GREAT GRAY OWLS (*STRIX NEBULOSA NEBULOSA*) AND FOREST MANAGEMENT IN NORTH AMERICA: A REVIEW AND RECOMMENDATIONS

JAMES R. DUNCAN Box 253, Balmoral, Manitoba, Canada ROC 0H0

ABSTRACT.-Great Gray Owl (Strix nebulosa nebulosa) populations in North America have likely been stable over the past 10-100+ yr. Local populations fluctuate in response to food supply and/or nestsite availability. Breeding Great Gray Owls require preexisting nest structures in forest stands that are adjacent to open foraging habitat, preferably with hunting perches. Current forestry practices have the potential to affect about 75% of the Great Gray Owls' breeding range in North America. Intensive timber management typically removes large diameter and deformed nest trees, leaning trees used by juveniles for roosting before they can fly and stands with dense canopy closure used by juveniles and adults for cover and protection. Modified forest management can, however, create new foraging habitat by opening up large, dense forest stands. Specific recommended guidelines include restriction of harvest unit size ($\leq 5-10$ ha), but within a mosaic of multi-sized units, retention of forest stands within 300 m of known or potential nest trees/sites, provision of hunting perches in cut-over areas, ensuring irregularly shaped harvest units and maintenance of forested travel corridors between cut-over areas. Because Great Gray Owls can breed on home ranges up to 800 km apart in successive years, integration of local management regimes at a landscape scale is recommended. Ideally, spatio-temporal patterns of natural disturbance (e.g., fire) should be emulated in a management plan to sustain the region's natural biological diversity, including Great Gray Owls when appropriate.

KEY WORDS: Strix nebulosa; North America; forest management; habitat use; Great Gray Owl.

El Gran Búho Gris Strix nebulosa nebulosa y administración forestal

RESUMEN.-Las poblaciones del búho Strix nebulosa nebulosa en norte américa han estado estable con seguridad los pasados 10 a 100+ años. Poblaciones locales fluctúan en reacción a suministros de comida y/o la disponibilidad a sitios de nido. Búhos en cría necesitan estructuras de nidos hechos en bosque que están pegados al hábitat de forraje libre preferible con perchas de cazar. Costumbres actualmente de forestales tienen la potencia para afectar casi 75% de el campo de cría de el búho en norte américa. La administración de madera con intensidad típicamente quita árboles con diámetros grandes y árboles deformados con nido, árboles inclinados usados por juveniles para percha antes que pueden volar, áreas con densidad cerrada usada por juveniles y adultos para cubrirse y protección. Administración de bosque modificados pueden, sin embargo, inventar nuevo hábitat de forraje con abriendo grandesy densas áreas de bosque. Recomendaciones específicos de las reglas incluyen: (1) restricciones de cosecha de cierta altura (<5-10 ha), pero dentro de un mosaico de varios tamaños, (2) retención de áreas de bosque conocido o en potencia de árboles/sitios con nido dentro de 300m, (3) provisión de perchas de cazar en áreas cortadas, sugiriendo conjuntos de cosecha con formas irreguladas, y (4) mantenimiento de corredores de viaje en áreas de bosque en parcelas cortadas. Porque búhos se pueden criar en campos naturales hasta 800 km aparte en años seguidos, integración de administración local con una escala de paisaje es recomendado. Idealmente, que muestras de spacio-temporal de disturbios naturales (e.g., lumbre) debe ser emulado en el proyecto de la administración para sostener las regiones, diversidad natural y biológica, incluyendo búhos cuando es oportunado.

[Traducción de Raúl De La Garza, Jr.]

In November 1995, a symposium on Holarctic raptor responses to forest management was held in Duluth, MN U.S.A. Presenters were asked to review information on a species according to guidelines provided and in response to specific questions. This paper is a review of such information for the Great Gray Owl (*Strix nebulosa*) in North America. The Great Gray Owl is unevenly distributed across the Holarctic over 30 million km² of boreal forests in Eurasia and North America (Clark et al. 1987). Throughout its range it occupies forest habitat; however, it also successfully breeds north to within the transition zone between the boreal forest and the treeless tundra (Lang et al. 1991). In western North America, it extends its range south by occupying montane forests in the Rocky Mountains, the Cascade Range and the Sierra Nevada Range (Duncan and Hayward 1994). It is the largest northern forest owl, although not the heaviest. Its yellow eyes, set in a facial disk with nearly concentric gray and white rings, are framed by a large round head that lacks ear tufts. Two subspecies are currently recognized: S.n. nebulosa in North America and S.n. lapponica in Eurasia (Bull and Duncan 1993).

Great Gray Owls in the boreal forest region of North America have greater diet similarity (% similarity) to populations in Eurasia ($\bar{x} = 95.3\%$, SD = 1.46, N = 3, range = 94-96.9%) than to those in the southwestern U.S. that occur in montane forests ($\bar{x} = 49.8\%$, SD = 13.9, N = 9, range = 39-69.4, Duncan 1992). Great Gray Owls from both continents exhibit similar plasticity in selection of nest sites, although ground nesting is more frequently reported from northern Europe (Mikkola 1983). They appear to use similar foraging habitat ın Eurasia and North America (Mikkola 1983, Duncan and Hayward 1994). Therefore, one would expect S.n. nebulosa and S.n. lapponica populations to respond similarly to forest changes that alter the availability of nest sites and/or foraging habitat. Eurasian Great Gray Owls are paler with more vertical barring, perhaps relating to habitat differences (Oeming 1955, Mikkola 1983); they also appear to be more aggressive toward humans at nest sites than North American Great Gray Owls (Nero 1980, Mikkola 1983).

Considerable attention has recently been directed toward evaluating the status of North American Great Gray Owl populations (Winter 1986, Hayward 1994). As with any species, this invariably requires an assessment of the habitats that are thought or known to sustain populations. Current forestry practices have the potential of affecting about three-quarters of the Great Gray Owls' breeding range in North America (Bull and Duncan 1993). McCallum (1994) provides a critical review of the complexities involved in determining owl-habitat relationships and the importance in distinguishing between habitat requirements, preference and use. To best evaluate the relationship between Great Gray Owl populations and forest management, one would ideally have knowledge of the species' habitat requirements and/or preference. Since these do not currently exist, except for a few habitat preference studies (e.g., Servos 1986), the following review of Great Gray Owls and forest management is based primarily on nesting and foraging habitat use data.

POPULATION TRENDS

Typically considered rare, the Great Gray Owl occurs at low densities within its range (Nero 1980, Bull and Duncan 1993). Nero estimated a continent-wide population of 5000–50 000 owls in North America; up to 25 000 breeding pairs have been estimated for Canada (Kirk and Hyslop pers. comm.). However, Great Gray Owls are easily overlooked and are probably more common. I estimate the current North American population of Great Gray Owls to be 20 000–70 000 breeding pairs. The range of this estimate reflects the dependence of this species on prey, primarily microtines (e.g., *Mucrotus* spp.), that exhibit unstable population fluctuations over 3–5-yr periods (Duncan 1992).

The degree to which local prey population fluctuations are synchronous over the Great Gray Owl's North American range is unknown. Extrinsic factors such as severe temperatures with little or no snow cover, occasionally synchronize (reduce) microtine populations over large geographic areas. More commonly, other factors (both intrinsic and extrinsic) appear to disrupt such synchronizing effects (Pruitt 1968, Lidicker 1988).

Great Gray Owls are most often seen in winter, and in more heavily settled areas along the southern portions of their breeding range. Irregular, large-scale, continental movements of bird populations are called irruptions (Collins 1980). The Great Gray Owl is one of several irruptive species of owls in North America. When large numbers of birds appear locally, it is commonly referred to as an influx or invasion. The fluctuations in winter occurrence of Great Gray Owls in these areas (Fig. 1) suggest that large-scale irruptions occur less frequently than local invasions. Large-scale irruptions are thought to be the product of one or more years of high Great Gray Owl reproductive success followed by a widespread decrease in prey availability on the breeding range. The recent apparent increase in Great Gray Owl winter occurrences is

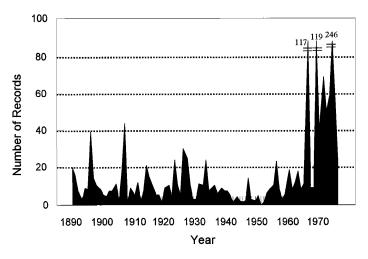


Figure 1. North American Great Gray Owl winter irruptions based on specimens and sight records, 1890–1976. Data from southern Canada and northern U.S.A. Modified from Collins (1980).

likely due to increased observer effort and increased access to winter habitat (Collins 1980).

The overall North American Great Gray Owl long-term (>10 yr) population trend is unknown. There are no long-term, rigorous or standardized Great Gray Owl breeding population trend data on a range-wide, regional or local scale. There is circumstantial evidence that some local and/or regional populations have either remained stable, increased or decreased over periods of <10 yr (Fyfe 1976, Collins 1980, Nero 1980, Nero et al. 1984, Winter 1986, Bryan and Forsman 1987, Franklin 1988, Collins and Wendt 1989, Bull and Henjum 1990, Duncan 1992). Ongoing local surveys are underway at a number of locations in Canada and the U.S. Nonetheless, it is useful to speculate on the relationship between forestry and local Great Gray Owl population trends.

Reliable population distribution data may only be available after widespread and standardized monitoring programs have been operating for several years. While classic "playback" survey techniques (Smith et al. 1987) can increase the number of Great Gray Owls detected by up to 40%, it is unlikely that they can yield data that identifies statistically significant population trends.

PRIMARY FACTORS ASSOCIATED WITH TRENDS

North American Great Gray Owl populations are relatively unaffected by human persecution or direct chemical effects (Nero 1980, Winter 1986, Hayward 1994), notwithstanding occasionally high local human-caused mortality (Nero and Copland 1981). The availability of nest sites and suitable foraging habitat are considered the most important factors limiting Great Gray Owl populations (Duncan and Hayward 1994). I will address these first, but some discussion is warranted on the shortterm (3–5 yr) influence of prey availability, which can profoundly affect conclusions drawn from short-term (<5 yr) local Great Gray Owl surveys.

Diet. Local Great Gray Owl breeding densities fluctuate considerably, primarily due to the instability of microtine prey populations (Henttonen 1986, Duncan 1992). Individual radio-marked owls in Manitoba and northern Minnesota have dispersed up to 684 km between breeding home ranges in response to prey population crashes ($\bar{\mathbf{x}} = 328.8$, SD = 184.9, N = 27, range = 41–684 km); those marked birds that did not disperse (N = 11) did not survive (Duncan 1992).

In contrast, breeding Great Gray Owl populations in montane regions of the western U.S. are thought to be relatively stable (Winter 1986, Bull and Henjum 1990, Bull and Duncan 1993). In northeastern Oregon, the maximum distance travelled from nest sites by adult radio-marked Great Gray Owls averaged 13.4 km (N = 23, range = 2.4– 43.2 km; Bull and Henjum 1990). Bull and Henjum (1990) speculate that in years when prey populations are low, Great Gray Owls in their study area remain as nonbreeding residents. In California, Winter (1986) suggested that under similar circumstances, Great Gray Owls possibly sustain themselves on pocket gophers (*Thomomys* spp.), as well as other prey species. Pocket gopher populations are relatively stable and noncyclical (Chase et al. 1982, Teipner et al. 1983).

Because breeding populations of Great Gray Owls in different parts of their North American range exhibit variable breeding dispersal strategies, owl surveys undertaken to determine distribution or local population trend data need to be conducted for at least as long as one prey population cycle to ensure reliable results. Therefore, ideally, one should concurrently monitor prey populations and Great Gray Owl diet. Great Gray Owls may or may not be present during years of low prey populations; if present at such times, they are less likely to respond to conspecific call playback used in surveys (Smith et al. 1987).

Nest-site and Foraging Habitat Availability. These factors are significantly affected by natural forest disturbances such as disease outbreaks, succession and the effects of fire and wind (Larsen 1980, Habeck 1994). The temporal and spatial scale of the impact of these ecological processes, and the relative stability of prey biomass productivity, have had a strong influence on the evolution of Great Gray Owl life history traits, such as breeding dispersal and post-fledging nest-site fidelity (Duncan 1992). Consequently, forest management does affect Great Gray Owl populations by altering natural disturbance regimes and by the application of management protocols. Anecdotal observations and current knowledge of Great Gray Owl ecology permit some speculation about how forest management likely impacts Great Gray Owl populations.

Nest sites. Great Gray Owls use preexisting structures for nesting, including deserted or vacant stick nests of some Buteo hawks, Northern Goshawks (Accipiter gentilis) and larger corvids (Duncan and Hayward 1994). They will also nest on a variety of artificial structures, in natural depressions in brokentopped snags or stumps, and, rarely, on the ground, on rock cliffs, or on top of haystacks (Mikkola 1983, Duncan and Hayward 1994). Nest-structure type or nest-tree species appears to be less important than nest-site habitat characteristics and the availability of foraging habitat (Duncan and Hayward 1994). Forest tree pathogens (e.g., ants and fungi) and fire can weaken trees, possibly resulting in tree death and subsequent snag or stump formation. More directly, dwarf mistletoe (Arceuthobium spp.) causes exaggerated branch configurations which are conducive to nesting and/or that promote nest-building activity by raptors and corvids (Bull and Henjum 1990). Nest-site availability generally increases with forest stand age (Duncan and Hayward 1994).

Tree pathogen outbreaks and other nest-site creating disturbances tend to have a clumped spatial and temporal distribution. The territories of the Northern Goshawk and Broad-winged Hawk (*Buteo platypterus*) often hold several stick nests (Palmer 1988, Goodrich et al. 1996). If nest sites are limiting and have a clumped distribution, perhaps it is no coincidence that Great Gray Owls have nested in what has been described as loose colonies (Wahlstedt 1976, Bull and Duncan 1993), a trait that undoubtedly also relates to their specialized diet (Mikkola 1983).

Nest-site availability appears to be important enough to Great Gray Owls that they have evolved the ability to relocate and use nest sites hundreds of kilometers apart over 2 or more yr (Duncan 1992). Therefore, forest management activities that reduce the number of nest sites (e.g., fire suppression, disease control and shorter rotation periods) have the potential to reduce Great Gray Owl breeding densities. Mitigation by installing artificial nest structures is impractical at larger spatial scales, but works well locally (Bull and Henjum 1990).

Foraging habitat. Voles and/or pocket gophers dominate the diet of Great Gray Owls (Duncan and Hayward 1994). Microtine voles generally occupy moist grass/sedge openings and open forests with herbaceous ground cover. Meadows considered in good ecological condition for voles, and hence Great Gray Owls, are dominated by a variety of climax perennial grasses, sedges, and forbes. Factors that reduce vole abundance (e.g., moderate to heavy grazing) decrease the suitability of foraging areas for Great Gray Owls (Winter 1986).

Great Gray Owl foraging habitat includes bogs, fens, muskeg, peatland, natural meadows, open forests and selective and clear-cut logged areas (Nero 1980, Mikkola 1983, Servos 1986, Winter 1986). Dense coniferous stands (e.g., jack pine, *Punus banksiana* and black spruce, *Picea mariana*), open areas with few or no trees and habitats with dense shrub layers are avoided by hunting Great Gray Owls (Servos 1986).

Great Gray Owls hunt primarily from perches, listening for prey and watching the ground intently. When prey is detected the owl usually stoops 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.

Bull and Duncan (1993) reported that Great Gray Owls also forage in open forests. In northeast Oregon, males foraged in stands with 11–59% canopy closure (Bull and Henjum 1990). These stands had meadowlike grass-dominated ground cover. Open tamarack (*Larix laricina*) stands with dense sphagnum/sedge/grass understory are often used by foraging Great Gray Owls in Manitoba.

While hunting, Great Gray Owls perch at varying heights, but usually 3–5 m above the ground, in both live trees and snags adjacent to or within open grassy areas (Duncan and Hayward 1994). Perch heights for male Great Gray Owls averaged 5.5 m in Oregon (Bull and Henjum 1990). In California, perch heights varied from 0–12.2 m above the ground ($\bar{x} = 3.3$, SD = 2.3, N = 143; Winter 1986). Great Gray Owls rarely hunt while perched on the ground or while flying (Bull and Duncan 1993).

Successful Great Gray Owl reproduction depends on the availability of suitable foraging habitat within 1–3 km of nest sites (Bull and Henjum 1990, Duncan and Hayward 1994). Such habitat can be ephemeral over shorter periods (e.g., postfire or post-cutting early succession habitat) or relatively permanent (e.g., sedge meadows, peatland and muskeg). Burned or cut-over areas can provide foraging opportunities for Great Gray Owls for 20 yr or more, depending on the rate of succession or on post-harvest management practices. Kirkland (1977) and Parker (1989) reported that meadow vole populations increase 3–18 yr after clear-cutting forests.

Great Gray Owl population declines from ancestral levels have been reported in California (Winter 1986). These were attributed to habitat changes, e.g., fire suppression and overharvesting of forests. Paradoxically, clear-cuts can create Great Gray Owl foraging habitat in dense forests in previously unoccupied areas.

Forest Management Recommendations

Throughout its North American range, the Great Gray Owl thrives in a variety of habitats (Duncan and Hayward 1994). It is adapted to capturing prey in permanent open habitats and in early forest successional stages (Nero 1980). Older and mature forest habitats adjacent to foraging areas provide suitable nest structures. Therefore, Great Gray Owl populations can likely persist with some amount of forest cutting. The following recommendations are based on what is generally known about Great Gray Owl ecology and not on specific responses of owls to measured habitat changes. New information should alter these specific conservation strategies through an adaptive management approach. The large lifetime home ranges of Great Gray Owls, e.g., in Manitoba and Minnesota (Duncan 1992), suggest that a coordinated landscape-level perspective to management is needed to maintain viable populations. With this in mind, I suggest the following management recommendations.

Occurrence Data. The occurrence of Great Gray Owls is poorly documented in many parts of its range (Duncan and Hayward 1994). A review of historic site-specific occurrence information (e.g., literature, specimen data and personal communications) is an appropriate first step. It should be determined if Great Gray Owls currently occur in the management area because pre- and post-harvest occurrence information can be used to adapt harvest guidelines accordingly. Secondly, the presence or absence of Great Gray Owls may influence the degree to which forest resources are managed. Assuming that forest resources are to be managed for this species (e.g., the management area is within suitable habitat and is within or adjacent to its expected North American range) then one must decide to implement a landscape-level or a specific management regime only at sites where Great Gray Owls are known to occur. The efficiency of various survey techniques have not been rigorously tested and survey methods may not be practical over large expanses and in remote areas. Therefore, in the absence of Great Gray Owl occurrence data, an appropriate landscape-level management recommendation would be the retention of a 300 m buffer area around natural openings such as meadows or fens (Winter 1986, Bouchart 1991).

Clear-cut Size. Clear-cuts up to 10 ha in size are probably ideal for Great Gray Owls, but these should occur within a mosaic of multi-sized units across a landscape. Great Gray Owls will use larger clear-cuts, but typically they catch prey within 50 m of hunting perches. While they hunt from isolated perches in open areas farther than 50 m from edges, in these situations they are more vulnerable to avian predators such as Northern Goshawks and Great Horned Owls (Bubo virginianus) (Duncan 1987).

Clear-cut Shape. Because Great Gray Owls frequently hunt from forest edges, irregular cut shapes with convoluted or scalloped-shaped edges would reduce mortality from avian predators. This design will therefore also increase access to newly created open foraging habitat. Because they catch prey within 50 m of hunting perches, larger cuts should therefore be elongated so that the maximum distance across the cut is <100 m.

Nest-site Availability. Timber management has reduced nesting opportunities for all forest raptors, including Great Gray Owls (Habeck 1994). Therefore, the impact of management practices on nest-site availability needs to be assessed.

Some types of nest structures (e.g., mistletoe brooms and snags) used by Great Gray Owls are either directly or indirectly created by tree pathogens (e.g., insects and fungi). These pathogens can cause significant financial losses on commercial forest land. Likewise, fire-killed trees can provide Great Gray Owl nest sites (e.g., snags), but fire also destroys valuable timber. Great Gray Owls often nest in stick nests built by large corvids and diurnal raptors. These sites occur more frequently in older forest stands with larger trees. Shorter rotation periods or selective removal of large-diameter trees has reduced nest-site availability. Forest pathogen control, fire suppression and shorter rotation periods are economically important forest management practices that impact Great Gray Owl nesting opportunities. The provision of artificial nest structures, while locally effective, is labor intensive and costly (Bohm 1985). Their use may still be justified in certain situations.

Influence of Residuals and Optimal Mix, Including Dispersal Corridors. Leaving residuals in cutovers (e.g., live trees and dead snags) provide important hunting perches. In Manitoba, the smallest Great Gray Owl nest stand was 4 ha (N = 18, median = 232 ha) and there were at least 69 ha (N= 15, median = 136 ha) of foraging habitat within 1 km of nest sites. Bull and Henjum (1990) reported that 52-99% of the area within 500 m of nest sites in Oregon was forested. While Great Gray Owls have successfully nested on the edge of foraging habitat, the distance to the nearest opening averaged 256 m in Manitoba (Bouchart 1991) and 143 m in Idaho and Wyoming (Franklin 1988). Therefore, retention of forest stands within 300 m of known or potential Great Gray Owl nest sites is

recommended as a minimum guideline (see also Winter 1986, Bouchart 1991). The provision or retention of leaning trees used by juveniles for roosting before they can fly and stands with dense canopy closure (>60%) for cover and protection (from heat stress and predators) of adults and juveniles is also thought to be critical (Duncan and Hayward 1994). Maintenance of forested travel corridors between nesting habitat is considered necessary to minimize predation of dispersing adults and juveniles.

Because Great Gray Owl breeding dispersal can be significant (e.g., up to 800 km, Duncan 1992), a coordination of local management regimes at a landscape scale is recommended. Ideally, spatiotemporal patterns of natural disturbance (e.g., fire) should be emulated in management plans to sustain a region's naturally occurring biological diversity, including Great Gray Owls when appropriate.

ACKNOWLEDGMENTS

I thank Gerald Niemi and others involved with organizing and hosting the November 1995 Symposium on Raptor Responses to Forest Management: A Holarctic Perspective, for the opportunity to write this paper. The Symposium was an event that I will fondly remember I also thank Evelyn Bull, Patricia Duncan, James Habeck, Seppo Sulkava and Daniel Varland for their review of earlier drafts of this manuscript.

LITERATURE CITED

- BOHM, R.T. 1985. Use of artificial nests by Great Gray Owls, Great Horned Owls, and Red-tailed Hawks in northeastern Minnesota. *Loon* 57:150–151.
- BOUCHART, M.L. 1991. Great Gray Owl habitat use in southeastern Manitoba and the effects of forest resource management. M.S. thesis, Univ. Manitoba, Winnipeg, Canada.
- BRYAN, T. AND E.D. FORSMAN. 1987. Distribution, abundance, and habitat of Great Gray Owls in southcentral Oregon. *Murrelet* 68:45–49.
- BULL, E.L. AND M.G. HENJUM. 1990. Ecology of the Great Gray Owl. USDA For. Ser. Gen. Tech. Rep. PNW-GTR-265, Portland OR U.S.A.
- BULL, E.L. AND J.R. DUNCAN. 1993. Great Gray Owl (Stnx nebulosa). Pages 1–16 in A. Poole and F.B. Gill [EDS.], The birds of North America. Academy of Nat. Sci., Philadelphia, PA and Am. Ornithol. Union, Washington, DC U.S.A.
- CHASE, J.D., W.E. HOWARD AND J.T. ROSEBERRY. 1982. Pocket gophers, Geomyidae. Pages 239–255 in J.A. Chapman and G.A. Feldhamner [EDS.], Wild animals of North America: biology, management and economics. John Hopkins Univ. Press, Baltimore, MD U.S.A.
- CLARK, R.J., D.G. SMITH AND L. KELSO. 1987. Distribu-

tional status and literature of northern forest owls. Pages 47–55 *in* R.W. Nero, R.J. Clark, R.J. Knapton and R.H. Hamre [EDS.], Biology and conservation of northern forest owls. USDA For. Serv. Gen. Tech. Rep. RM-142, Fort Collins, CO U.S.A.

- COLLINS, B.T. AND J.S. WENDT. 1989. The breeding bird survey in Canada 1966–1983. Analysis of trends in breeding bird populations. Tech. Rep. Ser. No. 75, Canadian Wildlife Service, Ottawa, Canada.
- COLLINS, K.M. 1980. Aspects of the biology of the Great Gray Owl, *Strix nebulosa* Forster. M.S. thesis, Univ. Manitoba, Winnipeg, Canada.
- DUNCAN, J.R. 1987. Movement strategies, mortality, and behavior of radio-marked Great Gray Owls in southeastern Manitoba and northern Minnesota. Pages 101–107 in R.W. Nero, R.J. Clark, R.J. Knapton and R.H. Hamre [EDS.], Biology and conservation of northern forest owls. USDA For. Serv. Gen. Tech. Rep. RM-142, Fort Collins, CO U.S.A.
- ——. 1992. Influence of prey abundance and snow cover on Great Gray Owl breeding dispersal. Ph.D. dissertation, Univ. Manitoba, Winnipeg, Canada.
- AND P.A. HAYWARD. 1994. Review of technical knowledge: Great Gray Owls. Pages 159–175 in G.D. Hayward and J. Verner [TECH. EDS.], Flammulated, Boreal, and Great Gray Owls in the United States: a technical conservation assessment. USDA For. Ser. Gen. Tech. Rep. RM-253. Fort Collins, CO U.S.A.
- FRANKLIN, A.B. 1988. Breeding biology of the Great Gray Owl in southeastern Idaho and northwestern Wyoming. *Condor* 90:689–696.
- FYFE, R.W. 1976. Status of Canadian raptor populations. Can. Field-Nat. 90:370–375.
- GOODRICH, L.J., S.C. CROCOLL AND S.E. SENNER. 1996. Broad-winged Hawk (*Buteo platypterus*). Pages 1–28 in A. Poole and F.B. Gill [EDS.], The birds of North America. Academy of Nat. Sci., Philadelphia, PA and Am. Ornithol. Union, Washington, DC U.S.A.
- HABECK, J.R. 1994. Dynamics of forest communities used by Great Gray Owls. Pages 176–201 *in* G.D. Hayward and J. Verner [TECH. EDS.], Flammulated, Boreal, and Great Gray Owls in the United States: a technical conservation assessment. USDA For. Ser. Gen. Tech. Rep. RM-253. Fort Collins, CO U.S.A.
- HAYWARD, G.D. 1994. Conservation status of Great Gray Owls in the United States. Pages 202–206 *in* G.D. Hayward and J. Verner [TECH. EDS.], Flammulated, Boreal, and Great Gray Owls in the United States: a technical conservation assessment. USDA For. Ser. Gen. Tech. Rep. RM-253. Fort Collins, CO U.S.A.
- HENTTONEN, H. 1986. Causes and geographic patterns of microtine cycles. Ph.D. dissertation. Univ. Helsinki, Helsinki, Finland.
- KIRKLAND, G.L., JR. 1977. Responses of small mammals to the clear cutting of northern Appalachian forests. J. Mammal. 58:600–609.
- LANG, A.L., J.R. DUNCAN, S. RAMSAY AND J.D. RISING.

1991. Great Gray Owl and Northern Hawk Owl nests at Churchill, Manitoba. *Blue Jay* 49:208–214.

- LARSEN, J.A. 1980. The boreal ecosystem. Academic Press, NY U.S.A.
- LIDICKER, W.Z., JR. 1988. Solving the enigma of microtine "cycles". J. Mammal. 69:225-235.
- McCALLUM, D.A. 1994. Methods and terminology used with studies of habitat associations. Pages 5-8 in G.D. Hayward and J. Verner [TECH. EDS.], Flammulated, Boreal, and Great Gray Owls in the United States: a technical conservation assessment. USDA For. Ser. Gen. Tech. Rep. RM-253. Fort Collins, CO U.S.A.
- MIKKOLA, H. 1983. Owls of Europe. Buteo Books, Vermillion, SD U.S.A.
- NERO, R.W. 1980. The Great Gray Owl—phantom of the northern forest. Smithsonian Inst. Press, Washington, DC U.S.A.
 - AND H.W.R. COPLAND. 1981. High mortality of Great Gray Owls in Manitoba—winter 1980–81. Blue Jay 39:158–165.
- NERO, R.W., H.W.R. COPLAND AND J. MEZIBROSKI. 1984 The Great Gray Owl in Manitoba, 1963–1983. *Blue Jay* 42:130–151.
- OEMING, A.F. 1955. A preliminary study of the Great Gray Owl (*Scotiaptex nebulosa nebulosa* Forster) in Alberta, with observations on some other species of owls. M.S. thesis, Univ. Alberta, Edmonton, Canada
- PALMER, R.S. [ED.]. 1988. Handbook of North American Birds. Vol. 4. Yale University Press, New Haven CT U.S.A.
- PARKER, G.R. 1989. Effects of reforestation upon small mammal communities in New Brunswick. *Can. Field-Nat.* 103:509–519.
- PRUITT, W.O., JR. 1968. Synchronous biomass fluctuations of some northern mammals. *Extrait de Mammalua* 32:172–191.
- SERVOS, M.C. 1986. Summer habitat use by the Great Gray Owl (*Strix nebulosa*) in southeastern Manitoba. M.S. thesis, Univ. Manitoba, Winnipeg, Canada.
- SMITH, D.G., T. CARPENTER, T. BOSAKOWSKI AND R.T. REYN-OLDS. 1987. Owl census techniques. Pages 304–309 in R.W. Nero, R.J. Clark, R.J. Knapton, and R.H. Hamre [EDS.], Biology and conservation of northern forest owls. USDA For. Serv. Gen. Tech. Rep. RM-142, Fort Collins, CO U.S.A.
- TEIPNER, C.L., E.O. GARTON AND L. NELSON, JR. 1983. Pocket gophers in forest ecosystems. USDA For. Ser. Gen. Tech. Rep. INT-154. Missoula, MT U.S.A.
- WAHLSTEDT, J. 1976. "Lappugglan Strix nebulosa i Sverige 1974." [The great gray owl in Sweden in 1974.] Vår Fågelvärld 35(1976):122–125.
- WINTER, J. 1986. Status, distribution and ecology of the Great Gray Owl (*Strix nebulosa*) in California. M.A. thesis, San Francisco State Univ., San Francisco, CA U.S.A.
- Received 2 November 1995; accepted 28 February 1997