patterns of habitat use at the landscape scale. Studies have not compared density, productivity, frequency of breeding attempts, or other measures indexing habitat suitability among landscapes with different mixes of forest cover. Neither have studies directly examined patterns of foraging habitat use across landscapes.

Indirect evidence from Europe and North America does suggest that boreal owls differentiate among forest habitats at the landscape scale. Evidence presented below supports the general statement by König (1969) that "in certain parts of [the study] area

the density of Tengmalm's owls was rather high, while in other ... forests no *Aegolius* existed."

Studies by Hayward *et al.* (1993) in Idaho provide some indirect information on landscape scale habitat use patterns. Nest sites and singing sites (considered representative breeding habitat) were not distributed randomly throughout the study area. Nesting was concentrated in mixed-conifer and aspen forests with no nesting in lodgepole pine forest and infrequent nesting in spruce-fir forests. In contrast, summer roost sites and foraging sites were concentrated in spruce-fir forests. Due to the natural segregation of forest types used for nesting and those used for roosting and foraging, habitat used for different ecological functions was segregated in the landscape. All the resources used by the owls were not provided by any single vegetation type leading to a complex pattern of habitat use. Spruce-fir forest in this study area had few potential nest cavities but small mammal sampling documented that this type supported the most abundant prey populations. In contrast, nest cavities were abundant in mixed conifer forest that supported few prey. Our discussion of microhabitat later provides some insight into landscape patterns through the examination of differences in habitat quality at the stand scale.

Korpimäki (1988a) provides a more direct examination of differences in habitat quality at the landscape scale from his studies in Finland. He rated territory quality of 104 nest sites based on frequency of use over 10 years. Territory occupancy varied from 0 to 9 nestings in 10 years. Poor territories (never occupied) occurred in extensive, uniform forests dominated by pine (*Pinus sylvestris*). These territories had little spruce forest and a high proportion of marshland. The proportion of pine forest decreased and the proportion of spruce forest (*Picea abies*) and agriculture land increased with increasing grade of territories (those with more frequent nesting). The conclusion that territories with spruce forest and agricultural land (in small patches) were the highest quality habitat was corroborated by evidence beyond the frequency of nesting. High quality sites supported breeding during prey crashes, mean clutch size was higher ($P < 0.05$), and number of fledglings was generally greater ($P < 0.05$) than other sites. Poor territories (occupied 0, 1, or 2 times) supported breeding only during peaks in the well-documented vole cycle (Korpimäki 1988a and references therein).

Korpimäki (1988a) explained this pattern based on variation in the abundance and stability of small mammal populations across the vegetation categories.

Spring and fall densities of *Clethrionomys glareolus*, a major small mammal prey, were three times higher in spruce than pine forests (Korpimäki 1981). The mean densities of small birds, important alternative prey, were also higher in spruce forests than in pine (331 versus 260 pairs/km²) (Korpimäki 1981). Furthermore, small mammal populations were more stable in the spruce forests than other types (Korpimäki 1988a). Korpimäki (1988a) pointed out that the pattern of habitat occupancy (virtually all habitats used in vole peaks but only "good" territories occupied during cyclic lows) fit the Fretwell and Lucas (1969) "ideal free" model of habitat use. Thus the size of the breeding population strongly influenced the pattern of habitat use at the landscape scale.

Home Range Scale Habitat Use

Home range size and movements within boreal owl home ranges was discussed in the Movements Within the Home Range section. Research in North America has not directly examined patterns of habitat use within individual home ranges except at the microhabitat scale which is discussed below. Patricia Hayward and I are currently analyzing data collected during the study reported in Hayward *et al.* (1993) at the home range scale but results are not yet available.

Sonerud *et al.* (1986) provide some data at this scale based on observations of a single radio-marked male owl followed on five nights. Because the results stem from observations of a single bird during a single week, general patterns cannot be inferred. The results are important, however, because they are the only data currently available and the pattern observed corroborates results reported throughout this section. The owl used an area of 205 ha during the 5 nights (based on 107 nocturnal locations using a minimum convex polygon estimator). Nightly use areas ranged from 40-78 ha and the maximum distance between foraging areas and the nest for each night varied from 1030-1320 m. While foraging, the owl favored old forest and avoided clear cuts and young plantations in spite of lower prey densities in the former (Sonerud *et al.* 1986:105).

Microhabitat

Nest Sites

A majority of nest site locations described in the literature have not resulted from efforts designed to survey a range of habitats to determine both habitats used and those not used. The results, then, can-

not be interpreted as an indication of selection but rather to describe some subset of used habitats. In Alaska, eight nests located near Fairbanks occurred in closed-canopy deciduous or mixed forest; none occurred in uniform conifer forest (Meehan and Ritchie 1982). Of five nests in natural cavities, four occupied flicker holes and one a natural cavity. In Canada, Bondrup-Nielsen (1978) located 6 nests, all in aspen—3 in live trees, 3 in snags. Minnesota nests have been documented in old aspen clones intermixed with conifers (Eckert and Savaloja 1979 and Lane 1988). In a more extensive investigation involving 9 National Forests in Montana and Idaho, 76% of 49 boreal calling sites (recognized as potential breeding sites) occurred in mature and older forest stands (Hayward *et al.* 1993). The exceptions were locations in lodgepole pine (*Pinus contorta*) stands in drainages where lodgepole was the only forest type. The majority (88% of 49 observations) of owls were located in stands on subalpine-fir habitat types. Proportions for other habitat types included Engelmann spruce (3%), Douglas-fir (6%), and western hemlock (3%).

During 4 years of study in the wilderness of central Idaho, Hayward *et al.* (1993) documented nests in stands of old mixed-conifer (11), old Engelmann spruce (7), old aspen (5), and old Douglas-fir (5) forest. A nest box experiment in the same area suggested that owls avoided nesting in forests lacking the structural features of mature and old forest when alternate sites in old forest were available (Hayward *et al.* 1993). This study did examine available forest structure and compared used sites with a sample of available sites. Forest structure at nest sites differed from the random sample (101 sites) of available forest. Used sites occurred in more complex forest, with higher basal area, more large trees, and less understory development than available sites. The forest immediately around nest trees had an open structure. Density of trees 2.5 to 23-cm-dbh (diameter at breast height) in a 0.01-ha plot around the nest tree averaged 398 ± 162 /ha (range 0-1,482). The density of trees at nests was three times lower than the average at winter roost sites. Nest sites averaged $57 (\pm 16)$ trees/ha over 38 cm dbh, $17.8 (\pm 3.1)$ m²/ha basal area, and 30% (± 4.3) overstory (> 8 m above ground) canopy cover (this is not total canopy cover but cover of upper canopy). Stands used for nesting supported an average of $9 (\pm 6.0)$ snags per ha over 38 cm dbh. Size of the stand containing the nest ranged from 0.8-1.3 ha in aspen and 1.6-14 ha in conifer forest.

The range of sites used by boreal owls is quite broad despite the evidence that the species chooses particular forest structures when a variety of nest

sites are available. In Idaho and Norway nest boxes in clearcuts have been used (see Sonerud 1989 and Hayward *et al.* 1992). The use of these sites, however, does not indicate that this is high quality habitat.

Nest Tree and Cavity Characteristics

Boreal owls are secondary cavity nesters and nest primarily in cavities excavated by pileated woodpecker (*Dryocopus pileatus*) and northern flicker (*Colaptes auratus*) in North America, and black woodpecker (*Dryocopus martius*) cavities or nest boxes in Europe. In central Idaho 18 of 19 nests were attributed to pileated woodpeckers; a northern flicker probably excavated the other. Cavity dimensions averaged 31 cm (± 7.61 ; $n=19$, range 7-50) deep and 9 cm (± 2.11 range 15-26) horizontally. Cavity entrances measured 102 mm (± 12.41 range 64-150) high and 95 mm (± 11.89 range 56-148) wide (Hayward *et al.* 1993).

Nests located in Idaho were generally in large trees or snags. Tree diameter at the cavity averaged 41 ± 5.21 cm (range 26-61 cm) and tree dbh averaged 64 ± 11.02 cm (range 33-112 cm). The smallest of these were all aspen and, therefore, still larger trees grew in the nest stand. Ten (of 19) nests occupied snags, including eight ponderosa pine, one aspen, and one Douglas-fir. Snag condition included 3 old branchless snags >11 m tall, 2 hard snags with sloughing bark and only large branches remaining, and 5 young snags with bark and complete limbs (Hayward *et al.* 1993).

In contrast with nest conditions in the United States, over 90% of some Scandinavian populations nest in artificial structures. This pattern is attributed to the scarcity of primary cavity nesters and paucity of large old trees (Korpimäki 1981, 1985).

Roost Sites

Three studies in North America addressed roosting habitat: one in Canada by Bondrup-Nielsen (1978), one in Colorado by Palmer (1986), and one in Idaho by Hayward and Garton (1984) and Hayward *et al.* (1993). These studies demonstrate that, unlike many forest owls, individual boreal owls roost at many different sites and choose roosts dispersed widely throughout their home range. The available evidence suggests that under some circumstances (see below) the owls select particular forest conditions for roosting but much of the time are unselective.

In Canada, 30% of 30 roosts located in spring and summer were in aspen or birch; the remainder were in conifers (Bondrup-Nielsen 1978). Based on com-

parison with paired random sites, Bondrup-Nielsen (1978) concluded that the owls were not selective in roost choice. In Colorado, 174 roosts located in winter and summer did not differ significantly between seasons although low statistical power may have led to this conclusion. It was not clear from the analysis whether forest structure at roosts differed from paired random sites. Combining seasons, roost sites averaged 14.7 trees/ha >39 cm dbh, 6 snags/ha, and 44% canopy cover (Palmer 1986). Average species composition of roost stands were 42% Engelmann spruce, 42% subalpine fir, and 6% lodgepole pine suggesting that the owls choose late successional stands for roosting.

In Idaho, based on habitat measurements from 430 roosts used by 24 radio-marked owls, habitat type (as defined by Steele *et al.* 1981) and forest structure differed between roosts used in winter and summer ($P < 0.001$, Hayward *et al.* 1993). Forest stands used for winter roosts averaged 58% canopy cover, 26 m²/ha basal area, 1,620 trees/ha with 2.5–23 cm dbh, and 165 trees/ha over 23.1 cm dbh. Summer roosts averaged 63% canopy cover, 30 m²/ha basal area, 2,618 trees/ha with 2.5–23 cm dbh, and 208 trees/ha over 23.1 cm dbh. Winter and summer roosts differed in all aspects of forest structure measured. All roosts ($n=882$) were in conifers; the owls were never observed roosting in cavities as is reported in Europe (Korpimäki 1981).

In the same study, roost sites were compared with paired random sites using a paired Hotelling's T^2 (189 winter, 241 summer sites). The results provided strong evidence for selection in summer, but results for winter also suggested selection (winter $P = 0.021$; summer $P < 0.0001$). Summer roosts occurred at cool microsites with higher canopy cover, higher basal area, and greater tree density than paired random sites (Hayward *et al.* 1993). When the authors compared temperature at the roost and in the nearest opening (both temperatures taken in the shade while the owl was roosting), roost sites were significantly cooler when ambient temperatures exceeded 4° C ($P < 0.001$). The difference in temperature increased with increasing ambient temperature and the owls gular fluttered when temperatures were as mild as 20° C. The authors concluded that in summer, the owls chose cool microsites for roosting to avoid heat stress. In winter, the owls did not appear to be thermally stressed and used a wider variety of roost conditions.

Foraging Sites

The nocturnal foraging pattern of boreal owls has hampered attempts to study foraging habitat use

(Hayward 1987). Therefore, the inferences concerning foraging habitat are largely based on indirect evidence.

Studies in Idaho (Hayward 1987, Hayward *et al.* 1993) based on roost locations (assumed to represent the end of a foraging bout) suggest that mature and older spruce-fir forests were important for foraging. Owls were observed successfully foraging in these forests and the locations of radio-tagged birds also indicated male owls were hunting in these forests while feeding young at nests located at lower elevations. Data on prey distribution and food habits further supported this contention (Hayward *et al.* 1993). Palmer's (1986) observations in Colorado also indicated older spruce-fir forest was used for hunting.

Studies in Norway also noted the importance of mature spruce forest for foraging (Sonerud 1986, Sonerud *et al.* 1986). Direct observations and diet indicated that during winter and summer the owls foraged primarily in older forest sites. In early spring, immediately following snowmelt, owls hunted clearcuts for a short period until lush vegetation developed. Owls favored mature forest during winter because snow conditions (uncrusted snow) facilitated access to prey. In summer, mature forest sites had less herbaceous cover than open sites that allowed greater access to prey. Following spring thaw, before herbaceous vegetation became dense, owls shifted to openings where densities of voles exceeded densities in forested stands.

In his 1987 address to the Northern Owl Symposium, Norberg (1987) highlighted the morphological adaptations of *Aegolius funereus* that facilitate foraging in forest stands at night. He noted the extreme skeletal asymmetry that facilitates ocular prey detection and localization under dark forest conditions. The short, broad, rounded wings of the boreal owl facilitate silent, agile flight in tight forest conditions. These morphological characteristics open up possibilities for exploiting habitat types unavailable to species lacking the traits. He also noted that the light wing-loading of boreal owls allow individuals to efficiently forage among habitat patches dispersed throughout their home ranges without expending excessive energy commuting between patches. Furthermore, the light wing-loading reduces the cost of foraging at distant sites and transporting prey back to the nest. This line of reasoning corroborates the limited observations that suggest that small, dispersed patches of high quality foraging habitat (high prey availability) are hunted by boreal owls who use large home ranges.

Morphology, of course, is not the only potential explanation for observed habitat use patterns. Predators and competitors may also influence foraging habitat use.

FOOD HABITS

Feeding

Foraging Movements

Boreal owls hunt primarily after dark except in northern regions without summer darkness (Norberg 1970, Mikkola 1983). In southern areas the species exhibits a biphasic rhythm with peaks of activity 2000-2200 h and 0200-0500 h (Mikkola 1983). Prey deliveries at monitored nests in Idaho (Hayward, G. D. and P. H. Hayward, unpubl. data) never occurred between sunrise and sunset; however, owls observed on daytime roosts ($n = 882$) occasionally hunted in daylight (13 observations in winter, 33 observations in summer) (Hayward *et al.* 1993). On 10 occasions the author observed owls capture prey from daytime roosts.

Boreal owls forage using sit and wait tactics (as opposed to pursuit). Four owls observed foraging on 13 occasions in Idaho moved through the forest in a zig-zag pattern, flying short distances ($\bar{x} = 25 \pm 8$ m; $n = 123$) between perches. Perch heights averaged $4 (\pm 0.6 \text{ } n = 114)$ m, and owls watched for prey for less than 5 minutes on 75% of 150 perches (Hayward *et al.* 1993). Norberg (1970) recorded perch heights averaging 1.7 (0.5-8) m ($n = 154$) and flight distances of 17 (2-128) m, and Bye *et al.* (1992) recorded similar observations.

Prey Capture

Boreal owls observed in Idaho usually attacked prey within 10 m of their hunting perch (Hayward *et al.* 1993). In Norway, Bye *et al.* (1992) reported attack distances (direct distance between the owl and the prey) from 2.2 to 12.6 m. Successful attacks averaged 5.3 m ($n = 10$) and unsuccessful attacks 6.1 m ($n = 10$). Norberg (1970) describes pouncing and killing behaviors in detail. He (Norberg 1970, 1987) notes observations of boreal owls capturing prey either under the snow surface (plunge diving) or obscured by vegetation. The ability to locate prey aurally is attributed to the extreme asymmetry of the owl's skull (Norberg 1978, 1987), which permits localization of sounds in vertical, as well as horizontal, directions.

Diet

In North America, usual prey species are voles, particularly red-back voles (*Clethrionomys gapperi*), heather voles (*Phenacomys intermedius*), northern bog lemming (*Synaptomys borealis*), and *Microtus* spp.; mice, including deer mice (*Peromyscus* spp.) and jumping mice (*Zapus princeps*); shrews, (*Sorex* spp.); northern pocket gophers (*Thomomys talpoides*); squirrels, including northern flying squirrels (*Glaucomys sabrinus*) and chipmunks (*Tamias* spp.); birds, especially thrushes (*Catharus* spp.), warblers, dark-eyed junco (*Junco hyemalis*), red crossbill (*Loxia curvirostra*), American robin (*Turdus migratorius*), mountain chickadee (*Parus gambeli*), common redpoll (*Carduelis flammeus*), kinglets, and woodpeckers; and insects, especially crickets (Bondrup-Nielsen 1978, Palmer 1986, Hayward and Garton 1988, Hayward *et al.* 1993). Weasel (*Mustela* spp.), woodrat (*Neotoma cinerea*), juvenile snowshoe hare (*Lepus americanus*), and pica (*Ochotona princeps*) represent unusual prey.

Within North America, little difference in diet is apparent between studies in Alaska (T. Swem, pers. comm.), Canada (Bondrup-Nielsen 1978), and the Rocky Mountains (Palmer 1986, Hayward *et al.* 1993). In each locale, red-backed voles (*Clethrionomys* spp.) and *Microtus* spp. were dominant prey.

Boreal owl food habits have been studied more thoroughly in Europe; for a summary see Cramp (1977). The results are surprisingly similar to North America. *Clethrionomys* sp. and *Microtus* sp. dominate the diet in most cases. Results suggest, however, that in Scandinavia, boreal owls consume more voles associated with open habitats than are recorded in the Rocky Mountains of North America. This could be due to differences in habitat characteristics in particular study areas, in the owls foraging behavior, in predation risks, or in competitive interactions.

Quantitative Analysis

Most samples of boreal owl prey in North America are small. Bondrup-Nielsen (1978) reported 58 individual prey from his two study sites in Canada, Palmer (1986) recorded 72 prey found in 4 years in Colorado, and Hayward *et al.* (1993) reported 914 prey identified from 4 years in Idaho (table 1). These data are not sufficient to make in-depth comparisons between geographic areas, examine functional or numeric responses to changes in prey populations, or predict changes in diet or owl demography in response to changes in prey populations. As a group, however, these investigations cover a broad geographic area and provide a sound basis for gen-

eralizations concerning boreal owl diet in North America.

The breadth of prey represented in the boreal owl diet contrasts with the narrow range of prey taken frequently. The data suggest that the boreal owls are vole specialists under most circumstances. *Microtus* and *Clethrionomys* constituted 45 and 31% (by frequency) of prey identified from the two study sites in Canada (Bondrup-Nielsen 1978). In Colorado, *Clethrionomys* and *Microtus* were 54 and 25% of the diet (Palmer 1986). In Idaho, red-backed voles were

the most frequent prey in summer (35% by frequency) and winter (49% by frequency) (32 owls over 4 years). In terms of prey biomass, red-backed voles accounted for 37% of the annual prey. Northern pocket gophers (26%) and *Microtus* spp. (11%) were the only other species accounting for over 10% of the annual prey biomass (Hayward *et al.* 1993). Northern flying squirrels were captured by female owls in winter and accounted for 45% of winter prey biomass. Overall, small mammals accounted for 79% of prey (95% of estimated biomass).

Table 1. – Diet of boreal owls in Idaho (Hayward *et al.* 1993), Colorado (Palmer 1986), and Canada (Bondrup-Nielsen 1978) based on pellets and prey identified from nests.

Prey	Idaho		Colorado	Canada
	% of prey items	Biomass ¹ (%)	% of prey items	% of prey items
Mammals				
Red-backed vole (<i>Clethrionomys</i> spp.)	36	37	54.2	31
Northern pocket gopher (<i>Thomomys talpoides</i>)	10	26		
Unidentified shrews (<i>Sorex</i> spp.)	11	3	5.5	2
Unidentified voles (<i>Microtus</i> spp.)	9	11	25	45
Deer mouse (<i>Peromyscus maniculatus</i>)	6	5	1.4	10
Heather vole (<i>Phenacomys intermedius</i>)	4	3		
Northern flying squirrel (<i>Glaucomys sabrinus</i>)	1	7		
Chipmunk (<i>Tamias</i> spp.)	2	3	1.4	
Jumping mouse (<i>Zapus princeps</i>)	2	1		
Woodland jumping mouse (<i>Napaeozapus insignis</i>)				3
Pica (<i>Ochotona princeps</i>)	tr ²	tr		
Woodrat (<i>Neotoma cinerea</i>)	tr	tr		
Unidentified weasel (<i>Mustela</i> spp.)	tr	tr		
Water vole (<i>Microtus richardsoni</i>)	tr	tr		
Birds	5	3	7	5
Insects	13	1		
Total count	914	-	72	58

¹ Biomass calculated using values from Hayward *et al.* (1993).

² tr indicates <1%.

Quantitative results from Europe demonstrate a similar pattern. *Microtus* and *Clethrionomys* dominate the diet in most locales but a more varied diet is evident in more southern populations (Korpimäki 1986b). In an 8 year study documenting contents of 67 owl nests in central Finland, Jäderholm (1987) found *Clethrionomys* spp. and *Microtus agrestis* together accounted for 80% of Tengmalm's owl prey biomass. Shrews were the next most important prey, accounting for 18% of individual prey and 8% of the biomass. Korpimäki's (1986c, 1988b, Korpimäki and Norrdahl 1989) work in western Finland reveals a similar pattern. *Microtus* spp. were the most abundant prey in nests (45% by frequency), followed by *Clethrionomys* spp. (32%), shrews (15%), and birds (5%). Values for prey identified from pellets differed in that shrews dominated the sample (33% by frequency), followed by *Microtus* spp. (27%), *Clethrionomys* spp. (24%), and birds (12%).

In Czechoslovakia, mice (especially *Apodemus* spp. and *Muscardinus avellanarius*, together 18% of prey biomass) were more important in the diet than in more northern populations and the diet included more species of mammals (24 species) (Kloubec and Vacík 1990). *Microtus* spp., *Sorex* spp., and *Clethrionomys* spp. were still major prey, together accounting for 39% of prey biomass. This study summarized information from 11 sites distributed throughout Czechoslovakia. Schelper (1989) summarized information from another southern population, in Germany. *Apodemus* spp. dominated the prey (39%) followed by *Microtus* spp. (25%), *Clethrionomys* spp. (14%), *Sorex* spp. (12%), and birds (6%).

Marti *et al.* (1993) summarized results of 20 papers from Europe and 4 from North America and found the geometric mean weight of prey for 4 regions in Europe, moving northward, to be 14.7, 17.6, 15.0, and 19.9 g; and 19.2 and 22.2 g for the Rocky Mountains and Alaska, respectively. In Europe, food-niche breadth declined from southern to northern populations while in North America food-niche expanded in northern populations (Marti *et al.* 1993).

Seasonal Variation

Boreal owl diets differ from winter to summer due to the natural variation in availability of prey due to snow cover and the hibernation of some small mammal prey. In Idaho, northern pocket gophers (one of the most frequent summer prey), western jumping mice, and yellow-pine chipmunks were all unavailable in winter. The owls relied on southern red-backed voles for nearly 50% of winter prey. Flying squirrels were captured far more frequently in winter than summer. Of 12 recorded flying squirrel prey,

11 were captured during winter, 10 of these by females. The squirrels represented 45% of prey biomass recorded for female owls during winter, indicating the importance of these prey when other prey are less available. During summer, southern red-backed voles continued to be the most frequent prey and accounted for 31% of prey individuals. The owl summer diet was diverse compared to winter with the addition of chipmunks, jumping mice, and crickets. The relative importance of birds in the diet did not change between seasons (5% by frequency).

In Finland, the owl's diet shows a marked seasonal pattern that varies depending on the stage of the multi-year vole cycle (tables 2 and 3). This study covered the period January-June from 1973-1985 and included four peak vole phases. In all years, birds were important from January through mid-March (24-24% of diet by frequency) and in late May and June (8 - 27%) while shrews increased in the diet as they matured in late April. In good vole years, *Microtus* spp. were taken most frequently in late March and April (74-84% of diet) and formed 35-49% of the diet in other months. During the high vole years, *Clethrionomys* captures increased in late April as *Microtus* became less important. In poor vole years the frequency of *Clethrionomys* in the diet increased earlier in March, when they accounted for 51% of the diet; *Clethrionomys* captures remained high through May.

Yearly Variation

In Idaho, *Clethrionomys gapperi* varied from 26 to 45% of the annual diet (by frequency) over 4 years (Hayward *et al.* 1993). Deer mice, pocket gophers, and heather voles (*Phenacomys intermedius*) increased in years when *Clethrionomys* was less frequent. Years with a low proportion of *Clethrionomys* were poor breeding years for the owl. The frequency of *Microtus* spp. remained relatively constant during this study and averaged 11%. The frequency of shrews and birds also remained relatively constant.

In Finland, the owl's diet varied sharply among years in response to the well documented (e.g., Hansson and Henttonen 1985) vole cycle (Korpimäki 1988b). The proportion of *Microtus* in diet correlated positively (Spearman rank correlation: $r_s = 0.86$, $P < 0.001$) with the abundance of these voles in spring trapping samples and varied from 6 to 71% of the diet (Korpimäki 1988b). Proportions of shrews and birds in the diet varied inversely with the numbers of *Microtus*. The proportion of *Clethrionomys* in the diet correlated positively with the proportion of *Microtus* ($r_s = 0.46$, $P < 0.10$) and varied from 3 to 45% of prey.

Table 2.—The seasonal changes in the food composition (as percentages by number) of the Tengmalm's owl during the first half of the year in peak vole years (pooled data from 1973, 1977, 1982, and 1985). The statistical significance of the differences between consecutive time periods was examined using chi-square tests. From Korpimäki (1986c).

	Time periods						Total	
Prey groups	1 Jan.-15 March	16-31 March	1-15 April	16-30 April	1-15 May	16-31 May	1-30 June	
Shrews	17.3	2.4	4.6	15.9	10.5	15.8	20.0	11.8
Water vole	-	-	-	-	0.2	-	-	0.1
Bank vole	17.3	11.2	15.5	34.0	34.1	27.2	20.0	27.7
<i>Microtus</i> spp.	34.7	84.0	74.0	46.6	49.0	45.1	48.0	52.4
Murids	6.7	2.4	5.5	2.8	5.6	-	-	4.1
Birds, adults	24.0	-	0.5	0.7	0.7	12.0	8.0	3.9
nestlings and young		-	-	-	-	-	4.0	0.1
total birds	24.0	-	0.5	0.7	0.7	12.0	12.0	4.0
No. of prey items	150	125	219	427	602	184	25	1732
Diet width	9.04	2.49	3.12	4.02	3.98	5.15	4.25	
χ^2	45.80	26.38	65.39	13.64	54.80	5.49		
df	4	4	5	5	5	4		
$P <$	0.001	0.001	0.001	0.05	0.001	ns		

Table 3.—The seasonal changes in the food composition (as percentages by number) of the Tengmalm's owl during the first half of the year when vole populations were not at a peak (pooled data from 1974-76, 1978-81, and 1983-84). Statistical analysis same as in table 1. From Korpimäki (1986c).

Prey groups	1 Jan.-15 March	16 March- 15 April	16-30 April	1-15 May	16-31 May	1-30 June	Total
Shrews	11.9	17.1	26.0	24.0	36.8	45.8	25.2
Red squirrel	-	0.3	-	-	-	-	0.0
Water vole	-	0.3	0.3	0.2	-	0.6	0.2
Bank vole	9.9	51.6	46.5	42.3	19.6	14.5	35.4
<i>Microtus</i> spp.	42.9	25.1	23.1	18.8	7.7	4.2	21.8
Murids	1.4	4.8	3.2	3.6	4.2	-	3.2
Birds, adults	34.0	0.9	1.0	11.2	26.7	18.7	12.3
nestlings and young	-	-	-	-	4.9	16.3	1.9
total birds	34.0	0.9	1.0	11.2	31.6	34.9	14.2
No. of prey items	294	351	624	421	285	166	2141
Diet width	8.18	3.05	3.24	3.95	5.20	4.13	
χ^2	222.10	9.02	50.47	84.56	6.28		
df	5	5	5	5	4		
P <	0.001	0.10	0.001	0.001	ns		

Energetics

During the nestling period, young owls in Finland consume an average of 21 g per bird per day and captive adults 65 g/day (Korpimäki 1981). Jäderholm (1987) calculated that during nesting, young boreal owls are provided about 650 g of prey,

which is similar to Korpimäki's estimate for a 29-30 day nestling period. Prey biomass provided for each nestling changed little for broods from 2-7 nestlings but was higher when only one nestling was present (about 1,600 g) (Jäderholm 1987:Fig 3).

As an indirect measure of prey consumed in Idaho, Patricia Hayward and I monitored four nests with

mechanical event recorders triggered by a perch mounted at the cavity. These records suggested that the female left the nest once each night during incubation (for gut clearing) and usually twice after the young had hatched. Assuming that all records other than female gut clearing were prey deliveries, deliveries averaged 3.5 (± 0.33 ; $n = 84$ nights of records; range 0-9) during incubation and 5.0 (± 0.61 ; $n = 76$ nights; range 0-12) during brooding. Clutches at the four nests were 2, 2, 3, and 3; each fledged two young. Korpimäki (1981) estimated 9.8 deliveries/night during brooding period and 8.0 after the female left the nest.

Temperature Regulation

No data have been published on thermal neutral zone, basal metabolic rate, and metabolism while active. Winter and summer roost characteristics indicate boreal owls in central Idaho were not stressed by winter conditions but chose roosts to reduce summer heat stress (Hayward *et al.* 1993). Gullar fluttering was noted only in summer but occurred when temperatures at roosts were as mild as 18°C and 23°C, suggesting the owls are easily heat stressed.

Food Caches

Immediately prior to nesting (1-2 weeks) and during nesting, prey are cached in the nest cavities (Norberg 1987). In Finland (13-year study, Korpimäki 1987a), the size of nest caches was related to phase of the vole cycle. During peak phase, caches averaged 6.9 items/nest weighing 89.3 g; in low phase, 1.5 items/nest weighing 19.6 g. *Clethrionomys glareolus* were the most common cached prey. Prey are also cached at roosts. In Idaho, owls were observed retrieving cached prey or caches were observed near roosting owls at 17% of summer and 4% of winter roost locations ($n = 882$).

ECOLOGY OF PRINCIPAL PREY

Forest dwelling small mammals dominate boreal owl diets in most regions (see previous Food Habits section). In North America, important species include red-backed voles, flying squirrels, deer mice, shrews, and pocket gophers. Microtine voles are also important throughout the species' range and seem to increase in importance in more northern latitudes. In this section I will briefly review the ecology of several prey species that occurred frequently in boreal owl diets in the United States: red-backed vole, deer mouse, flying squirrel, and other voles (Palmer

1986, Hayward *et al.* 1993). This review is intended only to give the reader a preliminary understanding of small mammal prey as a background for the remainder of the conservation assessment. I concentrate on habitat use and food habits of the selected prey species.

Red-Backed Vole

The genus *Clethrionomys*, or red-backed voles, occurs throughout the range of boreal owls and represents an important prey genus in all populations studied. These 20-30 g voles are active year-round and their circadian activity pattern includes periods of foraging throughout the 24 hour cycle (Stebbins 1984). Red-backed voles do not form colonies but nest singly or in family groups in natural cavities, abandoned holes, or nests of other small mammals near the ground surface. During winter they spend most of their time at the snow-ground interface.

The genus occurs almost exclusively in forest habitats although Whitney and Feist (1984) describe populations occurring in grassland habitats in Alaska. Merritt (1981:4) characterizes their habitat as "chiefly mesic habitats in coniferous, deciduous, and mixed forests with abundant litter of stumps, rotting logs, and exposed roots." In Idaho, red-backed voles were most abundant in mature and older spruce-fir forest where they were the most abundant small mammal (Hayward *et al.* 1993). The relationship between forest successional stage and red-backed vole abundance appears to vary geographically. In the western and northeastern portions of North America, red-backed voles are most abundant in mesic, mature conifer forest, particularly spruce-fir forests (Brown 1967, Scrivner and Smith 1984, Millar *et al.* 1985, Raphael 1988). In these regions red-backed voles decline sharply after clearcutting (Campbell and Clark 1980, Ramirez and Hornocker 1981, Halvorson 1982, Martell 1983a, Medin 1986). Martell (1983b) showed that the loss of red-backed voles from clearcuts may lag 2-3 years, but the voles were still rare after 13 years. In contrast to the radical population changes observed after clearcutting, red-backed vole populations remained abundant after patch cutting (3 acre clearcuts) and selection harvest in several locales (Campbell and Clark 1980, Ramirez and Hornocker 1981, Scott *et al.* 1982, Martell 1983b). Wywiałowski (1985), using voles caught in Utah and placed in an artificial experimental arena, showed that the voles preferred areas with greater overstory cover.

Observations in the central and southeastern portion of the species' range suggest a more varied pat-

tern of habitat use (see references in Merritt 1981). In Minnesota, Michigan, Maine, and Nova Scotia red-backed voles were common, or in some cases, most abundant in clearcut sites or sapling stages following cutting (Swan *et al.* 1984, Probst and Rakstad 1987, Clough 1987). The pattern seems to be associated with moist deciduous forests where sites remain mesic after deforestation.

Food habits of red-backed voles fit their association with forest habitats. Hypogeous ectomycorrhizal and surface fruiting fungi are dominant foods in many regions (see references in Merritt 1981 and Ure and Maser 1982). These fungi are associated with tree roots, rotting logs, and litter on the forest floor in mesic forest stands. Fruticose lichen, particularly the arboreal *Bryoria* spp., are important food across the species' range, especially in winter (Martell and Macaulay 1981, Ure and Maser 1982). In Ontario, lichen and fungi together formed 80-89% of the diet across four study sites (Martell and Macaulay 1981). Ure and Maser (1982) noted that lichen is especially important to voles at higher elevations where the fruiting season for fungi is brief. Other foods include green vegetation (e.g. leaves of *Vaccinium* spp.), seeds, berries, and some insects in summer and autumn.

Non-Forest Voles

Voles in the genus *Microtus* are consumed by boreal owls throughout the owl's range in North America (table 1). Predation on *Microtus* is especially significant because these 25-40 g rodents occur most commonly in nonforested habitats. *Microtus* are active year round; they nest on the ground surface in grass nests and live at the snow-ground interface during winter. *Microtus* feed almost exclusively on leafy vegetation and the inner bark of small trees and shrubs (Vaughan 1974). Numerous studies demonstrate that, aside from dispersing individuals, these voles do not occur in forest stands (see references in Johnson and Johnson 1983). Populations will occur in small (several acres) grassland or shrub openings in otherwise forested landscapes.

Deer Mouse

Deer mice (*Peromyscus* spp.) are eaten frequently by boreal owls throughout North America but never are the dominant prey. These 20-30 g mice are highly nocturnal (Stebbins 1984) and active year-round. Deer mice are partially arboreal (Getz and Ginsberg 1968). Their diet is omnivorous, being dominated by seeds (Martell and Macaulay 1981). Compared

with other small rodents their population densities are relatively stable (Van Horne 1982).

Deer mice occupy both forested and open habitats from desert to temperate rain forest. Within the geographic range and life zone used by boreal owls, deer mice occupy most habitats. In the mountains of Colorado deer mice were captured in a wider variety of montane habitats than other rodents (Williams 1955). In Idaho, deer mice were captured in spruce-fir forests, Douglas-fir forests, lodgepole pine forests, ponderosa pine forests, and sagebrush-bunchgrass openings. Wet meadows were the only habitats where the mice did not occur (Hayward *et al.* 1993). In most locales these mice increase or remain equally abundant with disturbance or deforestation (Campbell and Clark 1980, Ramirez and Hornocker 1981, Van Horne 1981, Halvorson 1982, Martell 1983a, Buckner and Shure 1985, Medin 1986). Deer mice tend to be more abundant than red-backed voles in drier, rockier, forested habitats that are dominated by pines rather than spruce or firs (Millar *et al.* 1985, Raphael 1988).

Northern Flying Squirrel

Northern flying squirrels have been identified as important prey in only a single study in North America (Hayward *et al.* 1993); however, in this study, northern flying squirrels represented 45% of the prey biomass for female owls during winter. These ~140 g squirrels are highly nocturnal and active year-round (Wells-Gosling and Heaney 1984). Their diet is poorly understood, but fungi and lichens are thought to be the major foods in areas without substantial mast crops. Other foods include buds, catkins, fruits, tree sap, and insects (Wells-Gosling and Heaney 1984). Lichen is also important to the squirrels as a winter nesting material (Hayward and Rosentretter 1994). As with diet, habitat relationships are poorly understood. Across their extensive range, northern flying squirrels are found in conifer, hardwood, and mixed forests (Wells-Gosling and Heaney 1984). Squirrel densities in Douglas-fir forests of the Oregon Cascade Range were not correlated with habitat characteristics (Rosenberg and Anthony 1992). The only substantial published study linking flying squirrels with older forest has been questioned (see Rosenberg *et al.* in press concerning Carey *et al.* 1992). It is therefore interesting that mature and older forests provide necessary foods such as fungi, lichen, and large mast crops that do not occur commonly in younger forests.

BREEDING BIOLOGY

Phenology of Courtship and Breeding

Data on the phenology of courtship and breeding for populations in North America stem from a handful of studies that were not designed to address this topic per se.

Courtship

In Colorado, singing began by mid-February, early March, late March, and mid-April in 4 years. Courtship singing by individual owls lasted up to 102 days with an average of 26 (4-59, $n = 4$) days for successful males (Palmer 1986). In Idaho, during 3 good breeding years, males were heard on 27 January, 30 January, and 16 February (each within 2 days of beginning field-work). During a poor breeding year, calling was first heard 9 February, 16 days after field-work was begun. At a similar latitude in Europe (Germany), singing begins around the first of January (Schelper 1989). In Sweden, Carlsson (1991) found individual males began singing on some successful territories over 2 months after the first males began singing. Late singers tended to be younger and may have immigrated into the area. Daylength, prey availability, and nightly minimum temperatures (Bondrup-Nielsen 1978, Korpimaki 1981) are purported to determine onset of the courtship period. The variation observed in courtship activity suggests that prey availability, weather conditions, and resident status interact to modify the influence of daylength, which likely acts as the primary factor.

During courtship, displays are limited to flights by the male between perches near the female and a potential nest cavity, accompanied by vocalization of the "prolonged song" or extended singing from the nest cavity. Courtship feeding may begin 1-3 months prior to nesting. The female occupies the nest up to 19 days and usually 1 week prior to laying (Hayward 1989) and is fed nightly by the male.

Nest Occupancy

Courting owls rendezvous nightly at the potential nest site toward the end of the courtship period where the male displays and presents food. Late in the courtship season, prior to laying, the female occupies the cavity day and night for 1-19 (usually ~6) days where she is fed by her mate. Over 4 years, known first day of occupancy ranged from 13-30 April for seven owls in Idaho (Hayward 1989).

Egg Laying

In Minnesota, clutches were initiated by 30 March and 12 April (Lane 1988). In Colorado, laying dates were estimated from 17 April to 1 June with half the known nests being initiated by 10 May (R. Ryder, Colo. State Univ., Ft Collins Co). In the central Idaho wilderness, initiation dates extended from 12 April to 24 May with half the nests begun by 1 May (5 years, 13 nests; Hayward 1989). Near Anchorage, Alaska, nests located in nest boxes were initiated from 27 March to 5 May with a median date of 10 April (T. Swem, U.S. Fish & Wildl. Serv., Fairbanks, AK). A population in Germany began laying as early as February in good vole years but more often in April (Schelper 1989). Finnish nests were initiated from 8 March to 15 May with over half begun before 10 April; nests were initiated earlier in good prey years (12 years; Korpimaki 1981). Studies in Norway suggest that second clutches of biandrous females were laid 50-64 days following the first (Solheim 1983a).

Fledging

The nestling period extends from 28-36 days (average 31.7) (Korpimaki 1981). First-hatched young stay in the nest an average of 2.3 days longer than the last hatched because adults feed young in the nest less when siblings beg outside the nest. In Idaho, the older nestlings left 27-32 days after hatching (Hayward 1989).

Mating System and Sex Ratio

The boreal owl's mating system has not been studied thoroughly in North America. Therefore, the differences in mating systems described for the New and Old Worlds may be artifacts of research emphasis rather than true biological differences. Boreal owls are considered monogamous for the duration of a breeding season in North America. The pair bond lasts only a single season; most individuals nest with a new mate each year. Extra-pair copulations have not been observed. In Europe, polygyny has been observed in most regions and is recognized as an important aspect of the species' mating system (Solheim 1983a, Schelper 1989, Korpimaki 1991). In Scandinavia and Germany, bigyny (male mated to two females), trigyny (male mated to three females), and biandry (female mated to two males) coincide with vole peaks (Solheim 1983a, Schelper 1989, Korpimaki 1991). An estimated 10-67% of males are polygynous in good years but polygamy was never recorded in poor years (Carlsson *et al.* 1987). In two good vole years, bigynous males reared an average

of 7.8 and 9.5 fledglings compared to 4.2 and 5.1 for monogamous males. Males achieve polygamy through polyterritorial behavior, advertising at multiple (up to 5) cavities within the home range (Carlsson 1991). Primary and secondary females were separated by an average of 1,050 m (median, $n = 17$) (Korpimäki 1991). Bigynous males feed primary and secondary females equally during laying but favor primary females during the brooding period (Carlsson *et al.* 1987). Secondary females produce fewer young than their primary counterparts (2.8 vs. 5.1 and 3.3 vs. 6.2 in two years, Carlsson *et al.* 1987). Biandrous females (multiple broods with the same male not recorded) cease caring for the first brood about three weeks after the young hatch (normal end of brooding) and may begin a second clutch with a new mate prior to departure of the first brood (Schelper 1989). The interval between clutches ranges from 50-64 days, the distance between nest sites ranges 0.5-10 km, and there is no significant difference in the number of eggs or mortality of young for biandrous vs. monogamous females (Solheim 1983a).

The sex ratio of adult boreal owls has not been estimated in North America. In Europe, where long-term studies of population ecology are more common, sex ratio of breeding individuals was estimated as 8:10, 0:10, 5:10, and 4.3:10 (females to males) during 4 years in northern Sweden using autumn playback and mist-net trapping (Carlsson 1991). These estimates may be biased, however, by sexual differences in response to playback of primary song.

Nest Site

Nest

Boreal owls nest exclusively in secondary tree cavities—in North America primarily pileated woodpecker, common flicker, or natural tree cavities or in artificial nest boxes. Boreal owl populations are likely limited in portions of their range by availability of cavities.

Maintenance or Re-Use of Nests

In Colorado, 2 (of 6 observed) nests were used 2 years in succession (R. Ryder, Colo. State Univ., Ft. Collins, CO). Both instances were in natural cavities in lodgepole pine. The owls were not captured so whether the same or different birds used the nests was unknown. Natural nest cavities were never used 2 years in succession in Idaho and rarely used again by the same individual (Hayward and Hayward 1993). Nest cavities may be reused by different individuals but generally after a “rest” period of more

than one year. Nest boxes in Idaho have been occupied in successive years but only by new individuals and after the box was cleaned. In Europe, where cavities are more limited, repeated use of nest boxes is more frequent (Sonerud 1985, Korpimäki 1988a).

Nesting

Egg Laying and Care of Young

Clutches in Idaho were begun 1-19 (usually about 6) days after the female occupied the cavity. In Finland, eggs were laid at intervals of 48 hours but varied from 0.3 to 0.7 eggs per day (Korpimäki 1981). The female does all incubation. There are no reports of egg dumping.

Brooding is performed exclusively by the female beginning immediately after hatching and lasting until the oldest nestling reaches 20-24 days. During the first 3 weeks the male brings all food to the nest for the female and young and the female feeds the young. The male continues to provide for the young throughout the nestling stage and the female supplies food to nestlings after ceasing brooding at some nests. After fledging the young are dependent on the adults for food for over a month.

Growth and Development

Variation in clutch size is reported under Demography, below. During the nestling period, which lasts 30 days for most young, nestlings gain about 5.2 g per day with the greatest absolute gains from 8-13 days (10 g/day). Young reach adult mass by 14-17 days; at 30 days nestlings average 156 (± 21.3 ; $n = 5$; range 130-174 g) (Hayward and Hayward 1993).

DEMOGRAPHY

Life History Characteristics

Age of First Reproduction

Banding records in the northern Rocky Mountains indicate that boreal owls breed the year after hatching. More intensive study in Finland indicates that, except in years of reduced food availability, both sexes can breed the year after hatching, but a larger proportion of females than males breed their first year (Korpimäki 1988c). Over an 8-year period, 16% of first-year males and 65% of second-year males bred (Korpimäki 1992). Both sexes are capable of breeding each year, but prey availability determines individual status year-to-year (Korpimäki 1988c). Second broods are not reported in North America;

see the Mating System and Sex Ratio section under Breeding Biology.

Clutch

Variation in clutch size is one of the most studied aspects of the species' biology, particularly in Europe. These studies have established that the number of eggs laid by boreal owls varies in relation to environmental conditions, particularly prey availability. Clutch size varies among geographic regions, among years, and among individuals within years. In both Europe and North America, northern populations that prey on fluctuating vole populations display the greatest variation in clutch size and have the largest potential clutches (Bondrup-Nielsen 1978, Korpimaki 1986a, Hayward *et al.* 1993) (table 4). Over 17 years, mean clutch size varied from 4.3 to 6.7 in western Finland (Korpimaki and Hakkarainen 1991) and over 4 years in Idaho from 2.5 to 3.5 (Hayward *et al.* 1993). The dramatic variation in clutch size within and among years is further shown in table 4.

Korpimaki (1987b, 1989) and Hornfeldt and Eklund (1990), using experimental and observational studies, demonstrated the direct link between vole abundance and clutch size in Finland. Further support for this pattern comes from observational studies in Norway (Lofgren *et al.* 1986), Sweden (Sonerud 1988), Germany (Schelper 1989), France (Joneniaux and Durand 1987), and Idaho (Hayward *et al.* 1993). Each of these studies reported larger clutches in years when indices of small mammal abundance, based on snap or live-trapping, were high.

To further demonstrate the variation in clutch size that has been observed I provide additional summary statistics from a sample of studies. Clutch size for separate populations in Idaho averaged 3.25 ($\pm$ 0.42 SD, n = 11, range = 2-4) and 3.57 ($\pm$ 0.34 SD, n = 31, range = 2-5) (Hayward *et al.* 1993, Hayward, G. D. and P. H. Hayward, unpubl. data) (table 4). From

a similar latitude in Europe (Germany), Schelper (1989) reported clutches of 3-4 eggs with larger clutches in years when voles dominated the diet. An earlier study in Germany reported 34 nests averaged 3.8 eggs (Konig 1969). In Finland, pooling results from 2 areas over 12 years shows clutches averaging 5.6 ($\pm$ 0.13 SD, n = 412, range = 1-10) (Korpimaki 1987b).

Fledging Success and Population Productivity

Patterns of fledging success reported for boreal owls in Europe and North America reflect the patterns reported for clutch size. Experimental and observational results strongly support the contention that prey availability influences fledging success and overall population productivity (e.g., Korpimaki 1987b, 1989, Hornfeldt and Eklund 1990). Therefore this section will not repeat results that simply duplicate those reported but will note important differences. Representative fledging rates include: 2.3 ($\pm$ 0.54 SD, n = 6, range = 2-3) fledglings/successful nest in Idaho (Hayward 1989); 3.4 young/nest in Germany (Konig 1969); and 3.2 fledglings/nest and 3.9 fledglings/successful nest over a 14-year period in Finland (Korpimaki 1987b).

Korpimaki's (1988d) studies in western Finland suggest that fledging success is more strongly influenced by prey availability during decrease and low phases of the vole cycle. Clutch size, in contrast, is more sensitive to prey availability during the increase phase.

Korpimaki (1988c) has also shown that breeding performance in Tengmalm's owl is dependent on the experience of both members of the breeding pair; pairs of older birds experience the highest productivity. These data suggest that annual reproductive success increases over time, within individuals.

Fledging success is usually reported as the mean

Table 4.—Summary of reproductive statistics for boreal owls from sites in North America and Europe.

Location ¹	Median laying date	Range laying dates	Mean clutch size	Mean no. young fledged ²
Colorado	10 May	17 Apr-1 Jun		
Idaho	1 May	12 Apr-24 May	3.25	2.3
Minnesota		30 Mar-12 Apr		
Alaska	10 Apr	27 Mar-5 May		
Finland	3 Apr	23 Feb-7 Jun	5.6	3.9
Germany			3.8	3.4

¹Sources of information: Colorado (Palmer 1986), Idaho (Hayward 1989), Minnesota (Lane 1988), Alaska (T. Swem, U.S. Fish & Wildl. Serv., Fairbanks, AK), Finland (Korpimaki 1987b), and Germany (Konig 1969).
²Calculated only for successful nests.

number of fledglings per successful nest. Productivity, however, is strongly influenced by nesting success (rate of unsuccessful nests). In some years, the small proportion of the population breeding has a greater impact on productivity than reduced clutch size or fledging success.

In central Idaho, 10 of 16 nests produced no young in a study where all but one nest was a natural cavity (Hayward 1989). In Norway, during a 13-year study employing nest boxes, 48% of 101 clutches were lost to predation (Sonerud 1985). A nest box study in Finland reported 85% of eggs hatched and 53% of the eggs laid ($n = 890$) produced a fledgling, averaging 3.2 fledglings/nest and 3.9 fledglings/successful nest over 14-year period (Korpimäki 1987b).

The influence of owl density on reproduction has not been directly addressed in the literature. The patterns described above do not suggest strong inverse density dependent reproduction. Clutch sizes and fledging rates tend to be highest in years when prey is abundant and the greatest number of owls are breeding. These results, however, do not preclude the potential for density dependent limitation of population growth. Perhaps density dependence is determined by the number of adult owls breeding per 1000 voles per km^2 . Because prey availability is a primary factor influencing reproduction, and boreal owls consume up to 17% of available *Microtus* (Korpimäki and Norrdahl 1989), a feedback loop is available to self-limit population growth to some degree. As discussed below, however, territoriality is not likely to be a mechanism for density dependent self-limitation.

Lifetime Reproductive Success

Lifetime reproductive success is difficult to study in any mobile vertebrate. No studies in North America have examined this topic. Based on 11 years of data, lifetime reproduction (LR) of 141 males in Finland varied from 0-26 fledglings (mean 5.2); 21% of males reared 50% of all fledglings (Korpimäki 1992). Among males hatched in a given year, 5% produced 50% of fledglings in the next generation. Offspring survival from egg to fledgling, lifespan of individual, clutch size of nests, and phase of the vole cycle at which an individual entered the populations were important components of LR for individual males. Offspring survival (as represented by the number of fledglings per nest) varied from 0 to 7. Most males breed for only a single season but the number of seasons ranged from 1-7 years ($\bar{x} = 1.5$). Clutch sizes varied from 2-8. Finally, the temporal variation in habitat quality due to fluctuating vole abundance was the most important environmental

determinant of LR. Males entering the population in the low and increase phases of the cycle had larger LR than those entering in decrease or peak (individuals raised in the low and increase phases had better food conditions in their first 1-2 years of breeding). The extreme variation among individuals in lifetime reproductive success is expected because prey availability varies greatly among years and within years among breeding sites in Finland. Other vertebrates exhibit similar patterns (e.g., Clutton-Brock *et al.* 1982, Grant and Grant 1989).

Proportion of Population Breeding

Sound estimates of the number of non breeding individuals are not available. Indirect evidence from North America and Europe, however, demonstrates extreme yearly variation in breeding attempts; e.g., in Sweden, nest box occupancy in one area varied from 0.8% to 40.2% in 1980-81, and 39.4%, 0.8%, and 23.8% in 1982-84 (Lofgren *et al.* 1986). In Idaho, the number of calling males heard per kilometer surveyed varied from 0.02 to 0.24 from 1984 to 1987 and some radio-marked individuals did not breed even in good breeding years (Hayward 1989).

The most direct estimates come from Korpimäki's studies based on 10 years of monitoring his smaller study area (100 km^2 , Korpimäki and Norrdahl 1989). The number of non breeding males (based on singing males who did not nest) varied from 0 to 66% of the population and averaged 47%.

Survivorship

In Idaho, adult annual survival estimated from 25 radio-marked birds was 46% (95% confidence interval 23-91%) (Hayward *et al.* 1993). In Finland, based on 281 banding recoveries, first-year male annual survival was 50% (95% confidence interval 43-57%) and adult male annual survival was 67% (95% confidence interval 61-75%). Based on re-trapping birds for 11 years in an intensive study area, 78% of fledgling males died before their first breeding attempt (Korpimäki 1992). In Germany, results of a long-term banding study in an area with natural and artificial nest sites suggested juvenile survival of 20% and adult survival of 72% (Franz *et al.* 1984). In Norway, Sonerud *et al.* (1988) estimated 62% adult annual survival.

Breeding males remain in the breeding population an average of 1.5 (range = 1-7) years (Korpimäki 1988c) with an average life span of 3.5 (range = 2-11) years (E. Korpimäki, pers. comm.). In Germany, females in a nest box study were documented living 8 ($n = 6$), 9 ($n = 5$), and 10 ($n = 1$) years (Franz *et al.* 1984).

Ecological factors influencing survival have not been explored in any detail. Korpimäki (1992) established that owls in his population survived in the breeding population longer during increase than decrease phases of the vole cycle. Although starvation is often presumed to be a major mortality factor, direct and indirect causes of mortality have not been identified for any populations.

Movements as Related to Demography and Metapopulation Structure

As described earlier, boreal owls usually remain resident within a multiannual home range but are capable of moving long distances between breeding sites. In Sweden, young females that bred the year after fledging moved 24 km (median) from their natal territory while males moved less far (median 4.5 km). In Finland, adult females disperse up to 580 km (median 4 km) between successive breeding seasons while males rarely move more than 5 km (median 1 km; Korpimäki *et al.* 1987). During prey declines, more than half of females in Sweden were nomadic (Lofgren *et al.* 1986). Adult nomadism occurs in response to prey shortage, which may be more acute and regular in northern geographic areas. Juvenile boreal owls frequently remain within the same breeding population but also have been documented moving long distances. Research methods are biased toward detecting residency, however, so movements between populations may be quite common. Both adult and juvenile movements have not been studied carefully in North America so inferences concerning the influence of movements on demography stem from European studies.

The nomadic life history of boreal owls and the capacity for juveniles to disperse long distances may result in a strong metapopulation structure within North America. Suitable habitat in the western United States occurs in numerous patches separated by tens to hundreds of km (figure 1). The habitat distribution, then, provides a landscape that will support small populations each separated by distances greater than the normal daily movement and normal yearly movement distances of individual owls. Linkage among populations, then, results from the nomadic movement of adults or exceptional long distance dispersal of some young owls. Subpopulations of boreal owls that occur in disjunct locales may be linked through nomadic movements and juvenile dispersal. These movements are potentially important in the species' population dynamics. Individual populations may act alternately as sources and sinks depending on the status of prey, cavity

availability, weather events, predators, and competitors. The long-term persistence of individual populations may be determined in large part by the rescue effect (Brown and Kodric-Brown 1977) resulting from interpopulation movements of owls, particularly experienced breeding adults.

Local Densities

There are no reliable estimates of population density for boreal owls in North America. Estimates from Europe all refer to breeding season populations, rarely include estimates of non-breeding individuals (Korpimäki and Norrdahl 1989), and most frequently refer to calling male owls. Korpimäki and Norrdahl (1989) for the period 1977-1987 reported a minimum of 1 breeding pair and 2 non-breeding males, and a maximum of 26 breeding pairs and 8 non-breeding males within a 100 km² study area in western Finland.

Indices of density based on calling surveys or number of active nests exhibit extreme yearly variation that corresponds with fluctuating indices of rodent abundance. Density estimates include: 0.6-1.3 nests/km², averaging 0.25/km² in France (Joneniaux and Durand 1987); 0.05-0.46/km² with some small areas as high as 4/km² in Southern Lower Saxony (Schelper 1989); and 0.19 to 0.48/km² in Sweden (Källander 1964).

Spacing and Population Regulation

Behavioral interactions, particularly territoriality, function to limit population size in many bird species (e.g., Hensley and Cop 1951, Krebs 1971, Watson and Moss 1980). Studies in Europe and North America suggest that under most circumstances, territoriality has no influence on abundance of boreal owls. The direct effects of prey abundance and cavity abundance are the most likely factors influencing population size; however, the links between these and other proximate factors are not established. Figure 5 displays the array of environmental factors thought to affect boreal owls based on the studies discussed in this report.

Spacing

Individuals, including mated pairs, are seldom found together except during courtship rendezvous at the nest site. Five mated pairs radio-marked prior to nesting in Idaho roosted within 150 m of one another on 7 occasions ($n = 121$) (Hayward *et al.* 1993); 1 pair accounted for 4 of these observations. Locations where paired individuals roosted together oc-

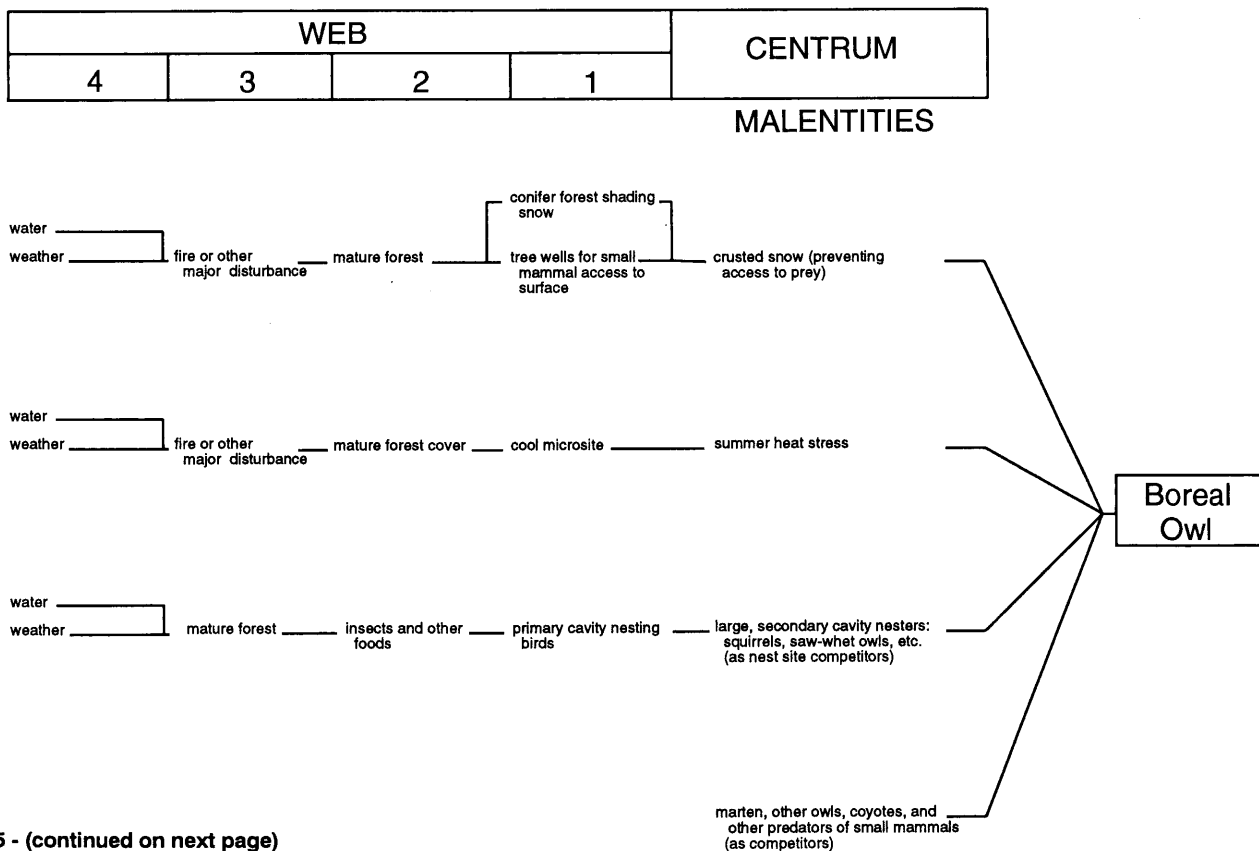
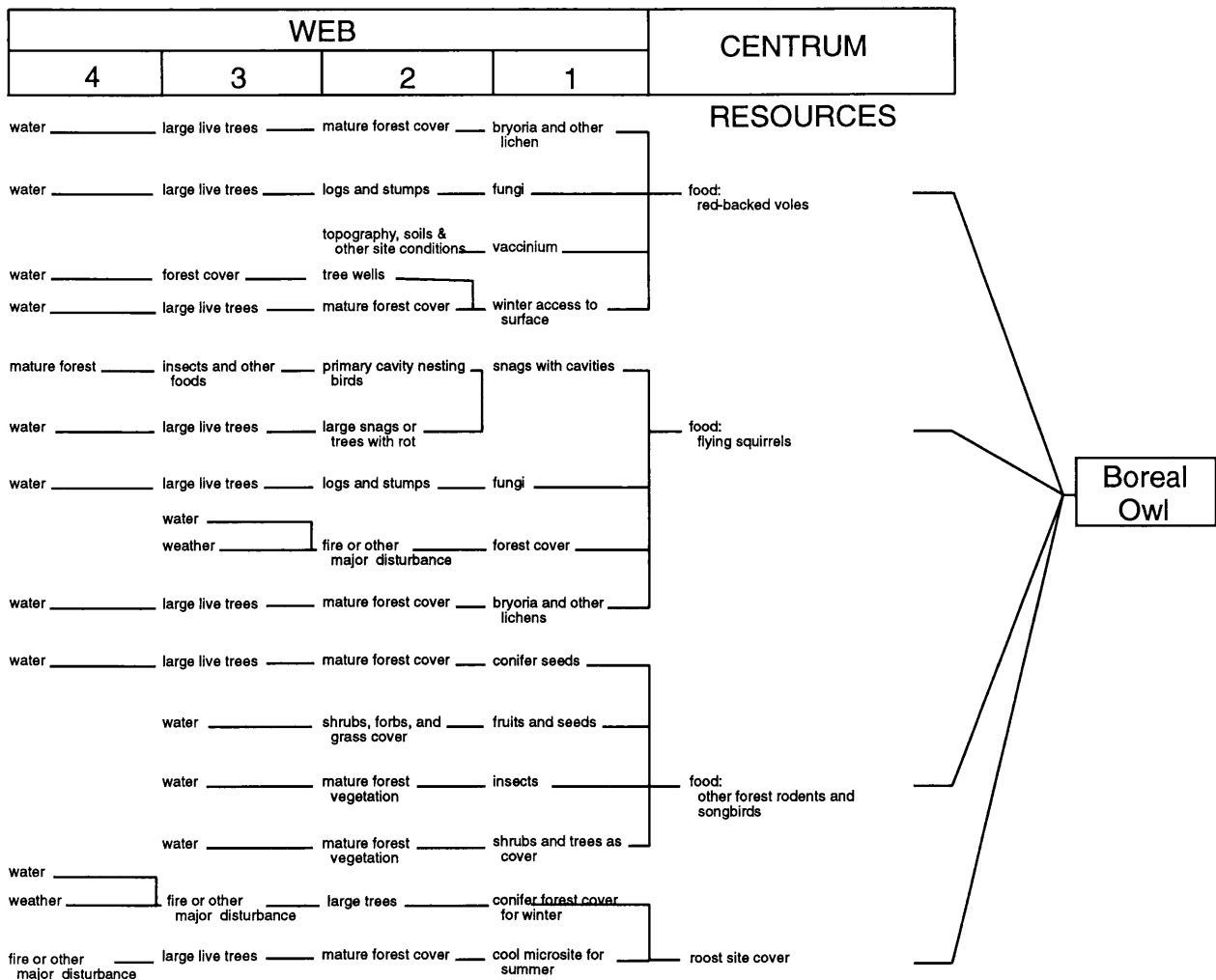


Figure 5 - (continued on next page)

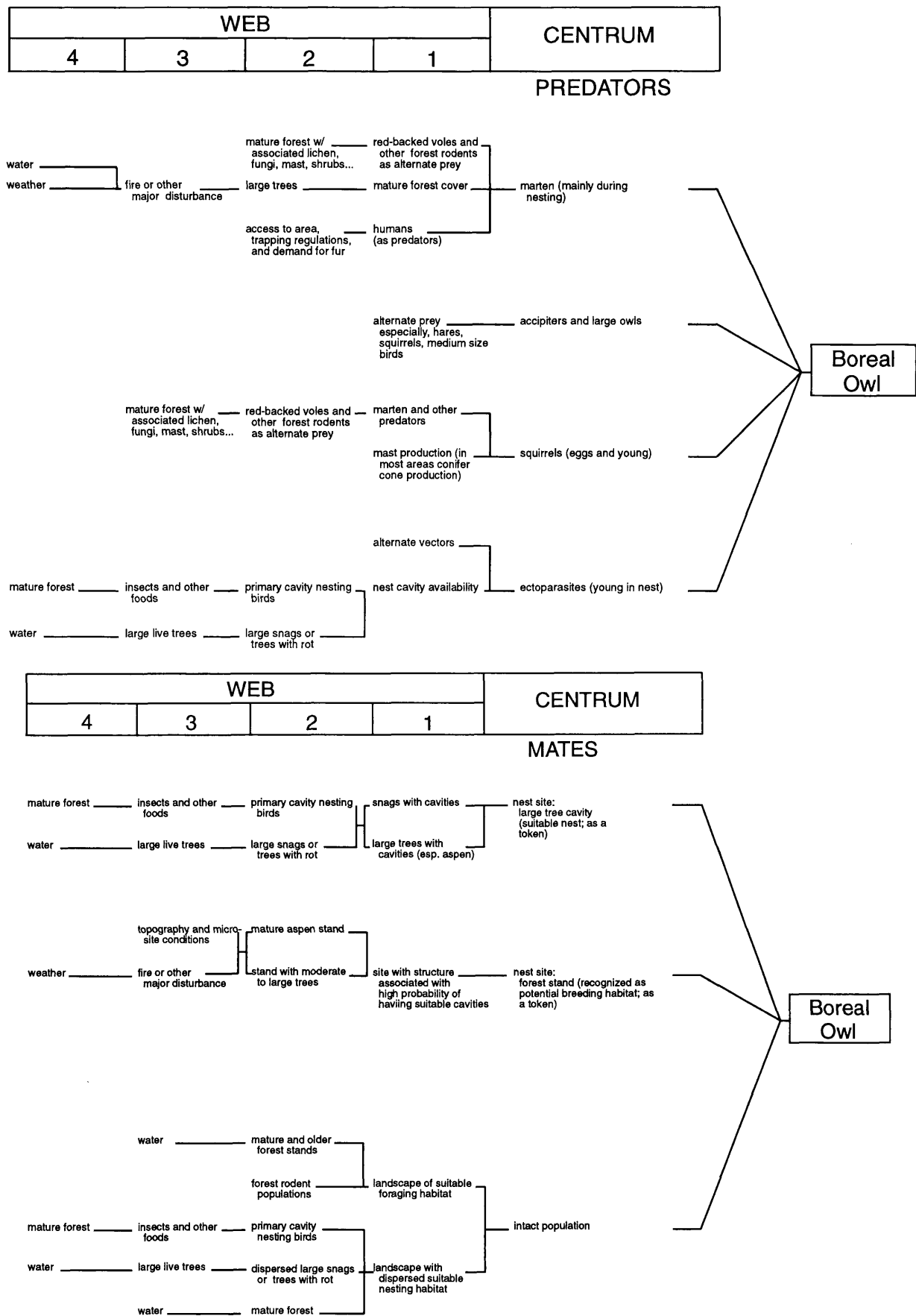


Figure 5.—Envirogram representing the web of linkages between boreal owls in the western United States and the forest ecosystem they occur in. This web should be viewed as a series of hypotheses based on the ecology of boreal owl as described throughout this assessment. For more on the application of envirograms in conservation biology see Andrewartha and Birch (1984) and Van Horne and Wiens (1991).

curled up to 6.5 km from the nest and never at the nest (Hayward *et al.* 1993). Unmated owls were located within 150 m of one another on 2 occasions: 2 males in May and an unmated male and a female caring for young in June.

Although individual owls rarely interact closely, home ranges of individuals living in the same drainage overlap extensively. In Colorado, Palmer (1986) observed > 90% overlap in ranges of two males. In Idaho, ranges of 13 owls monitored in two adjacent drainages overlapped another owl's by at least 50% and the degree of overlap was not dependent upon sex (Hayward *et al.* 1987b and Hayward *et al.* 1993).

Territoriality

Boreal owls do not exhibit strong territorial behavior. Males sing to maintain a territory only in the immediate vicinity of potential nest cavities. Territory defense is confined to the nest site and seems to include less than a 100-m radius around the nest (Mikkola 1983). Carlsson (1991) reports a male calling within 200 m of another male's nest. The paired male flew within 50 m of the calling bird and uttered a "screech" call but did not pursue the caller. Minimum distances reported between nests were 100 m (Mikkola 1983) and 0.5 km (Solheim 1983b). The distance between territories depended on prey abundance (Schelper 1989, Korpimäki and Norrdahl 1989). How factors other than prey abundance (e.g., cavity availability, habitat structure) influence territorial spacing has not been studied.

Territorial behavior is thought to be confined to the courtship and breeding period (January - July), but Kampfer-Lauenstein (1991) reported warning calls and direct flight attacks (suggesting territorial behavior) in response to playback from August-November. This suggests that the autumn territory is within the year-round home range but may not coincide with breeding territory.

Population Regulation

The availability of nest cavities and prey are the most likely environmental factors to limit populations of boreal owls (when populations are limited). The role of prey availability in observed nomadic movement patterns and the yearly variation in productivity suggests that food may regulate boreal owl abundance at times in some locales. The mechanism of limitation by food is not completely understood; but prey available to the female prior to nesting may be a critical factor in laying date and clutch size. Prey availability during the nestling period strongly influences the number of young fledged (Korpimäki 1989, Hornfeldt and Eklund 1990). Large clutches

have been shown to produce more young leaving the nest (Korpimäki 1989). In his 1989 paper, Korpimäki reported an experiment in which he manipulated the abundance of food available to females prior to laying during a peak in the vole cycle. Despite the abundance of natural prey, females provided additional prey laid earlier, laid larger clutches, and fledged more young than control individuals.

Other investigators, using nonexperimental approaches, have concluded that prey availability has a direct positive correlation with boreal owl productivity (e.g. Lofgren *et al.* 1986, Sonerud *et al.* 1988, Hayward *et al.* 1993). The number of owls nesting (Lofgren *et al.* 1986), laying date (Hörnfeldt and Eklund 1990), clutch size (Lofgren *et al.* 1986), nest abandonment (Hayward *et al.* 1993), number of fledglings (Hayward *et al.* 1993), and movements of individuals following nesting (Sonerud *et al.* 1988) have all been linked with abundance of small mammals. Prey limitation leads to nomadic movements and likely results in higher mortality.

These demographic data have not been incorporated into a model (verbal or quantitative) describing population growth. Whether the absolute abundance or changes in prey populations is more important has not been pursued. Neither have the links between prey availability and changes in other environmental features been explored. And finally, the role of stochastic events in the pattern of population change has not been addressed.

In some areas of Europe, natural cavity availability is thought to limit population size and distribution (Korpimäki 1981, Franz *et al.* 1984). In North America, in regions with few (or no) pileated woodpecker or flicker cavities, nest site availability may limit boreal owl abundance. Within the geographic range of pileated woodpeckers, the absence of the woodpeckers at higher elevations may limit abundance (Hayward *et al.* 1993).

Cavity availability and abundance of prey likely interact to influence boreal owl population growth. Tree cavities occur nonrandomly across the landscape as do small mammal populations. The spatial arrangement of cavities and prey (in relation to one another) are important in determining boreal owl abundance.

Other factors potentially play a role in boreal owl population growth but research has not addressed these possibilities. Indirect evidence suggests that the owl's southern distribution and its lower elevation range in montane areas may be related to summer heat stress (Hayward *et al.* 1993). Boreal owls are easily heat stressed and seek cool roost locations

in summer. The owl's physiological response to heat stress has not been measured, however.

COMMUNITY ECOLOGY

Predation on Boreal Owls

Marten (*Martes* spp.) are the most important predator of owlets and adult females at the nest site. Over 13 years, 48% of clutches were preyed upon in Norway, most by marten (Sonerud 1985). In Idaho, loss of nests are also most frequently attributed to marten; red squirrel (*Tamiasciurus hudsonicus*) predation upon eggs is also suspected (Hayward, G. D. and P. H. Hayward, unpubl. data). Aside from predation by marten at the nest, Cooper's hawk (*Accipiter cooperi*), northern goshawk (*Accipiter gentilis*), great-horned owl (*Bubo virginianus* or *Bubo bubo*), Ural owl (*Strix uralensis*), and tawny owl (*Strix aluco*) are the most important predators of young and adults (Herrera and Hiraldo 1976, Mikkola 1983, Reynolds *et al.* 1990). Research has not examined the impact of predation away from nests on population dynamics.

Relationship With Prey Populations

As described earlier, small mammal abundance has a direct and significant impact on boreal owl movements, reproduction, and survival. This relationship between prey abundance and boreal owl demography has been studied by several scientists in Europe (e.g., Korpimäki 1984, 1987a, Lofgren *et al.* 1986, Sonerud 1986) and to a lesser extent in North America (Hayward *et al.* 1993). In contrast, the influence of boreal owls on the dynamics of their prey populations has not been studied.

Korpimäki and Norrdahl (1989) provide the only focused discussion of this topic based on a 10 year study in western Finland. This work combined monitoring of owl breeding activity, owl breeding success, owl diet, and small mammal abundance in a 100 km² area. The results suggested that Tengmalm's owls had a direct effect on *Microtus* and to a lesser extent *Clethrionomys* populations. Predation by boreal owls likely dampens fluctuations in vole populations through the combined influence of the numerical and functional response of the owls to changing vole abundance.

Korpimäki and Norrdahl (1989) reported up to a 21-fold year-to-year variation in the number of Tengmalm's owls. Breeding population size was correlated with vole abundance ($r = 0.80$, $P < 0.01$). The nomadic nature of the owls in Finland, their potential to produce large clutches, and a breeding

system that promotes bygamy and biandry in good prey years accounted for the dramatic numeric response that showed no time lag with the vole fluctuations. The owls exhibited a type 1 linear functional response with respect to vole (*Microtus* and *Clethrionomys*) abundance with no leveling off in capture rate even at the highest vole densities. The proportion of *Microtus* in the diet varied from 0-89%.

Combining the observed numeric and functional response of the owl population revealed that the proportion of available *Microtus* and *Clethrionomys* captured was higher in years when voles were most abundant (11 and 8% of the respective mammal populations) than in other years (4 and 5% of the respective mammal populations). Korpimäki's argument that Tengmalm's owl directly impacts the dynamics of its primary prey stems from his data on the owls' demographics and behavior. As a nomadic vole specialist, which can rapidly switch prey, the owl responds rapidly to changes in vole abundance. The owl's functional response indicates a lack of satiation at high vole densities which, when combined with the numeric response, leads to increased predation with increased prey abundance.

South of Finland, Tengmalm's owl is characterized as a resident-generalist, rather than a nomadic-specialist. Korpimäki and Norrdahl (1989) argue that these two life histories lead to similar impacts on fluctuating prey. Therefore, although the results can not be directly generalized to other regions, the evidence suggests that boreal owls may influence prey populations elsewhere.

Competitors

The influence of competitors on boreal owl populations has not been studied. Hayward and Garton (1988) described the pattern of resource partitioning among montane forest owls in central Idaho, and Korpimäki (1987c) described community dynamics in Finland.

Korpimäki (1987c) indicated that boreals were the most numerous species in a spruce forest in locations where populations of Ural owl were scarce. He suggested that Ural owls may limit the density and distribution of boreal owls. In North America, in sympatric situations, there is a potential for exploitative competition (when prey is limited) with saw-whet owls (Hayward and Garton 1988), great gray owls, and maybe most important, American marten (*Martes americana*). The degree to which this competition limits the distribution or abundance of boreal owls is unknown.

Potential competition for nest cavities may have the most direct influence on boreal owl distribution

and abundance. Northern flying squirrel, roosting pileated woodpeckers, northern hawk owl, and saw-whet owl are the most likely competitors. Again these relationships have not been examined.

BOREAL OWL RESPONSE TO FOREST CHANGE

Individual and population response of boreal owls to forest change has not been studied directly using either experimental or observational studies. Below I interpret the results of studies examining habitat use and population dynamics as they relate to this question. Because much of the knowledge necessary to infer the owl's response has been described in earlier sections, this section is brief in relation to its importance.

Nesting Habitat

As an obligate cavity nester, boreal owl populations may be influenced by changes in cavity availability resulting from changes in snag abundance or woodpecker populations. The strength of the relationship is dependent on the relative abundance of nest sites. Changes in forest structure that reduce the number and dispersion of trees larger than ~45 cm dbh could limit the owls. Similarly, changes in forest structure that alter woodpecker prey availability or the foraging ability of flickers and pileated woodpeckers will affect boreal owl nest site availability. Finally, changes in tree species composition, regardless of tree size class, could influence nest site availability as tree species differ in their longevity as a snag and in suitability for cavities (McClelland 1977).

Because nest cavities are a species requirement, the function relating cavity availability to boreal owl breeding population density is likely a complex curve. In landscapes where nest sites are not limiting, a steady linear reduction in cavities may initially have no impact on the owls. As cavities become less abundant, breeding owls may decline initially, not due to an absolute lack of nest sites but due to the imperfect ability of the owls to locate suitable cavities or due to the juxtaposition of cavities and foraging habitat and their dispersion. As cavities become still more scarce, breeding owl abundance will decline in direct, linear response to the decline in cavity abundance.

Franz *et al.* (1984) demonstrated that cavities were limiting for boreal owls on their study site in Germany. Nest box studies in Sweden, Norway, and Finland also suggest that natural cavities were limit-

ing. Biologists suggest that the long history of forest management that has removed old forest and large trees from Fennoscandia has led to significant natural nest site limitation. Up to 90% of the owls in these studies rely on nest boxes for nesting structures.

Changes in forest structure may also impact aspects of nest quality rather than nest site availability. Nests may become more vulnerable to predation or owls may have more difficulty locating suitable cavities under various forest structures. Results of a small nest box experiment in Idaho (Hayward *et al.* 1993) suggested that the owls prefer old forest sites for nesting. The results were not conclusive, however, and other studies of nesting habitat have been strictly observational (Bondrup-Nielsen 1978, Palmer 1986). The pattern of nest site use does indicate that older forest sites are used for nesting by these owls and therefore nesting opportunities may decline if the distribution of forests change toward younger age classes.

Roosting Habitat

The elimination of forest from a portion of an individual owl's home range will reduce roosting opportunities. The impacts of less dramatic changes in forest structure are not so clear. Observational studies of roosting habitat in Canada and Idaho led to different conclusions regarding the potential impact of forest change. A small sample of roosts and paired random forest sites in Canada did not differ from one another, implying the owls were not selective among the range of available sites (Bondrup-Nielsen 1978). In Idaho, owls did select forest with particular structural features, especially during summer (Hayward *et al.* 1993). Results from this study suggest that a reduction in the abundance or distribution of mature and old spruce-fir forest sites could limit roost sites during summer. Because cool roost locations dispersed throughout the home range may be important in boreal owl thermoregulation, a reduction in the quality of roost sites may influence owl survival rates.

Forest change involving type conversion (shift in tree species composition) could similarly influence roosting habitat. Old spruce-fir forest would provide a greater degree of microhabitat amelioration than old lodgepole pine forest.

Foraging Habitat

Changes in forest structure and/or species composition will influence boreal owls by changing prey abundance or availability. Prey availability will be

influenced by changing the dispersion of hunting perches or the owls' access to prey. Because boreal owls hunt from perches, forest removal affecting patches larger than several hectares will always eliminate foraging habitat even if prey populations are increased. Dense ground vegetation or crusted snow will reduce access to prey.

Sonerud (1986) described the importance of old spruce forest as foraging habitat for boreal owls in Norway despite the lower abundance of small mammals in this habitat. In winter, uncrusted snow facilitated the movement of prey to the snow surface providing the owls access to prey. In summer, the lack of dense forest-floor vegetation provided the owls clear access to small mammals. These results stress the importance of conifer canopy cover in maintaining small mammal availability.

Red-backed voles represent important prey for boreal owls in much of North America (Bondrup-Nielsen 1978, Palmer 1986, Hayward *et al.* 1993). Changes in forest structure or composition that influence red-back vole populations will likely influence boreal owl populations. The effect of forest structure and composition on red-backed vole population dynamics is not well known aside from the decline in red-backed vole populations usually observed following forest removal. Similar knowledge for other prey species (northern flying squirrels, northern pocket gophers, heather voles, etc.) is also lacking.

Broad-Scale Habitat Change

As the reader can well imagine, the influence of regional changes in habitat conditions on boreal owl populations is unknown. Changes at this scale will influence metapopulation structure through dispersal and local extinction. Changes in the size of subpopulations, distance between neighboring subpopulations, changes in productivity of source populations, and characteristics of habitat separating subpopulations likely influence metapopulation stability and would be important to manage on a regional scale.

BOREAL OWL RESPONSE TO HUMAN OR MECHANICAL DISTURBANCE

Boreal owls tolerate human and machine noise. In Colorado, owls have nested within 30 m of a major highway (R. A. Ryder; pers. comm.). In Europe, nests have been located within farmsteads and are associated with agriculture (Korpimäki 1981). Owls tolerate frequent (every 4-5 days) direct nest inspec-

tion (except during laying) and will deliver prey to the nest while humans observe from several meters away. There is no evidence that disturbance is an important factor in nest loss or owl movements.

ASSESSMENT OF SCIENTIFIC BASIS FOR PARTICULAR MANAGEMENT TOOLS

Monitoring

Intensive management of wildlife populations, particularly threatened, endangered, and sensitive species, requires information on population trend of the target species and on habitat trend. Monitoring regional trends in boreal owl populations may be approached intensively or extensively. An intensive approach involves tracking a measure of abundance for sample populations within the target region over time. An extensive approach tracks presence/absence for a large sample of populations over time.

These approaches differ in method and objective. The intensive approach facilitates examination of environmental features associated with trends in individual populations but requires a large field effort, as described below. The extensive approach costs less and tracks the "winking" on and off of populations throughout the region, but it provides no insights into the causes of population changes.

Methods for monitoring boreal owl populations have received little attention. Playback surveys have been used extensively to determine the geographic distribution of the species (Palmer and Ryder 1984, Hayward *et al.* 1987a) and have been promoted as a promising monitoring technique for other owls (Johnson *et al.* 1981, Forsman 1983, Smith *et al.* 1987). Playback surveys cannot be considered the best technique to assess trends in boreal owl populations, however, because many factors influence calling rate. Lundberg (1978) suggested that the number of boreal owls singing may be inversely related to breeding success. He found that "territorial and breeding pairs were more silent than non-territorial individuals" and concluded that "censuses made at roadside stops give unacceptable results for population studies of both the Ural owl and Tengmalm's [*boreal*] owl" (Lundberg 1978:171).

Although Lundberg's (1978) results suggest that playback surveys should not be used for intensive population monitoring, playback could be useful in developing methods of presence/absence monitoring. Playback methods seem to be the most efficient method to determine the occurrence of boreal owls in an area. These provide the basic data necessary in

a presence/absence sampling design. Research to date has not explored the potential of these techniques for monitoring owls on a regional basis. These methods would fit well into a scheme designed to approach management in a metapopulation framework.

Some work has been done to develop more intensive population level monitoring. Hayward *et al.* (1992) examined the sampling efficiency of employing nest boxes to monitor response of boreal owls to changes in foraging habitat. The results suggest that when boreal owls are moderately abundant (nest box occupancy >7%), modest changes in clutch size and occupancy rate could be detected with a system of 350 nest boxes. When owls are less abundant, the number of nest boxes necessary to detect modest changes would be prohibitively large. Research has not addressed the underlying assumptions of the methods suggested in this study (Hayward *et al.* 1992).

An understanding of boreal owl vocalizations is necessary in designing surveys to determine distribution or to develop a presence/absence monitoring program. Difficulties observing behaviors associated with vocalizing boreals and problems interpreting phonic representations of calls have led to some confusion in describing the array of sounds produced and the function of various vocalizations. Authors within the United States and in Europe have used a variety of names to describe vocalizations and no one set of names is preferable. Meehan (1980) and Bondrup-Nielsen (1984) provide the most complete vocal analysis for the boreal owl. Cramp (1977) and Johnsgard (1988:221) summarize information for North America and Eurasia. Throughout this discussion I refer to Meehan (1980) as RHM and Bondrup-Nielsen (1984) as SBN.

The call most important in terms of management is the primary song (staccato song--SBN, song--RHM). This is the call that can be attributed most certainly to boreal owls and is the call most frequently elicited in springtime playback surveys. The primary song is uttered loudly only by males from a perch near a potential nest cavity, is not commonly used outside the breeding season, and isn't used during antagonistic encounters among individuals. It is presumed to function in mate attraction as a long distance advertisement song. The call is a loud vocalization uttered as a series of trills consisting of 11-23 notes at ~0.74 kHz that increase in volume during a trill lasting 1.8 (1.32-2.32) seconds (SBN). The trill is repeated after a silence of 1 to several seconds; singing bouts frequently last 20 minutes but may extend 2-3 hours with infrequent pauses of sev-

eral minutes. The song is frequently heard by humans over 1.5 km and up to 3.5 km.

Singing in Idaho began by 20 January, reached greatest intensity by late March, and became uncommon by late April (Hayward 1989). In Colorado, Palmer (1987) reported singing 18 February - 21 June; singing peaked in late April and a lull followed in early May with renewed frequency late May through June. Palmer (1987) speculated that calling in June resulted from first-time breeders and unmated males. In Alaska, singing peaked by mid-February to March (RHM).

See Hayward and Hayward (1993) for a summary of the characteristics of other songs.

Viability Analysis

Biologists working with land management agencies are often asked to evaluate the impact of management activities on sensitive plants and animals. Biologists must document their judgments about whether or not a proposed management action will increase the likelihood of sensitive species becoming threatened or endangered. The basis for the "determination of effect" necessarily involves some kind of population viability analysis (PVA). Gilpin and Soule (1986) described PVA as a complex process of considering all factors that affect the processes of species extinction or persistence while Boyce (1992) discussed both theoretical and practical aspects of PVA.

Tools necessary to conduct PVA for boreal owls are not available. Neither mathematical nor word models linking the relevant factors have been developed. Furthermore, the ecological understanding of the owl's ecology in North America has not reached the level of maturity necessary to conduct formal viability analyses. The biological and ecological information summarized in this chapter, however, could provide the background necessary to structure assessments for individual impact analyses until more general guidelines for PVA are developed. Further ecological research will be necessary, though, before developing any formal analysis tools.

Effects Criteria Identification

Although PVA is an important tool for impact analysis, the identification of criteria upon which to base statements of effects is important in most environmental assessments. Therefore, guidelines from which to build effects criteria are important for resource managers. These types of guidelines are not currently available to managers. The paucity of in-

formation on boreal owl ecology and life history specific to different management regions precludes development of elaborate criteria. Based on the ecological relationships depicted in figure 5, however, some basic guidelines can be outlined. These will be stated generally here but could be elaborated for particular regions:

(1) Large trees are required for nesting boreal owls.

(2) Primary cavity nesters (e.g., pileated woodpeckers, common flickers) provide a majority of nesting sites in most areas and the status of populations of these birds is important to the productivity of boreal owls.

(3) The availability of small mammals limits populations of boreal owls in many areas; therefore, factors that influence small mammal abundance and availability will directly influence the abundance of boreal owls.

a) Red-backed voles are important prey for boreal owls everywhere the owl has been studied. In the western United States the abundance of red-backed voles is related, at least in part, to forest age, fungi abundance, and lichen abundance.

b) Prey availability is related to forest structure characteristics as the structure influences mobility of boreal owls. Dense shrub cover or high tree density will limit the access of boreal owls to small mammals. Conditions that promote snow crusting (large openings) will also reduce small mammal availability.

(4) In the western United States, boreal owl distribution may be limited, in part, by warm summer temperatures. Cool microsites for daytime roosts may be important in determining the species' current distribution. In Idaho, old forest sites provided cool microsites used for roosting (Hayward *et al.* 1992).

Stand and Watershed Scale Silviculture Prescriptions

Guidelines with which to develop specific stand and watershed scale silviculture prescriptions are not published. Knowledge of boreal owl ecology and habitat choice limits the specificity of any guidelines. As shown above, some general statements can be made with certainty.

Current understanding of boreal owl habitat use suggests that the maintenance of forested landscapes is required for boreal owls. Furthermore, silvicultural prescriptions must provide for large diameter trees well dispersed over space and time. The roosting, nesting, and foraging ecology of boreal owls in the western United States also suggests that mature

and older forest must be well represented in the landscape to support a productive boreal owl population. In most cases, uneven-aged management or other silvicultural practices that maintain canopy structure and forest floor moisture will maintain boreal owl nesting, roosting, and foraging habitat. Forest clearcuts provide little or no habitat for boreal owls for two to several decades after disturbance and may not provide high quality habitat for one to two centuries.

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