Chapter 14

Review of Technical Knowledge: Great Gray Owls

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INTRODUCTION

The great gray owl (*Strix nebulosa*) is the longest, but not heaviest, of the northern forest owls. Distributed holarctically across the boreal forests of North America and Eurasia, the great gray owl extends its range southward into the contiguous states by inhabiting forests other than the boreal type. The subalpine and montane forests of the Cascade Range, Sierra Nevada Range, and the Rocky Mountains support great gray owl populations in central Washington; central and northwestern Oregon; north-central and eastern California; northern, central, and southeastern Idaho; western Montana; and northwestern Wyoming. Despite its large size, broad distribution, and relatively bold nature, the great gray owl remains poorly understood. European investigations focus primarily on how *Microtus* populations affect the owl's productivity and movements (Hilden and Helo 1981, Mikkola 1983, Stefansson 1983, Cramp 1985, Korpimaki 1986). We have found no studies that examine great gray owl poplation characteristics or habitat use. In North America, Bull *et al.* (1988a, 1988b, 1989a, 1989b) intensively studied great gray owl demography, movements, and habitat use. Their study area in northwestern Oregon, however, may not be characteristic of the entire North American range. Franklin (1988) observed the breeding biology of great gray owls in southeastern Idaho. Duncan (1992) examined great gray owl movements as they relate to several factors, including prey abundance, for a Canadian population. The remaining studies (e.g., Winter 1986, Osborne 1987, Spreyer 1987) are largely limited to describing nest sites. Though the great gray owl has not been targeted for expansive ecological studies, a useful body of knowledge has accumulated through more specific research and incidental sources.

DISTINGUISHING CHARACTERISTICS

Distinctly colored, the great gray owl wears a dusky gray to sooty overall plumage. Grayish white mottles the crown, nape, back, rump, and shoulders; but the underparts are boldly streaked over fine barring. Its wings and long, wedge-shaped tail are strongly barred. The great gray owl's head supports no horn-like feather tufts, but the facial disk, common to all owls, is conspicuously patterned with concentric bands of pale gray on a dusky white background. Bright yellow eyes punctuate the face and appear small for the size of the bird. The yellow or ivory bill contrasts a black chin sharply defined by prominent white jowl patches. The legs, feet, and toes are completely feathered. Great gray owls exhibit pronounced reversed size dimorphism (McGillivray 1987). Males weigh 700-1,175 g and females 925-1,700 g (Duncan 1992). Total length is 61-84 cm. Cramp (1985) and Voous (1988) provide measurements from the Palaearctic.

SYSTEMATICS

The great gray owl is the only member of the genus *Strix* that breeds in both the Old and New Worlds (Voous 1988). Of the two recognized subspecies, *Strix nebulosa nebulosa* inhabits North America and *Strix nebulosa lapponica* inhabits Europe and Asia. Although minor plumage differences exist between the subspecies, Oeming (1955), Mikkola (1981), and Duncan (1992) concluded that the two subspecies were very similar in size. The size similarity probably reflects three important circumstances. First, diet, climate, and other ecological factors are similar across the species' range. Second, the species is probably a recent arrival to North America (Oeming 1955, Voous 1988). Third, current theory (Eldredge and Gould 1972) suggests the great gray owl exhibits species stability. Sibley and Ahlquist (1990) used DNA analysis to identify the mottled owl (*Ciccaba virgata*) and the barred owl (*Strix varia*) as the great gray owl's closest relatives.

Strix nebulosa is not represented in the fossil record of North America. However, fossil material does yield related species (Olson 1985). *Strix dakota* (Miller 1944:95) has been found in South Dakota's Tertiary

deposits. Dating back 18-19 million years, *S. dakota* was associated with the early Hemingfordian group in the North American Land Mammal Age (NALMA). Unlike living species in this genus, it was a small owl, and Ford (1967:69) has questioned its generic allocation. A fossil tarsometatarsus of an undescribed *Strix* species dates back 9 million years to the late Clarendonian-early Hemphillian (NALMA) group in the Tertiary deposits of north-central Nebraska. It is in the size range for males of *Strix nebulosa*. Finally, Olson has commented on two late-Pleistocene specimens (Olson 1984:44-46). One of them, an unnamed species of *Strix* from Ladds, Georgia, was larger than any living North American owl. *Strix brea* from Rancho La Brea, CA (Howard 1933:66), was comparable to *Strix nebulosa* in size except that it had very long tarsometatarsi.

DISTRIBUTION AND ABUNDANCE

North American Breeding Range

In Canada, the great gray owl ranges from near tree line in northern Yukon, northwestern and central Mackenzie (Lockhart River, Great Slave Lake), northern Saskatchewan, northern Manitoba (Churchill, The Pas), and northern Ontario (probably Severn River, Moose Factory) south through southern Yukon and interior British Columbia, northern and central Alberta, central Manitoba (Dauphin Lake, South Junction), and central Ontario (Godfrey 1986); it also occurs in Quebec but breeding has not been confirmed in this province. In the United States, great gray owls nest commonly in central and southern Alaska; but the species exhibits uneven distribution throughout its southern range, which includes central and northwestern Washington, northern and central Idaho, western Montana, northwestern Wyoming, northeastern and central Oregon, east-central California, west-central Nevada, and portions of Minnesota, Michigan and Wisconsin (Map 3).

North American Winter Range

The winter range of the great gray owl coincides with its breeding range except for a tendency to wander irregularly south in winter (Nero 1969, Brunton and Pittaway 1971), occasionally as far as Pennsylvania and Long Island, New York, in the east. Movement patterns of southwestern populations are unknown but are thought to be more stable and sedentary (Duncan 1992, Bull and Duncan 1993).

Eurasian Range

In Eurasia, great gray owls breed from northern Scandinavia, northern Russia and northern Siberia south to central Russia, northern Mongolia, northern Manchuria, Amurland, and Sakhalin (Cramp 1985). Southern extensions in boreal forest of some central Asiatic mountains (Salair and Kuznetsk Alatau in the northern Altai and the Kentei Mountains in eastern Mongolia at 54°N) correspond to similar extensions into the Rocky and Sierra Nevada Mountains in the United States (Voous 1988).

Abundance

Counts or estimates of great gray owl abundance differ among studies and are likely influenced by estimate methods, researcher bias, the phase of prey cycle in northern populations, and nest site availability. Nero (1969) estimated the North American great gray owl population to be between 5,000 and 50,000 birds. This estimate was arbitrary and not based on a sample from the "population" of interest. The highest reported nesting density in North America is 1.88 pairs/km^2 in Manitoba and northern Minnesota (Duncan 1987). Bull and Henjum (1990) calculated densities of 1.72 pairs/km^2 and 0.74 pairs/km^2 on two Oregon study sites. Their calculations were based on nests located during systematic searches. Winter (1986) recorded a nesting density of 0.66 pairs/km^2 in California. Spreyer (1987) recorded 0.15 pairs/km^2 in Minnesota. These study areas were generally chosen because great gray owls were abundant in the area.

European researchers report substantially higher maximum densities. In fact, some classify the species as a "loose colonial nester" that is extremely tolerant of intraspecifics on its breeding home range (Wahlstedt 1974, Mikkola 1983, Duncan 1987, Bull and Henjum 1990). Wahlstedt (1974) discovered 7 pairs over a distance of 3 km in Sweden. Hoglund and Lansgren (1968) documented nests in Sweden as close as 100 m apart. In Finland, 3 nests were found within 400 m of one another (Mikkola 1976). Although nests may be clumped, the species' breeding strategy does not fit the definition of a colonial nester (Lincoln *et al.* 1982).

Population Trends

No long-term, rigorous, or standardized data on regional or local breeding populations are available. At a local scale, southern populations in the west-

ern United States are thought to be relatively stable with individuals breeding every year and/or at least remaining in the same general area all year (Winter 1986, Bull and Henjum 1990). Northern populations appear to be less stable (Nero 1980, Duncan 1992). Duncan (1992) related great gray owl population stability to that of prey biomass productivity (see the Food Habits section later in this chapter).

The North American Breeding Bird Survey (BBS) methodology does not effectively detect nocturnal species. A standardized survey protocol specific to great gray owls, or to owls in general, needs to be used across the species' range if long-term population trend data are to be obtained. Local population studies from within the breeding range for North America (Collins 1980, Nero 1980, Winter 1986, Franklin 1987, Bull and Henjum 1990, Duncan 1992) and Eurasia (reviewed in Mikkola 1983) typically last fewer than 8 years. Caution must be exercised in drawing regional, or even local, population trend conclusions from short-term studies where prey populations are cyclic or fluctuate multi-annually (see also Movements).

Breeding populations of Finland's great gray owls showed long-term regional increases from 1954 to 1981, but these probably related to more intensive search efforts and to an increasingly colder climate (Mikkola 1983). Collins and Wendt (1989) summarized breeding bird survey data for many Canadian birds from 1966 to 1983. For species with low densities, they compared a simple abundance index for the time periods 1966-1977 and 1978-1983. Great gray owls were detected in 4 of 10 Canadian regions covered by the BBS. Between the two periods, increases were noted in the maritime provinces, central Ontario and Quebec, and southern British Columbia whereas a decrease was noted for the central prairies. Collins and Wendt (1989) caution against inferring regional population trends for species with such low densities or small samples and they say that changes noted are possibly due to changes in BBS techniques. Fyfe (1976) reviewed the population status of raptors in Canada based on correspondence with bird observers. Great gray owl population trends were noted as "fluctuating" in Ontario, southern Quebec, the prairie provinces, and British Columbia. Trends were reported as "unknown" for the Northwest Territories and the maritime provinces. Nero *et al.* (1984) speculated that more great gray owls now inhabit southern Manitoba than in the past.

Conversely, Winter (1986) surmised from limited data that great gray owl populations in California have declined from ancestral levels due to habitat degradation. A breeding population in the Targhee National Forest, Idaho, increased then decreased from 1974 to 1989. Groves and Zehntner (1990) felt the changes were related to a specific timber harvest regime but this speculation was also based on limited data rather than on long-term monitoring. Bryan and Forsman (1987) believed Oregon populations must have declined as a result of habitat loss since all (n = 63) of their locations occurred in mature to old-growth timber, but the suspected decline cannot be substantiated.

No data substantiate historical changes in distribution although some have suggested possible changes in Europe (Mikkola 1983, Voous 1988) and in North America (Oeming 1955, Nero 1980). Reliable information on population trend and changes in great gray owl distribution will only become available after monitoring programs have been in place for several years.

MOVEMENTS

Great gray owls have been described as both nonmigratory and nomadic (Nero 1980, Mikkola 1983). Movement patterns are variable, being stable in some areas and/or years while highly irruptive in others. Movements appear to be influenced by prey availability and the stability of prey biomass productivity (Nero 1980, Mikkola 1983, Duncan 1992). In southern latitudes great gray owls appear to shift to lower elevations and, presumably, lower snow depths (J. Winter; pers. comm., Franklin 1987). In northeast Oregon adult owls moved 2-43 km from their nest sites to areas with thinner snow cover (Bull *et al.* 1988a); but 39% of radio-marked pairs nested on the same nest site a second year, and 39% nested within 1 km of their previous nests. Only 22% nested > 1 km from their previous nests and the average distance between successive nests was 1.3 km (0.2-4.5 km).

In boreal forests of Canada and Alaska, individuals can migrate up to 700 km (Nero 1980, Duncan 1992). In Manitoba and northern Minnesota, migration (breeding dispersal, c.f. Greenwood and Harvey 1982) is generally independent of snow cover. Among dispersing birds 62% of females and 27% of males moved before snow accumulated, and all adults dispersed before snow depths reached 45 cm. In fact, although great gray owls dispersed to areas of lower elevation, snow levels increased. Dispersal did, however, follow rodent population crashes (Duncan 1992); and interaction between dispersal strategy and prey population phases was significant ($P < 0.001$). Owls failing to disperse following prey

declines frequently die (Duncan 1992). Cramp (1985), however, noted no correlation in European literature between the *extent* of movement and rodent population levels.

For North America, records of irregular southward winter invasions of this species date back to 1831 when at least one individual flew as far south as Marblehead, Maine. Other winter incursions are reported by Godfrey (1967), Collins (1980), Nero (1980), and Campbell *et al.* (1990). See also figure 1. Large invasions rarely occur in all or many regions in the same year, implying asynchronous prey population crashes over large regions (Duncan 1992). Nine sporadic great gray owl invasions between 1955 and 1981 have been observed (generally in different years from North America) in Scandinavia (Cramp 1985). This species is known to occasionally winter well north (as well as south) of its taiga breeding range (Dement'ev and Gladkov in Nero 1980, Cramp 1985).

Duncan (1992) also documented that breeding great gray owls in southeastern Manitoba and northern Minnesota (within the southern portion of their North American taiga breeding range) disperse northward following prey population crashes. This dispersal more closely resembles a migratory type dispersal rather than nomadism (c.f. Baker 1978). Radio-tracking shows individuals can travel (day and night) up to 40 km in 24 hours and 650 km in 3 months (Duncan 1992). Great gray owls loosely congregate, probably in response to abundant prey (Nero 1980, Duncan 1992). For example, during the winter of 1978-1979, about 40 birds gathered near Toronto, Ontario; and >100 were found in southeastern Manitoba within a 30 km radius (Bull and Duncan 1993).

Sex Differences

In Manitoba and northern Minnesota, radio-marked adult females migrated farther and earlier (mean = 372 km; October) than did adult males (235 km; January-February) but no gender difference was observed in mean direction of migration (Duncan 1992). Sex ratios were calculated by Duncan (1992) based on winter-caught great gray owls (n = 412) sexed by discriminate function analysis. For a combined 14-year period, sex ratios were significantly female biased (294 females:118 males).

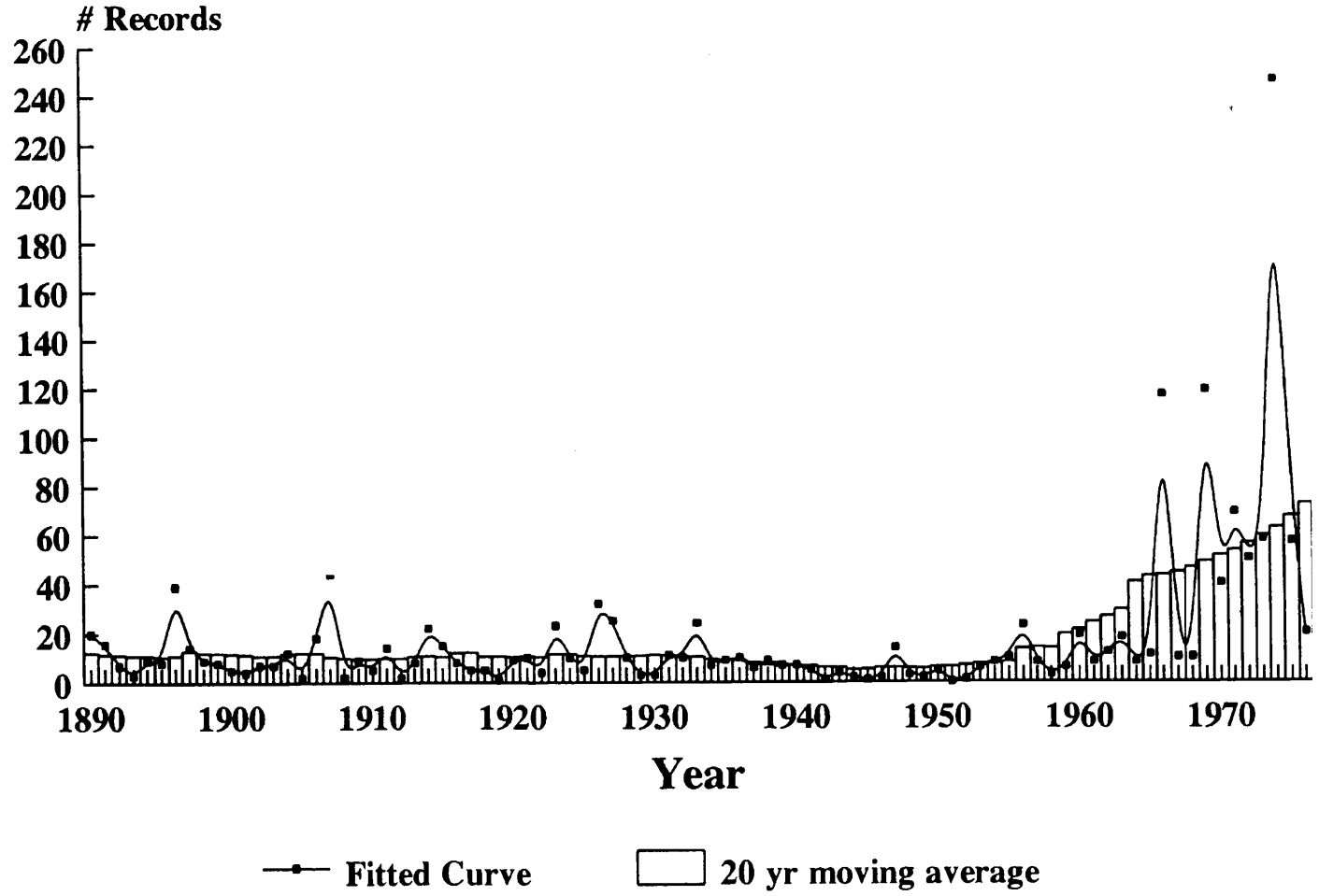

Figure 1.--Numbers of great gray owls observed in southern Canada and northern United States during winter 1890-1979 (data from Collins 1980).

HABITAT USE

Few experimental studies have analyzed habitat associations, although Servos 1986, Bull *et al.* 1988b, and Bouchart 1991 conducted qualitative studies. Abundant anecdotal descriptions of owl-occupied habitat exists. Availability of nest sites and suitable foraging habitat are considered the most important factors governing habitat use by breeding great gray owls (Lundberg 1979, Collins 1980, Nero 1980 Mikkola 1983).

Nesting Habitat

Nest Structure

Great gray owls rely on old hawk and raven stick-nests or natural depressions on broken-topped snags or stumps for nest sites (Nero 1980, Mikkola 1983) (see tables 1 and 2). They also nest on natural platforms formed by dwarf-mistletoe (*Arceuthobium spp.*) and, rarely, on the ground, rock cliffs, or haystacks (Mikkola 1983, Duncan 1992). Great gray owls readily accept artificial nest structures (Nero *et al.* 1974, Collins 1980, Bohm 1985, Bull and Henjum 1990). Thus, the actual nest structure and its support may be relatively unimportant in nest site selection compared to the nest site habitat and availability of foraging habitat. In evaluating long-term habitat quality, it is important to consider factors that influence populations of nest-building species (*Accipitridae* and *Corvidae*) and tree-pathogen/insect interactions that can influence tree branching. Some authors report that the relative use of broken-topped snags decreases northward through the great gray owl's breeding range (Mikkola 1983, Winter 1986, Franklin 1987) corresponding with a decrease in tree size and circumference in northern latitudes.

Broad Scale Nesting Habitat

In Canada great gray owl breeding habitat is generally described as extensive taiga interspersed with sphagnum bogs, muskegs, and other open spaces (Nero 1980, Harris 1984, Godfrey 1986, Campbell *et al.* 1990, Semenchuk 1992). Tamarack (*Larix laricina*) bogs appear to be preferred nesting habitat in Manitoba (Nero 1980, Servos 1986, Lang *et al.* 1991, Duncan 1992). In southeast Manitoba three studies have investigated breeding habitat used by great gray owls, primarily at the forest stand scale. Ser-

Table 1. – Tree species used for nesting (1), or dominant trees in nest stands (2) used by great gray owls in Canada and the United States. A "3" designates tree species used for nesting that also represent the dominant tree in nest stands. Data from: Bouchart (1991), Osborne (1987), Spreyer (1987), Harris (1984), Nero (1980), Duncan (1992), Servos (1986), Bull & Henjum (1990), Winter (1986), Oeming (1955), Campbell *et al.* (1990), Semenchuk (1992), Kondla (1973), and Sent (1938). Tree species abreviations: LL *Larix laricina*, PT *Populus tremuloides*, PB *Populus balsamifera*, PS *Populus spp.*, PI *Picea inariana*, PG *Picea glauca*, BP *Betula papyrifara*, TO *Thuja occidentalis*, AB *Abies balsamea*, PB *Pinus banksiana*, FN *Fraxinus nigra*, TA *Tilia americana*, UA *Ulmus amaricana*, AS *Acer saccharum*, AR *Acer rubrum*, PC *Pinus contorta*, PP *Pinus ponderosa*, PM *Pseudotsuga menziesii*, PE *Picea engelmannii*, LD *Libocedrus decurrens*, AC *Abies concolor*, LO *Larix occidentalis*.

	Tree species																					
Location	LL	PT	PB	PS	PM	PG	BP	TO	AB	PB	FN	TA	UA	AS	AR	PC	PP	PM	PE	LD	AC	LO
Ontario	3	3	1		3					1												
Manitoba	3	3	1	1	2		2	1	1				1									
Saskatchewan	3	3			2																	
Minnesota	3	2	3				1				1	1	1		1							
Wisconsin	3	3																				
Alberta	1	3	3	1	1	2				1												
British Columbia		3			3	1										2		2	2			
Alaska			3			3	2															
Northwest Territories						3																
Yukon																						
Washington																2	2	2				2
Idaho		3		1												3		3	1			
Montana																						
Oregon																3	3	3				3
Wyoming		3		1												3		3	1			
California																	2			2	2	

Table 2.—Nest platform types used by great gray owls in Canada and the United States. See table 1 for sources.

Location	Stick	Stump	Witch's broom	Ground	Artificial
Ontario	x	x			
Manitoba	x	x		x	x
Saskatchewan	x				
Minnesota	x				x
Wisconsin	x				
Alberta	x				x
British Columbia	x		x		
Alaska	x	x			
Northwest Territories	x				
Yukon	x				
Washington	x	x			
Idaho	x	x			x
Montana	x	x			
Oregon	x	x	x		x
Wyoming	x	x			x
California		x			x

vos (1986) looked at habitat use by post-fledging family groups rather than actual nest sites. The dominant tree species within a 1-km radius around 14 nest sites were tamarack (6), quaking aspen (*Populus tremuloides*) (4), black spruce (*Picea mariana*) (2), paper birch (*Betula papyrifera*) (1), and tree-grown muskeg (1). The distribution of these sites reflected the availability of habitat (Bouchart 1991). Collins (1980) looked at dominant tree species in nest stands within 800 m of 9 nests in southeastern Manitoba. Tamarack/black spruce dominated at seven sites and quaking aspen dominated at the others. See table 1 for descriptions of other sites.

Tamarack and black spruce wetlands were associated with 25 of 27 suspected breeding sites in Saskatchewan (Harris 1984). In Alberta, Oeming (1955) found that great gray owls frequently nested in poplar woods adjacent to extensive treed muskegs. Spreyer (1987) conducted a detailed floristic analysis within 20 m of 14 nest sites in Minnesota. Nest site stands were dominated by hardwood tree species, especially black ash (*Fraxinus nigra*), basswood (*Tilia americana*), American elm (*Ulmus americana*), red maple (*Acer rubrum*), and sugar maple (*Acer saccharum*). All were characterized as being in habitats with high soil moisture.

Great gray owls bred in forests (all types) in the vicinity of marshes, lakes, muskegs, wet meadows, and pastures in British Columbia (Campbell *et al.* 1990). The forests were primarily Douglas-fir (*Pseudotsuga menziesii*) with patches of aspen but also Douglas-fir/lodgepole pine (*Pinus contorta*), lodgepole pine/Engelmann spruce (*Picea engelmannii*), black spruce, and Engelmann spruce-dominated stands between 900 and 1,220 m elevation. In Alaska, great gray owls nested primarily in balsam poplar (*Populus balsamea*) forest and less frequently in white spruce/birch forest (Osborne 1987).

In southern parts of their range, great gray owls nest in relatively xeric, montane evergreen, or deciduous forests up to 2,800 m elevation. Winter (1986) and Reid (1989) concluded that access to suitable hunting meadows restricts population densities and range expansion in California since owls rarely foraged in forest habitat. For example, preferred breeding habitats were pine and fir forests adjacent to montane meadows between 750 m and 2,250 m elevation (Winter 1986). Ponderosa pine (*Pinus ponderosa*) was the dominant tree species within the home ranges of breeding owls, followed by incense cedar (*Calocerdrus decurrens*) and white fir (*Abies concolor*). In southeastern Idaho and northwestern Wyoming, 10 nests were in mid- to late-successional stages of Douglas-fir forests on flat land with herbaceous understory, which is the most abundant habitat available (Franklin 1987). In addition, clear-cut and natural meadows were associated with all 10 nests. More than 90% of sightings of this species in Idaho and Wyoming were in the lodgepole pine/Douglas-fir/aspen zone (Franklin 1987). In central Oregon, meadow systems associated with coniferous forests were used (Bryan and Forsman 1987). In northeastern Oregon, all forest types sampled had nests, with 50% found in Douglas-fir/grand fir (*Abies grandis*) forest types, 29% in lodgepole pine/western larch, 15% in ponderosa pine/Douglas-fir, and 7% in pon-

derosa pine (Bull and Henjum 1990).

Mikkola (1983) found that great gray owls in Finland use damp heath coniferous forests (45%), spruce bogs (35%), dry heath coniferous forests (11%), pine peat bog (6%), and other herb-rich forests (3%). These were also associated with open grassy areas.

Home Range Area

Great gray owl home ranges are often relatively small, depending on food supply (Mikkola 1981). Average home range size calculated for breeding adults in Oregon was 4.5 km^2 (n = 5 males, range 1.3 - 6.5 km^2, minimum convex polygon [MCP]) (Bull *et al.* 1988a, Bull and Henjum 1990). Craighead and Craighead (1956) calculated 2.6 km^2 (MCP) in Wyoming. Males have been observed hunting up to 3.2 km from their nest (Bull and Henjum 1990). Maximum distance traveled by adults from their nest averaged 13.4 km (Bull and Henjum 1990). Bryan and Forsman (1987) observed owls moving 3-4.8 km/d.

Microhabitat

Nesting

Bull and Henjum (1990) erected 158 artificial platforms to determine preference for nest type (open vs. box), height (9 m vs. 15 m), and distance to a clearcut (adjacent vs. 100-200 m). Great gray owls always chose open structures, preferred higher nest structures, and selected nest sites within forest stands. Distance to the nearest opening averaged 256 m (range 0 to 1,000 m) in Manitoba (Bouchart 1991) and 143 m in Idaho and Wyoming (Franklin 1987). Canopy closure exceeded 60% at most Oregon nest sites (Bull and Henjum 1990), and the percentage of forested area within 500 m radius of nests varied between 52% and 99%.

Roosting

Great gray owls typically roost in trees near the trunk. They lower their heads, close their eyes, and "fold" their facial disks, thus dividing the face with a vertical dark line that often matches the bark pattern (Cramp 1985). They roost in trees with fairly dense canopy during hot weather and close to the trunk in inclement weather. Winter (1986) noted that great gray owls roosted at lower heights during warmer weather, possibly as a thermoregulatory response. In California, roosts averaged 90 m from openings and 10.9 m above ground; trees <23 cm dbh were avoided (Winter 1986).

Unlike spotted owls, which roost in the same location over long periods (Forsman 1976, Winter 1986), great gray owls frequently change trees to roost throughout their home range. In winter and late spring (April), owls occasionally roost in sunny open areas and atop snags (Winter 1986, Bull and Duncan 1993). Although great gray owls frequently use meadows for foraging, they typically roost away from the meadow's edge. Winter's (1986) roosts averaged 90 m from openings and Bryan (1985) also noted owls roosting within forest stands.

Because fledglings leave the nest before they can fly, forested habitat around the nest is considered important for their survival. Bull and Henjum (1990) noted that roosts accessible to flightless young, such as leaning and deformed trees and perches high enough to avoid terrestrial predators, may increase reproductive success. In another study area, roost height correlated positively with the age of recently fledged young (Franklin 1987).

Foraging

Several authors cite foraging habitat throughout the great gray owls' range as relatively open, grassy habitat, including bogs, selective and clear-cut logged areas, natural meadows, and open forests (Nero 1980, Mikkola 1983, Winter 1986). These authors maintain that great gray owls avoid hunting in timbered stands. Bryan and Forsman (1987) and Bull and Henjum (1990), however, report great gray owls foraging in and, in fact, preferring open forests for foraging. In northeast Oregon, male owls foraged in stands with 11-59% canopy closure (Bull and Henjum 1990). These stands had heavy ground cover (average 88%) dominated by grasses. While hunting, great gray owls perch at varying heights but usually 3-5 m high in both live trees and snags adjacent to or within open grassy areas. Perch heights for Oregon males averaged 5.5 m (Bull and Henjum 1990). Great gray owls rarely hunt while sitting on the ground or while flying (Collins 1980, Nero 1980, Winter 1986, Duncan 1987, Reid 1989, Bull and Henjum 1990). Perch to prey distances averaged 10.5 m in Bull and Henjum's (1990) study. Downed wood was present within 1 m of the capture point at 77% of prey capture sites (Bull *et al.* 1988b).

Based on relocations of radio-marked individuals (five males, five females and six young), Servos (1986) found that owls in southeastern Manitoba used tamarack bogs and treed muskeg in greater proportion than their availability. Jack pine (*Pinus banksiana*), black spruce stands, open areas with few or no trees, and habitats with dense shrub layers were avoided (Servos 1986).

Winter Use

Winter habitat is generally the same as the breeding habitat. In some mountainous portions of its breeding range, the great gray owl often descends to lower elevations (Yosemite National Park, California: J. Winter, pers. comm.). The ecotone between grassland meadows and tall willows, balsam poplars and white spruce (*Picea alba*), is the preferred winter habitat in Alaska (Osborne 1987). In Manitoba, the owls use tamarack, black spruce, and aspen forests in winter months (Bouchart 1991). Elsewhere in Canada the owl also occupies open fields with scattered large trees, shrubbery, and fence-rows (Brunton and Pittaway 1971, Nero 1969), especially during irruptive winters when many individuals move south.

FOOD HABITS

Great gray owls prey upon relatively small prey. Their diets consist primarily of small mammals, especially rodents. Voles (*Microtus* spp.) dominate their diets over most of their range (Collins 1980, Nero 1980, Mikkola 1983, Bull *et al.* 1989a, Duncan 1992). Pocket gophers (*Thomomys* spp.) are the primary prey in Yosemite National Park, California (Winter 1986), southeast Idaho and northwest Wyoming (Franklin 1988), and northeast Oregon (Bull and Henjum 1990). Occasional prey include shrews (*Sorex* spp., *Blarina brevicauda, Microsorex hoyi*), moles (*Scapanus* spp.), red-backed voles (*Clethrionomys gapperi*), deer mice (*Peromyscus maniculatus*), red squirrels (*Tamiasciurus* spp.), flying squirrels (*Glaucomys* spp.), jumping mice (*Zapus* spp.), and grasshopper mice (*Onychomys* spp). In Canada, star-nosed moles (*Condylura cristata*), northern bog lemmings (*Synaptomys borealis*), heather voles (*Phenacomys intermedius*), least chipmunks (*Eutamias minimus*), weasels (*Mustela* spp.), snowshoe hares (*Lepus americanus*), sharp-shinned hawks (*Accipiter striatus*), broad-winged hawks (*Buteo platypterus*), gray jays (*Perisoreus canadensis*), American robins (*Turdus migratorius*), spruce grouse (*Dendrogapus canadensis*), and wood frogs (*Rana sylvatica*) were also consumed (Duncan 1992).

In most years the great gray owl diet overlaps very little with great horned owls (*Bubo virginianus*), long-eared owls (*Asio otus*), and boreal owls (*Aegolius funereus*). Competition for food is more likely to occur during years when prey species are scarce. In northeast Oregon, the long-eared owl diet is most similar to that of the great gray owl, although the latter eats mostly adult pocket gophers while the former takes juveniles (E.L. Bull, pers. comm.). Whether this difference reflects the owls' diets or sample bias is not clear.

Quantitative data on food habits presented herein are derived primarily from pellet analysis. Prey remains in pellets are a reliable indicator of diet, but caution is needed when analyzing pellets collected at nest sites because breeding males have been observed to deliver larger prey items to the nest and to eat smaller prey themselves (Bull and Henjum 1990).

Great gray owl diets from various locations in North America are compared in table 3. Vole species (weights ranging from 30 to 50 g) dominate diets of northern populations, often comprising > 90% of diets (Hoglund and Lansgren 1968, Mikkola and

Table 3.—Food of the great gray owl from selected regions of North America. Figures indicate percentage of prey by numbers; data derived primarily from analysis of pellets.

Prey	Oregon[1]	Idaho[2]	California[3]	Manitoba[4]
Microtus	51.6	34.1	30.8	83.5
Thomomys	28.8	57.9	52.6	—
Sorex	2.2	1.4	1.5	1.6
Peromyscus	0.9	1.6	3.8	0.2
Clethrionomys	13.9	0.7	—	3.0
Bird	0.1	2.2	0.4	1.7
Other	2.5	2.1	10.9	10.0
Prey items (n)	4,546	435	662	2,004

[1]*Bull et al. (1989).*
[2]*Franklin (1987).*
[3]*Winter (1986).*
[4]*Duncan (1992).*

Sulkava 1970, Pulliainen and Loisa 1977, Mikkola 1983, Osborne 1987). *Microtus* and *Synaptomys* species comprise 91.3% (84% is *Microtus pennsylvanicus*) of great gray owl diets in boreal forest regions of North America (Duncan 1992) and are more similar to that of European great gray owls than to that of owls in Oregon, Idaho, or California. Michigan great gray owls consumed 96% (by number) *Microtus pennsylvanicus* (Master 1979). Cramp (1985) noted that diet varies little between individuals or within years. Even changes between years consist largely of alterations in proportions of vole species rather than the overall proportion of voles. In Manitoba and Minnesota, owls select *Microtus* spp. in proportions greater than their availability, while shrews (Soricidae) and *Clethrionomys* spp. were underutilized (Duncan 1992). In Oregon, however, pocket gophers comprise 67% of the diet's biomass and voles 27% (Bull and Henjum 1990). In California, owls shift prey emphasis between microtines and pocket gophers as prey availability changes (Winter 1986).

In general, peak hunting times are thought to coincide with peak activity of prey species (Nero 1980, Mikkola 1983, Winter 1986, Reid 1989). During the breeding season, the male regularly hunts nocturnally and diurnally in addition to his normal crepuscular pattern. Brunton and Pittaway (1971) reported that in winter great gray owls are crepuscular and diurnal hunters, but great gray owls have also been observed to hunt nocturnally in winter (J.R. Duncan, unpubl. data).

Great gray owls hunt primarily from perches, listening and watching the ground intently. When prey is detected, the owl usually flies only a short distance, generally no more than 50 m. Bull and Henjum (1990) recorded an average perch to prey distance of 10.5 m. Great gray owls can detect and capture prey by sound alone, which permits the capture of prey beneath snow (Law 1960, Godfrey 1967, Nero 1969). Individuals typically hover above the snow and then plunge face downward breaking through the snow with clenched feet and then attempting to grasp prey with their feet and talons (Collins 1980, Nero 1980, Duncan 1992). Nero (1980) observed owls breaking through snow crust hard enough to support an 80-kg person. Great gray owls can reach prey as deep as 45 cm below the snow surface (Collins 1980). Duncan (1992) observed successful foraging in snows exceeding 70 cm. In summer the owls break into the earthen burrows of pocket gophers (*Thomomys* spp.) in much the same way (Tryon 1943, Winter 1986). Bull *et al.* (1989b) observed a 33% capture rate in 90 attacks. Snow-plunging owls achieved a 65% success rate (Duncan 1992).

Asymmetrical ear openings undoubtedly help this owl detect prey by sound alone, as has been shown experimentally in the barn owl (Payne 1971, see also reviews in Voous 1988 and Marti 1992). Voous (1988) describes the external ear openings of the great gray owl. The asymmetry in the size and position of the great gray owl's ear opening is enhanced by skull asymmetry, which Voous (1988) reports "[promotes] precise directional hearing."

The daily food intake was from 60 to 80 g per day for an incubating wild female (Cramp 1985). In winter, wild adults can consume up to 7 *Microtus*-sized prey (45 g each) per day (Duncan 1992). Bull and Henjum (1990) calculated an individual great gray owl's yearly consumption as > 1,400 voles.

INFLUENCE OF PREY SPECIES BIOLOGY ON OWL MOVEMENTS

Microtine voles generally occupy moist grass/sedge openings and open herbaceous forests (Anderson 1987) whereas pocket gophers (*Thomomys* spp.) prefer drier meadows (Chase *et al.* 1982). Microtines undergo dramatic, geographically asynchronous population fluctuations while pocket gopher populations exhibit less annual variation. The contrasting dynamics of primary prey populations likely influence great gray owl population dynamics. Andersson (1980) compared the relative merits of adult avian nomadism to site tenacity based on a model relating Malthusian fitness of an individual to the pattern of food production. The model predicts that nomadism is most likely when food production fluctuates in an unpredictable manner. Conversely, it predicts site tenacity or migration under stable food production or when fluctuations are regular or predictable. The pattern of food production, then, is likely to influence movements of great gray owls. The semi-nomadic movement pattern of northern populations and the relative site tenacity observed in southern populations fit the predictions of this model.

Northern vole populations are thought to fluctuate with a larger amplitude than southern populations. Explanations for this pattern abound, although none seems completely satisfactory. Hypotheses concerning vole cycles include those based on optimal versus suboptimal habitats (Martell and Fuller 1979), geographical (climatic) gradients (Hansson and Henttonen 1989), dispersal sinks and predation (Tamarin 1978, Gliwicz 1980, Hansson and Henttonen 1989), food and cover (Birney *et al.* 1976, Cole and Batzli 1979, Taitt *et al.* 1981), habitat het-

erogeneity and dispersal (Abramsky and Tracy 1979, Gaines *et al.* 1979, Stenseth 1980), and immunological disfunction and opportunistic, pathogenic microparasitism (Mihok *et al.* 1985). More recently, Halle and Lehmann (1987) investigated the phasic relationship among circadian activity pattern, photoperiod responses, and population cycles in voles. They concluded "that vole population cycles are not triggered by overriding (e.g., climatic) conditions, but depend on population properties themselves." No hypothesis, model (Stenseth 1980), or statistical analysis (Mihok 1981, Garsd and Howard 1981, 1982) has provided an all-encompassing explanation of microtine multi-annual population cycles. Given the diversity of population cycle patterns observed, Lidicker (1988) suggested a multivariate, synthetic approach.

BREEDING BIOLOGY

While great gray owls are typically monogamous, polygyny is occasionally suspected (Cramp 1985, J.R. Duncan, unpubl. data). In boreal forest regions the pair bond does not appear to be maintained over winter. However, individuals may nest with the same mate in the subsequent year if local prey populations remain high (Duncan 1992). In Oregon, Idaho, and California, pairs possibly remain together as long as both live, but either sex will remate if its mate disappears (E. L. Bull, pers. comm.).

Chronology of Courtship and Breeding

In Manitoba and Minnesota, great gray owls are mostly solitary in autumn and early winter, becoming increasingly gregarious toward March. Groups of up to 15 individuals have been observed in late winter (Nero 1980, J.R. Duncan, unpubl. data). Pair formation occurs as early as January and as late as 2 weeks prior to egg laying in April and May (Collins 1980, Franklin 1988). In Manitoba, courtship behavior and nest site inspections have been observed as early as November (Duncan 1987) but more typically in late February through April. In California, Oregon, and Manitoba, clutches are initiated as early as late March. Mean date of the first egg laid is 5 April in Manitoba (J.R. Duncan, unpubl. data) versus 5 May in Idaho and Wyoming. Egg laying is apparently delayed in years of heavy snow cover (Franklin 1988), and Bull *et al.* (1989b) observed earlier nesting in areas with lower snow cover. No second broods have been reported unless the first nesting attempt fails. One record of a renesting after 2-week old nestlings died is known (Bull and Henjum 1990). The timing of egg laying probably depends on the availability of prey (Voous 1988).

Only females develop a brood patch; and only females incubate, beginning with the first egg laid. Eggs are laid at 1 to 3-day intervals. Reported average incubation periods vary: 29.7 days (Idaho and Wyoming; Franklin 1988), 28-36 days (Scandinavia: Mikkola 1981), and 31 days in captivity (Ontario: K. McKeever, pers. comm.).

During incubation, females leave the nest only briefly and at long intervals to defecate and regurgitate pellets (Mikkola 1981, Bull and Henjum 1990). Males feed the incubating/brooding females and bring three to five prey per day to the female. Collins (1980) reports 0.27 feeding trips per hour by the male to the nest during the nestling stage in 135 hours of observation. Young great gray owls are fed at all times of day, but primarily around dawn and dusk.

Young either fall or jump from their nest at 3 to 4 weeks of age (Franklin 1988, Bull *et al.* 1989b). Owlets leave the nest over several days, with the oldest usually leaving first (Oeming 1955, Nero 1980, Bull and Henjum 1990). After leaving, young owls can readily climb leaning trees and roost off the ground. They can fly 7-14 days after leaving the nest (Franklin 1988).

Reported weights of juveniles just out of the nest range from 360 to 755 g. The mean weight at fledging was 507 g in Manitoba (Collins 1980, J. R. Duncan, unpubl. data) and 609 g in Oregon (Bull *et al.* 1989b). Females stay near their fledged young to protect them. After 3-6 weeks females abandon their young, but males continue to feed them for up to 3 months (Bull and Henjum 1990, Duncan 1992). Females may visit other adjacent family groups, occasionally returning to their own mate and progeny (Duncan 1987). Fledged young are known to join other fledged broods and may be fed by more than one male (J.R. Duncan, unpubl. data). Juveniles start hunting on their own at about 3 months, are independent by September/October, and disperse in late fall and winter.

Courtship Songs

Collins (1980), Nero (1980), and Winter (1986) describe vocalizations in North America. Cramp (1985) describes vocalizations of this species in Europe. Here we describe the dominant songs and calls that may be heard during surveys for this owl.

The territorial call given by both sexes is a repetitious series of low, evenly spaced *hoos*. Males have a lower pitch. This call is given most frequently during the pre-nesting season and while the male is near

a nest. It is audible for 400 m to 800 m (Cramp 1985). A second call of low, soft double hoots may be a contact call associated with defense of territory (Collins 1980, Nero 1980). A low, softer version of the territorial call is sometimes given by the male just before he delivers prey to the female. Another variation of *hoos* is given by the female when agitated, usually by human disturbance.

The repertoire of calls is greatest during the breeding season. Great gray owls are much less vocal when not breeding. An increase in vocal activity has been noted in autumn (J.R. Duncan, unpubl. data). The territorial call is primarily nocturnal. Winter (1986) found calling activity in California was greatest at 0100 hr, with a second peak at 2200 hr with 56% of calls heard between 0100 and 0400 hr. Calling declined conspicuously around midnight.

Parental Care

Only females incubate eggs and brood nestlings. After about 2-3 weeks, the female starts roosting near the nest. Males bring prey to the female and the female feeds the young. After fledging, the young are usually fed directly by the male. Owlets depend on adults until 130-160 days old. Few data document feeding rates at nests. Four young (> 14 days old) at a nest in Finland were fed, on average, 10.3 voles per day over 9 days (Pulliainen and Loisa *in* Cramp 1985). Females consume feces and pellets of their young until about a week before they fledge.

DEMOGRAPHY

Life History Characteristics

Nesting Success

Great gray owls rarely breed at 1 year, sometimes at 2 years, and more commonly at 3 years (Bull and Duncan 1993, J.R. Duncan, unpubl. data). One brood is produced per year. In 67 nesting attempts during 4 years in northeast Oregon, 78% fledged young (Bull *et al.* 1989b). In Idaho and Wyoming, 70.5% of nests fledged young (Franklin 1988); and in Manitoba and Minnesota 81% fledged (J.R. Duncan, unpubl. data). Of 427 Finnish nests, 95% hatched eggs and 69% fledged (Cramp 1985). Forty-two Finnish nests experienced 80.5% hatching success and 72.1% of chicks fledged. Fifty-eight percent of eggs survived to fledging.

Average clutch sizes in Europe vary from 0 to 4.6 eggs, seemingly in response to *Microtus* numbers (Mikkola 1983); Korpimaki (1986) cited a mean clutch size of 4.4 eggs. Mean clutch sizes reported in North America are: 3 - 3.3 in Idaho and Wyoming (Franklin 1988); up to 5 in Oregon (Bull and Henjum 1990) and in Manitoba (Collins 1980); and 2 - 3 in California (J. Winter, pers. comm.). Mean number of fledged young per successful nest are 2.3 (SD = 0.87, range 1-5) in Oregon (Bull *et al.* 1989b), 2.7 - 3.0 (SD = 0.4, range 1-4) in Idaho and Wyoming (Franklin 1988), 2.8 in Manitoba (J.R. Duncan, unpubl. data), and 2.4 in Finland (Mikkola 1983). Producing 1.9-2.4 young per successful nest, great gray owls showed little annual variation in reproductive success during a 6-year Oregon study (Bull and Henjum 1990). In Scandinavia, however, Hilden and Helo (1981) reported fledging rates varying from 0 in poor prey years to 2.7 -3.9 young/nest in good years. Twenty-one nests in Sweden fledged an average of 3.6 young/nest. No data establish lifetime reproductive success. In Manitoba, 91% of 32 radio-marked fledgling owls died before they were 1 year old (Duncan, unpublished data). Numbers of breeding owls corresponded with the number of *Microtus* in Canada but not to total numbers of small mammals or any other subgroup of prey (Duncan 1992). Non-dispersing adults died during population declines, but some individuals that had dispersed several hundred kilometers reproduced successfully. In Oregon, however, all radio-tagged adults nested each year (Bull *et al.* 1989b).

Survival

Franklin (1987) reported that a young great gray owl had a 63% chance of surviving from egg to flight stage; Mikkola (1983) reported a 58% chance. In Oregon, the probability of a juvenile surviving its first year is 53% and its first 2 years is 31% (Bull *et al.* 1989b). Annual probability of survival for nesting females in Oregon was 84% (95% confidence limit [CL] 70% - 100%) and for nesting males 91% (CL 78% - 100%) (Bull *et al.* 1989b). In Manitoba, 29% of 51 radio-marked adult owls (10 of 23 males and 5 of 28 females) died within 2 years (Duncan, unpublished data).

Individuals can be long lived. Cramp (1985) reported a 7-year-old owl and Oeming (1964) a wild 9-year-old bird. A female banded as an adult was recaptured 13 years later (R. W. Nero, pers. comm.). Korpimaki (1986) cited a life span of 11 years. In Canada, great gray owls failing to disperse following prey declines died over winter (Duncan 1992).

In Oregon, Manitoba, and Minnesota, avian predation accounts for most juvenile mortality (Bull and Duncan 1993). Starvation is also probably a significant cause of juvenile mortality but is difficult to quantify. Common raven (*Corvus corax*) predation

on eggs and young was significant in Oregon. Great horned owl predation on young and adults is reported from Manitoba and Oregon. Other reported sources of mortality include entanglement on barbed wire and electrocution on transmission lines. Collisions with automobiles are a major cause of mortality in some years (Nero and Copland 1981). Mikkola (1981) reported mortality of young resulting from mosquito and black fly bites.

Ecological Influences on Survival and Reproduction

Two principal factors appear to limit great gray owl populations through their influence on reproduction and survival: the availability of pre-existing nest sites and prey abundance/availability. Because great gray owls do not construct their own nests, factors affecting the availability of nest sites directly affect great gray owl breeding habitat. For example, outbreaks of certain insects can result in damaged tree tips or leaders. This damage can cause several tree branches in the whorl immediately below the lost leader to grow vigorously, creating a branch structure ideal for stick nests of hawks or ravens. Suppression of insect outbreaks may reduce the number of deformed trees and ultimately great gray owl nests. If successful, genetic improvements for trees used in plantations may lead to the same consequence. Pathogen resistance and selection for straight boles could reduce the number of trees suitable for primary platform nesting species.

Stick nests collapse after a few years of owl use. So, factors negatively affecting nest-building hawks and corvids may decrease productivity of great gray owl populations through a decline in available nest platforms. The availability of nest structures may fluctuate with cyclic prey populations of primary nest-building raptors. Patterns in great horned owl populations, which compete with great gray owls for nest platforms, will also influence nest availability.

Forestry practices that reduce the number of potential nest sites include the removal of diseased trees, removal of large trees, and forest stand alterations not compatible with the habitat requirements for nest-building species. Conversely, harvest prescriptions may increase nest site availability by altering habitat in a manner that favors primary nest building species, by promoting growth of large trees capable of supporting a large nest platform, or by leaving snag and snag replacements that will favor broken top nest structures.

Although many factors influence great gray owl survival, prey availability is thought to be a primary factor. Despite of their large size, great gray owls prey almost exclusively on small mammals weighing less than 100 g. In the northern portion of their range, great gray owls depend on microtine rodents that exhibit multi-annual population fluctuations. When local prey populations crash, owls must disperse. Individuals that remain either starve or are predisposed to other mortality factors through decreased prey availability. Dispersing birds may experience increased mortality through increased risk of predation, accidents, or inadequate prey.

In the western United States, pocket gophers are thought to be an important buffer species allowing great gray owls to avoid nomadic movements. When vole populations decline, great gray populations may experience limited reproduction but can survive and remain resident on or close to their breeding home range. Pocket gophers, then, alter survival and movement patterns in these populations compared to northern populations. Gene flow and metapopulation structure are changed as a consequence.

Finally, annual mortality patterns in great gray owl populations are influenced by the abundance of raptors and prey available to those raptors. If raptors that occasionally prey upon great gray owls are abundant and their prey base declines, predation on great gray owls can be severe (Duncan 1987).

Social Pattern for Spacing

More research is needed on factors influencing territoriality, especially in relation to prey abundance. Adult males establish territories by vocalizing in the vicinity of the nest site (Bull and Duncan 1993). Territories can be established as early as the autumn prior to nesting (Duncan 1987). Given adequate prey, adult males in Manitoba and Minnesota may maintain a territory around the nest site all year (J.R. Duncan, unpubl. data).

Great gray owls appear to defend only the area immediately surrounding the nest site (Bull and Henjum 1987, Duncan 1987). Reid (1989) and Winter (pers. comm.) suggest that in California great gray owls defend foraging habitat, but the speculation is not based on thorough study of owl behavior. In other areas home ranges overlap (Servos 1986, Duncan 1987, Bull and Henjum 1990) and pairs readily nest within 0.5 km or less of each other (Nero 1980, Cramp 1985, Duncan 1987, Bull *et al.* 1988a). Duncan (1987) observed up to four adult males and their fledged young hunting in the same field. During the post-fledging period, adult females visit adjacent family groups (Duncan 1987).

Mikkola (1983) suggested that great gray owls may nest in loose colonies as short-eared owls (*Asio flammeus*) do and that they can be extremely tolerant of intraspecifics. The term "colony" may be a misnomer because the social unit likely does not function as a colony. Hoglund and Lansgren (1968) documented nests in Sweden as close as 100 m apart. In Finland, three nests were found within 400 m of one another (Mikkola 1976). Wahlstedt (1974) discovered seven pairs over a distance of 3 km in Sweden. Similar clusters of great gray owls have also been described by Duncan (1987) and Bull and Henjum (1990) in North America. An immature male was observed feeding a mated female brooding young while her mate, an adult male, was hunting 30 m away (Duncan 1987). Lower breeding densities may be more typical over the vast majority of its range.

Some observed agonistic encounters suggest winter territoriality, probably when prey are scarce (Brunton and Pittaway 1971, Nero 1980, J.R. Duncan, unpubl. data). Interpreting late winter behaviors, however, creates problems since they may be either agonistic or related to courtship.

Limiting Factors

Food supply likely regulates abundance of great gray owls in much of its range. When prey is scarce, many individuals abandon their breeding range. In one case, immediately after a prey decline in Canada, all non-dispersing birds died (Duncan 1992). In Oregon, all adult deaths occurred in fall and winter (Bull *et al.* 1989b). Although data suggest that prey availability influences great gray owl abundance in some areas, nest site availability likely limits owl abundance in other localities. Artificial nest sites allow breeders to settle new habitat. The relative importance of these factors in limiting population size has not been addressed. Geographic patterns in population limitation must be studied to provide a basis for conservation management.

Patterns of Dispersal of Young

The maximum distance that radio-tagged juveniles dispersed from natal sites in their first year ranged from 7.5 to 32 km in Oregon (Bull *et al.* 1988a). Two birds were found nesting 8.5 and 33 km from their natal site (Bull and Henjum 1990). In Manitoba, some immatures did not disperse from their natal site until March of the following year. Adults and juveniles travel much greater distances in the northern parts of their range; some to 753 km in Canada (Duncan 1992, see also the Movements section earlier in this chapter).

Characteristics of Non-Breeding Segment of Population

This important aspect of great gray owl population biology has not been studied, aside from the characteristics of pre-breeding individuals reported earlier.

Metapopulation Structure

In Oregon, great gray owls typically nest in the same home range year after year (Bull *et al.* 1989a). They will change nest sites but usually move < 5 km. Some birds in Oregon stay in the same area year round if snow is not deep; others move to areas with less snow. In Manitoba, some individuals returned to former nest sites after dispersing up to 500 km (Duncan 1992). Especially in the southern portion of the species' range, the demographic link between populations is provided by dispersing juveniles.

Because of the relatively continuous dispersion of suitable habitat throughout much of the species' range, great gray owls may not have a strong or well-defined metapopulation structure, as compared to the boreal owl for example (Hayward *et al.* 1993). The degree to which small populations of great gray owls in the Sierra, Cascade, or Rocky Mountains of the United States are separated from other local populations is unknown.

COMMUNITY ECOLOGY

Predators

Northern goshawks (*Accipiter gentilis*) and great horned owls frequently prey on juvenile great gray owls, particularly in years when grouse and hares are scarce (Nero 1980, Duncan 1987). Red-tailed hawks (*Buteo jamaicensis*) also attack juveniles (Bull and Henjum 1990). In Manitoba, juvenile owls were killed by black bear (*Ursus americanus*), fisher (*Martes pennanti*), and great horned owls (Duncan 1987). Adult birds are occasionally killed by Canada lynx (*Lynx canadensis*) and great horned owls (Duncan 1987, A. Franklin, pers. comm.).

The nest site is actively defended against common ravens, broad-winged hawks, northern goshawks, and great horned owls (Mikkola 1983, Bull and Duncan 1993, J.R. Duncan, unpubl. data). Intruders are chased and occasionally attacked. European ornithologists use a helmet and face mask when check-

ing nests. Mikkola (1983) reports several instances in which people without such protection suffered wounds or lost an eye to this species.

Competitors

Prey and nest sites likely limit great gray owl populations in various geographic settings. Great horned owl, broad-winged hawk, red-tailed hawk, northern goshawk, northern hawk owl (*Surnia ulula*), boreal owl, and long-eared owl nest sites have been found within 500 m of great gray owl nests (Lane and Duncan 1987, J.R. Duncan, unpubl. data; J. Winter, pers. comm.). The proximity of these nests, however, does not indicate that these species do not compete with great gray owls. Great horned owls are most likely to compete with great gray owls for nest sites since both species favor the open, abandoned nests of other large raptors (Nero 1980, Voous 1988). Potential exploitative competition for food among great gray owls and these raptors may exist because each consume small mammals from similar habitat.

Voous (1988) summarized the ecological relationships between this owl and others sharing its habitat. He indicated that, although the great gray owl is longer and larger in appearance than either the great horned owl in North America or the eagle owl (*Bubo bubo*) in the northwestern Palaearctic, its body mass is only 84% of the great horned owl's and 40% of the eagle owl's. Thus, despite its impressive size, the great gray owl takes relatively small prey and is unlikely to compete strongly with *Bubo* owls for food. Competition for food with long-eared owls, barred owls, northern hawk owls, and boreal owls is minimal or nonexistent during prey population highs, especially in northern regions. During prey population lows, however, competition is likely more important (Mikkola 1983, Johnsgard 1988).

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