BOREAL OWL
NESTING AND ROOSTING HABITAT

HABITAT SUITABILITY INDEX MODEL
VERSION 5

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1. INTRODUCTION

Habitat Suitability Index (HSI) models predict the suitability of habitat for a species based on an assessment of habitat attributes such as habitat structure, habitat type and spatial arrangements between habitat features. This HSI model for the boreal owl (*Aegolius funereus*) applies to habitats in the Foothills Model Forest (FMF) in west-central Alberta. The intended use is to predict habitat suitability at landscape scales and over long time periods. The model will be used to determine potential changes in boreal owl habitat area and carrying capacity throughout an entire forest management cycle (200 years). The model was developed using literature review and some nesting data that was collected on the FMF.

2. SPECIES DESCRIPTION AND DISTRIBUTION

The boreal owl is a small brown owl with a large round head and a distinct brown and white facial disc (Johnsgard 1988). This nocturnal owl feeds on a variety of small mammals and birds. Near the Arctic, boreal owls will also feed during the day. They roost in coniferous trees and nest in natural tree cavities or cavities built by other birds such as woodpeckers (Johnsgard 1988).

The boreal owl, referred to as Tengmalm's owl outside of North America, occurs worldwide in boreal forests (Hayward et al. 1993). In North America, the northern limit of boreal owls extends along the arctic tree line from Alaska to the coast of Labrador (Johnsgard 1988). Prior to 1979, boreal owls were rarely found south of Canada, although infrequent irruptions into north-eastern United States have been recorded (Catling 1972). Breeding populations have now been recorded in Montana, Minnesota, Idaho, Colorado, Wyoming, Washington, Oregon and New Mexico (Eckert and Savolja 1979, Hayward and Garton 1983, Palmer and Ryder 1984, Hayward et al. 1987b**,** O'Connell 1987, Whelton 1989, Stahlecker and Rawinski 1990). Although the true extent of the boreal owl range in North America is unknown, there may be a contiguous distribution throughout lower Canada and south via the Rocky Mountains (Whelton 1989, Hayward et al. 1993).

In Alberta, boreal owls were observed across the northern portion of the province and along the Rocky Mountains and Foothills (Semenchuk 1992). Boreal owls are considered a sensitive species because they are associated with habitats that are or could potentially deteriorate (Wildlife Management Division 1996).

In Northern Europe (Scandinavia, Poland, Germany and Russia), Tengmalm's owls are found in pine and spruce forests, while in Central Europe they occur in montane forests of the Alps, Carpathian and Jura mountain ranges

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(Wardhaugh 1983). Often densities are increased in these areas by providing artificial nest boxes (J. Grosse, personal communication).

Boreal owls are typically associated with structurally diverse (old growth) stands. These stands have large trees with decreased growth rates and a heightened susceptibility to damage caused by climatic extremes, insect or fungal infestations. This results in an abundance of dying trees (Spurr and Barnes 1980) which provides natural or woodpecker cavities for nesting.

3. FOOD

Boreal owls are primarily nocturnal hunters except near the Arctic where they experience 24-hour daylight (Hayward 1994). Studies have shown that moving prey is taken significantly more often than stationary prey, indicating the importance of auditory cues to locate prey (Palmer 1986). Boreal owls were observed capturing voles under moderate cover by plunging through the shrub layer. Shrubs were *vaccinium* spp. and were less than 10 cm tall (Palmer 1986). Boreal owls use the sit and wait approach (Hayward 1994). Low (4 m) perches in branches of trees are used and prey is usually attacked within 5 m of their perch (Hayward et al. 1993).

The main prey species of the boreal owl in North America are red-backed voles (*Clethrionomys gapperi*), heather voles (*Phenacomys intermedius*), northern bog lemming (*Synaptomys borealis*), other voles (*Microtus* spp.), deer mice (*Peromyscus maniculatus*), western jumping mice (*Zapus princeps*), shrews (*Sorex* spp.), northern pocket gophers (*Thomomys talpoides*), flying squirrels (*Glaucomys sabrinus*), and chipmunks (*Eutamias* spp.; Catling 1972, Bondrup-Nielson 1978, Hayward et al. 1993). Small birds are taken in relatively small proportions (Korpimaki 1981, 1992, Carlsson 1990). Voles made up > 90% of the boreal owl's diet in Sweden (Hornfeldt et al. 1990).

The abundance of prey may influence distribution and habitat use of boreal owls (Korpimaki 1986, Lofgen et al. 1986, Carlsson and Hornfeldt 1989, Boutin et al. 1996). In Kluane, Yukon, boreal owl densities were linked with *Microtus* spp. (Boutin et al. 1996). The owls favored the older stands due to the lack of a crust layer on the snow which facilitated plunge diving. During early spring, boreal owls feed in openings and clear-cuts due to earlier snow melt and then move into mature spruce-fir forest (summer, fall and winter) when vegetation becomes too thick in the clearings (Palmer 1986).

4. COVER AND ROOSTING

Boreal owls depend on areas that provide nesting, roosting and feeding habitat (Korpimaki 1988, Hayward et al. 1993). This indicates that boreal owls need a mixture of mature spruce-fir stands, deciduous stands and clearings. In north-eastern Minnesota, boreal owls were found in sawtimber-sized aspen-dominated habitats during nesting (Lane et al. 1997a). In Europe, habitat used by Tengmalm's owls were coniferous stands, intermixed with agricultural land (Korpimaki 1988). Spruce (*Picea* spp.), fir (*Abies* spp.), mountain pine (*Pinus sylvestris* and *Pinus uncinata*) and beech (*Fagus* spp.) were most commonly used by Tengmalm's owls (Korpimaki 1981, 1988, Solheim 1983b, Joneniaux and Durand 1987, Dejaifve et al. 1990). In Colorado, boreal owls avoided large, unbroken stands of lodgepole pine and were found most often above 2,800 m in spruce-fir forests (Palmer 1986).

Roost sites are highly variable (Catling 1972). Boreal owls roosted mainly in coniferous (spruce, fir and pine) trees in Idaho (Hayward and Garton 1984). In Ontario and Alberta, 14% of roost sites (N = 28) were in aspen and the rest were in conifers, with 46% being in balsam fir (Bondrup-Nielson 1978). Balsam fir was preferred for roosting because few needles and branches were close to the trunk where the owls tended to roost but needles and branches were abundant on the outer portion of the trees thus providing good cover. Boreal owls typically roosted in trees with an average height of 14 m, and used Englemann spruce significantly more often than subalpine fir or lodgepole pine in Colorado (Palmer 1986). Cavities were not used (Palmer 1986). In Idaho, spruce-fir stands and occasionally pine seem the preferred roosting habitat because these trees provided thermal and hiding cover (Hayward and Garton 1984). In northeastern Minnesota, roost sites and foraging areas were typically in thick, homogeneous conifer stands in lowland areas (Lane et al. 1997b). Black spruce was used as the roost tree 82% of the time, balsam fir 9% and northern white cedar 4% (Lane et al. 1997b).

Boreal owls roost close to the tree trunks to take advantage of their cryptic coloration (Hayward and Garton 1984). Roosting heights have been found to be 5-7 m in trees with an average diameter at breast height (dbh at 1.3 m) of 25-28 cm (Hayward et al. 1993). Canopy closures of roost sites ranged from 58-63% in Idaho (Hayward et al. 1993).

5. REPRODUCTION

The mating system of the boreal owl can be monogamous, polygynous or biandrous (Solheim 1983a, Carlsson 1990, Korpimaki 1992). Male boreal owls are poly-territorial (defend more than one nest) and will feed the females prior to egg laying and feed the young exclusively during the early nestling period (Korpimaki 1992).

Boreal owls in North America nest primarily in cavities excavated by pileated woodpeckers (*Dryocopus pileatus*) and occasionally northern flickers (*Colaptes auratus*; Hayward et al. 1993). They will also nest in nest boxes (Howard et al. 1993). Nests are often found in live trees or snags of aspen, balsam poplar (*Populus balsamifera*), spruce, lodgepole pine, ponderosa pine (*Pinus ponderosa*) and Douglas-fir (Bent 1961, Palmer and Ryder 1984, Palmer 1986, Hayward et al. 1993). In the FMF, boreal owl nests were most frequently found in old pileated woodpecker cavities (R. Bonar, Weldwood of Canada Ltd, Hinton, Biologist, personal communication).

Egg laying dates range from the middle of March to the end of May in North America (Hayward 1994). Clutch size averages 2-4 eggs (Hayward et al. 1993). Eggs are laid in the bottom of the cavity without any nesting material (Wardhaugh 1983). Average nest dimensions for 19 nests in Idaho were 31 cm deep by 19 cm horizontally and openings averaged 9.5 cm by 10.2 cm (Hayward et al. 1993). These nest sites were located in trees with dbh ranging from 33-112 cm and greater than 11 m in height (Hayward et al. 1993). In central Ontario and northern Alberta, 12 nest cavities (6 confirmed and 6 that were suspected of being used by boreal owls) were found 11-17 m above the ground and were 5-35 cm deep with a cavity diameter of 20-25 cm. The cavity openings ranged from 6 cm by 6 cm to 14 cm by 7 cm (Bondrup-Nielson 1978).

Nesting sites are highly variable regionally. Boreal owls in central Ontario occurred in mixed coniferous and deciduous forests rather than pure coniferous forests with nests mainly in aspen (Bondrup-Nielson 1978). In Montana, Idaho and Washington, boreal owls used mature conifer forests consisting of Englemann spruce, subalpine fir and western hemlock (*Tsuga heterophylla*) at elevations above 1500 m (Hayward et al. 1987a, Holt and Hillis 1987, O'Connell 1987). Nest trees used by boreal owls in Idaho were in relatively open areas with average tree densities of 398 trees/ha with a dbh of 2.5-23.0 cm and 212 trees/ha for trees larger than 23 cm dbh (Hayward et al. 1993).

6. HABITAT AREA

Breeding male boreal owls tend to remain on the same territory even when food abundance is limited, while females will move between successive breeding attempts (Lofgren et al. 1986, Korpimaki 1988). Information on home range and population densities is limited. In central Ontario and northern Alberta, estimated boreal owl densities were 0.001 singing male boreal owls/ha for both regions (Bondrup-Nielson 1978). In Kluane, estimated boreal owl density was 0.005 pairs/ha (Boutin 1996). In the FMF, 10 broadcast surveys conducted along 16 km transects detected 90 and 23 boreal owls during the spring of 1995 and 1996 respectively (Takats 1998).

Home range size of boreal owls is highly variable. Lane et al. (1997b) found the home range for nesting male boreal owls to be 1,202 ha (n = 4, range = 742-1,444 ha). Palmer (1986) estimated home ranges of two male boreal owls in Colorado to be 296 ha during the breeding season and 1,132 ha in the post-breeding season. Male singing territory size during the courtship season was between 0.2-11 ha and expanded to 100-500 ha for hunting in Ontario and Alberta (Bondrup-Nielson 1978). Hunting areas are generally larger than courtship areas (Hayward et al. 1987a, Howard et al. 1993). In Idaho, winter home ranges averaged 1,451 ha in winter and 1,182 ha in summer (Hayward et al. 1993). Home ranges of owls may overlap up to 50% (Hayward et al. 1993) and up to 98% during the post-nesting period (Palmer 1986).

7. HSI MODEL

7.1 MODEL APPLICABILITY

Species: Boreal owl (*Aegolius funereus*).

Habitat Evaluated: Nesting and roosting habitat.

Geographic area: The model is applicable to the Foothills Model Forest in west-central Alberta.

Seasonal Applicability: Full year roosting, spring nesting.

Cover types: This model applies to all forest and non-forest habitat areas of the Lower and Upper Foothills, Montane and Subalpine Natural Subregions (Beckingham et al. 1996) since suitability is determined from structural characteristics within stands rather than classified forest stands directly. The model should also be broadly applicable to other habitat areas dominated by vegetation similar to that in this region, including pure deciduous, mixedwood and pure coniferous forest types, as well as wetland and riparian forests, meadows, shrublands, and areas regenerating after forest harvesting.

Minimum Habitat Area: Minimum habitat area is defined as the minimum amount of contiguous habitat required before an area will be occupied by a species (Allen 1987). It is unknown whether boreal owls require a large contiguous forest or whether small patches of suitable habitat in a managed landscape are suitable, so no minimum habitat area is defined for this model.

Model Output: The model will produce Habitat Units (HU) for all cover types for roosting and nesting based on HSI value and stand area. Habitat units are calculated by multiply the HSI score for the area by the number of hectares. The performance measure of this model is carrying capacity (boreal owl breeding pairs per ha). Model output must be correlated to estimates of carrying capacity to verify model performance.

Carrying Capacity (Breeding Pairs per ha where HSI = 1.0): Based on Bondrup-Nielson (1978), the best density estimate for Alberta in optimal habitat is 0.001 males per ha.

Verification Level: The reliability of this model has not been evaluated against local data. The verification level is 1: model developed based on literature review and published models for the species.

Application: This HSI model is designed to assess habitat suitability for relatively large forest landscapes using generalized species-habitat relationships and stand-level vegetation inventory. Its purpose is to predict relative changes in boreal owl habitat supply at the landscape level over long time periods (200 years), for integration with forest management planning. The model is not designed to provide accurate prediction of suitability or use at the stand level. Approximate population size can be calculated by assuming linear habitat-population relationships, but the model is not designed to provide accurate population density estimates. Any attempt to use the model in a different geographic area or for other than the intended purpose should be accompanied by model testing procedures, verification analysis, and other modifications to meet specific objectives.

7.2 MODEL DESCRIPTION

The critical components of boreal owl habitat appear to be the availability of large trees for nest cavities and trees that provide thermal cover for roosts. This model is based on the assumption that reproductive habitat, which includes nesting and roosting habitat, is the most limited year-round habitat. If trees of sufficient size and number are present to ensure there will be suitable nest sites, it is assumed that reproductive requirements of boreal owls are met.

The availability of prey is an important component of boreal owl habitat. Small mammals such as voles and mice make up the majority of their diet (Catling 1972, Hayward et al. 1993, Hayward 1994) and occur in high densities in mature conifer forests, particularly spruce and fir (Hayward et al. 1993). Since spruce-fir forests are also the preferred roosting habitat, this model assumes that boreal owl food requirements will be met in the same habitats that provide suitable roosting habitat. A forest must be of sufficient height and canopy cover to meet the roosting requirements.

This model will produce HSI values that are assumed proportional to a forest stand's ability to provide suitable reproductive habitat for boreal owls. A stand with an HSI value of 0 is assumed to represent unsuitable habitat and occurs in young stands (i.e. small trees dominate the stand), with no suitable cavities and sparse cover values. An HSI value of 1 is assumed to represent the best habitat and indicates high reproductive habitat quality and high densities of breeding pairs.

7.2.1 Habitat Variables and HSI Components

A. Nesting

High quality nesting habitat for the boreal owl requires large trees in structurally diverse forests to provide suitable nest cavities. Boreal owls nested primarily in pileated woodpecker cavities in the FMF, so the nesting component used in the pileated woodpecker model is used as the first component in the boreal owl model (S_1, Table 1).

B. Cover and Roosting

Adequate cover occurs in mature dense stands with high tree canopy closure. Roosting habitat quality is assumed to decline as tree canopy closure decreases. Component S_2 is predicted from canopy closure. Roosting habitat was associated with mature coniferous forests, so conifer canopy height (S_3) ensures the forests are old enough to provide the structure needed by roosting boreal owls. Boreal owls roost primarily in spruce and fir and occasionally in pine and deciduous species. Spruce trees are preferred because of the high thermal and hiding cover provided. To reflect the importance of spruce and fir, the component S_4 is defined using a weighted conifer composition (Table 1).

Table 1. Relationship of habitat variables to life requisites for the boreal owl HSI model.

HSI Component	Life Requisite	Habitat Variable	Habitat Variable Definition
S_1	Nesting	Deciduous Trees/ Conifer Snags ≥ 35 cm dbh (stems/ha)	Number of deciduous trees and conifer snags ≥ 35 cm dbh/ha.
S_2	Cover	Tree Canopy Closure (%)	Percent of ground covered by a vertical projection of tree crown areas onto the ground. Includes trees ≥ 8 cm dbh.
S_3	Roosting	Conifer Canopy Height (m)	Top height of 100 conifer trees/ha that have the largest dbh.
S_4	Roosting	Weighted Spruce, Fir and Pine in Tree Canopy (%)	% Spruce (Black + White) + % Fir + 0.25 x % Pine in the tree canopy.

7.2.2 Graphical HSI Component Relationships

S_1 S_1 is set so suitability increase linearly from 0 suitability at 0 large trees/ha to a suitability of 1 at 30 large trees/ha (Figure 1a).

S_2 Roosting habitat quality for the boreal owl is related positively to overstory canopy closure. Stands with closure values < 20% are assumed to be unsuitable ($S_2 = 0$), between 20-50% the stand has increasing value, and at values greater than 50% the stand is fully suitable ($S_2 = 1$) (Figure 1b).

S_3 The mean height of conifer canopy trees determines the developmental state of the stand. Boreal owls typically perched 5-7 m high in roost trees (Hayward et al. 1993) and trees are generally 2-3 times taller than the perch height (Hayward et al.1993). Roost trees with a mean height of 5 m are unsuitable ($S_3 = 0$). Palmer (1986) found roost had an average height of 14 m, therefore S_3 was set equal to 1 at heights of ≥ 14 m (Figure 1c).

S_4 Stands with ≥ 50% weighted conifer are the best for roosting ($S_4 = 1$). Stands with < 30% are unsuitable ($S_4 = 0$) (Figure 1d).

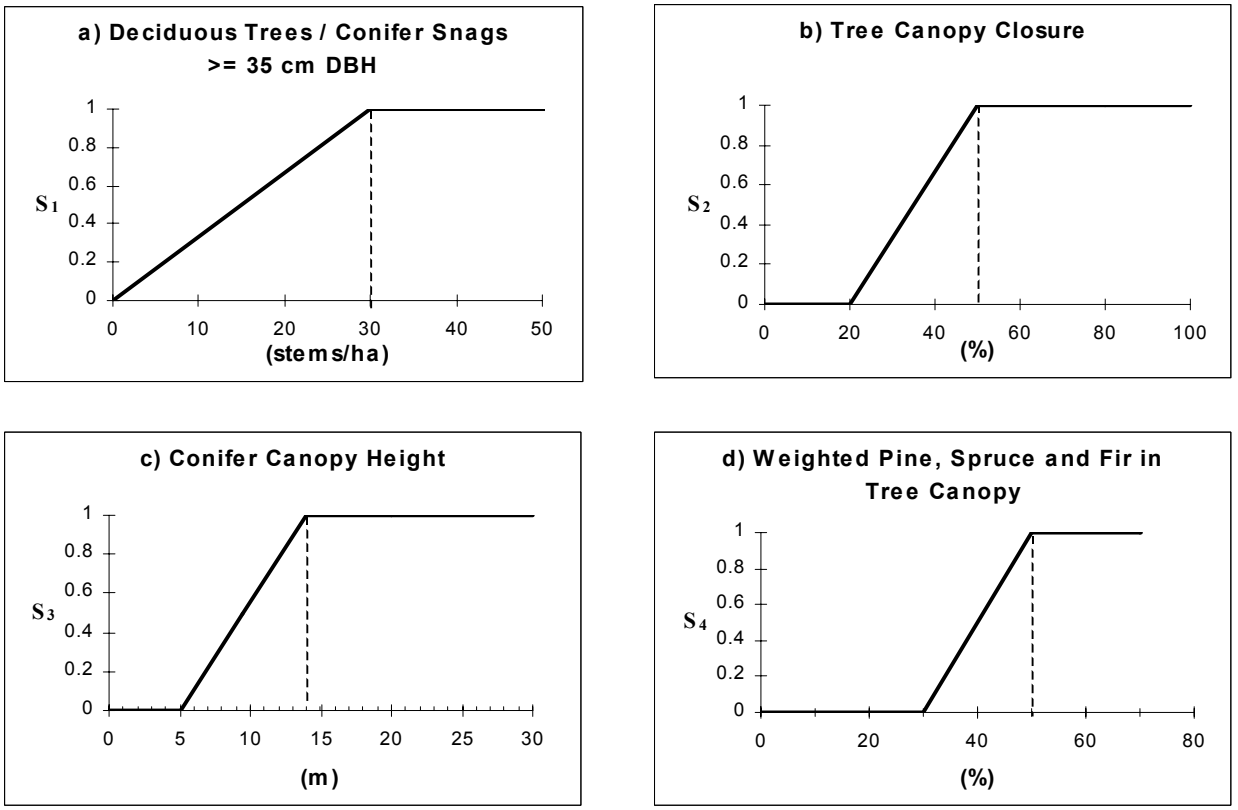

Figure 1. Graphical relationships between habitat variables and HSI components in the boreal owl model.

7.3 MODEL ASSUMPTIONS

1. The availability of nesting and roosting habitat limits the year-round boreal owl distribution.
2. Foraging habitat will be provided if suitable nesting and roosting habitat is available.
3. Water is not limiting.
4. Nesting and roosting habitat quality increases as forest stands develop structurally to have taller trees, more dying or dead trees, and more likelihood of trees with broken tops or branches for nest locations.
5. Mean height of conifers is indicative of stand structural complexity and is therefore representative of potential nesting habitat quality.
6. Aspen and balsam poplar likely to contain suitable nest sites for boreal owls because they are more often excavated by pileated woodpeckers.

7.4 EQUATION

The equation assumes that all components are equally important and non-compensatory.

$$HSI = S_1 \times S_2 \times S_3 \times S_4$$

8. SOURCES OF OTHER MODELS

There were no other HSI models for boreal owls found in the literature.

Model History

All of the HSI models for the Weldwood Forest Management Area have undergone several revisions, and they will be revised again as new information becomes available. Contact Rick Bonar for information about the most current version.

- Version 1 (1989) was developed by the Weldwood Integrated Resource Management Steering Committee (IRMSC).
- Version 2 (1994) was revised by Barb Beck and Melissa Todd.
- Version 3 (1995) was written by Ralph Heinrich and Jody Watson in a habitat modeling course at the University of Alberta.
- Version 4 (1996) was edited and reformatted by Wayne Bessie.
- Version 5 (1999) was revised by Karen Graham, Rick Bonar, Barb Beck and Jim Beck to incorporate information from recent literature.

9. LITERATURE CITED

Allen A. W. 1987. Habitat Suitability models: barred Owl. U.S. Fish and Wildlife Service. Biological Report 82. Washington D.C.

Beckingham, J. D., I. G. W. Corns and J. H. Archibald. 1996. Field guide to ecosites of west-central Alberta. Natural Resources Canada, Canadian Forest Service, Northern Forestry Centre, Special Report 9, Edmonton, Alberta.

Bent A. C. 1961. Life histories of North American birds of prey. Dover Publications, New York, New York.

Bondrup-Nielson S. 1978. Vocalizations, nesting and habitat preferences of the boreal owl (*Aegolius funereus*) in North America. Thesis, University of Toronto, Toronto, Ontario.

Boutin, S., C. J. Krebs, R. Boonstra, M. R. T. Dale, S. J. Hannon, K. Martin, A. R. E. Sinclair, J. N. M. Smith, R. Turkington, M. Blower, A. Byrom, F. I. Doyle, C. Doyle, D. Hik, L. Hofer, A. Hubbs, T. Karels, D. L. Murray, V. Nams, M. O'Donoghue, C. Rohner and S. Schweiger. 1996. Population changes of the vertebrate community during a snowshoe hare cycle in Canada's boreal forest. OIKOS 74:69-80.

Carlsson B. G. 1990. Recruitment of mates and deceptive behaviour by male Tengmalm's owl. Behavioral Ecology and Sociobiology 28:321-328.

Carlsson B. G. and B. Hornfeldt. 1989. Trigyny in tengmalm's owl (*Aegolius funereus*) induced by supplementary feeding. Ornis Scandinavica 203:155-156.

Catling P. M. 1972. A study of the boreal owl in southern Ontario with particular reference to the irruption of 1968-69. The Canadian Field-Naturalist 86:223-231.

Dejaifve P. A., C. A. Nova and R. Prodon. 1990. Habitat et densite de la chouette de Tengmalm (*Aegolius funereus*) a l'extremite orientale des Pyrenees. Alauda 58:267-273.

Eckert K. R. and T. L. Savaloja. 1979. First documented nesting of the boreal owl in Canada. American Birds 33: 135-137.

Hayward G. D. 1994. Flammulated, boreal and great gray owls in the United States: a technical conservation assessment. USDA Forest Service General Technical Report RM-253.

Hayward G. D. and E. O Garton. 1983. First nesting record for the boreal owl in Idaho. Condor 85:501.

Hayward G. D. and E. O. Garton. 1984. Roosting habitat selection by three small owls. Wilson Bulletin 96:690-692.

Hayward G. D., P. H. Hayward and E. O. Garton. 1987a. Movements and home range use by boreal owls in central Idaho. Pages 175-184 *in* R. W. Nero, R. J. Clark, R. J. Knapton and R. H. Hanre, editors. Biology and conservation of northern forest owls. USDA Forest Service General Technical Report, RM-142.

Hayward G. D., P. H. Hayward and E. O. Garton. 1987b. Revised breeding distribution of the boreal owl in the northern Rocky Mountains. Condor 91:431-432.

Hayward G. D., P. H. Hayward and E. O. Garton. 1993. Ecology of boreal owls in northern Rocky Mountains, USA. Wildlife Monographs 124:1-59.

Holt D. W. and M. Hillis. 1987. Current status and habitat associations of forest owls in western Montana. Pages 281-286 *in* R. W. Nero, R. J. Clark, R. J. Knapton and R. H. Hanre, editors. Biology and conservation of northern forest owls: symposium proceedings. USDA Forest Service General Technical Report, RM-142.

Hornfeldt B., B. G. Carlsson, O. Lofgren and U. Eklund. 1990. Effects of cyclic food supply on breeding performance in tengmalm's owl (*Aegolius funereus*). Canadian Journal of Zoology 68:522-536.

Johnsgard P. A. 1988. North American owls: biology and natural history. Smithsonian Institution Press. Washington.

Joneniaux A. and G. Durand. 1987. Forest management and population ecology of tengmalm's owl. Rev. Ecol. Terre et la Vie, Suppl. 4: 84-87.

Korpimaki E. 1981. On the ecology and biology of tengmalm's owl (*Aegolius funereus*) in southern Ostrobothnia and Suomenselka, western Finland. Acta Universitatis Ouluensis Series A. Sciential Rerum Natualium No. 118. Biologica 13:1-84.

Korpimaki E. 1986. Gradients in population fluctuation of Tengmalm's Owl (*Aegolius funereus*) in Europe. Oecologia (Berlin) 69:195-201.

Korpimaki E. 1988. Effects of territory quality on occupancy, breeding performance and breeding dispersal in Tengmalm's owl. Journal of Animal Ecology 57:97-108.

Korpimaki E. 1992. Fluctuating food abundance determining lifetime reproductive success of male Tengmalm owls. Journal of Animal Ecology 61:103-111.

Lane, W. H., D. E. Andersen and T. H. Nicholls. 1997a. Distribution, abundance, and habitat use of territorial male boreal owls (*Aegolius funereus*) in northeast Minnesota. Pages 246-247 *in* J. R. Duncan, D. H. Johnson and T. H. Nicholls, editors. Biology and conservation of owls in the northern hemisphere, Second International Symposium. USDA Forest Service General Technical Report, NC-190.

Lane, W. H., D. E. Andersen and T. H. Nicholls. 1997b. Habitat use and movements of breeding male boreal owls (*Aegolius funereus*) in northeast Minnesota as determined by radio telemetry. Pages 248-249 *in* J. R. Duncan, D. H. Johnson and T. H. Nicholls, editors. Biology and conservation of owls in the northern hemisphere, Second International Symposium. USDA Forest Service General Technical Report, NC-190.

Lofgren O., B. Hornfeldt and B.G. Carlsson. 1986. Site tenacity and nomadism in tengmalm's owl (*Aegolius funereus*) in relation to cyclic food production. Oecologia 69:321-326.

O'Connell M. W. 1987. Occurrence of boreal owls in northeastern Washington. Pages 185-188 *in* R. W. Nero, R. J. Clark, R. J. Knapton and R. H. Hanre, editors. Biology and conservation of northern forest owls. USDA Forest Service General Technical Report, RM-142.

Palmer, D. A. 1986. Habitat selection, movements and activity of boreal and saw-whet owls. Thesis, Colorado State University, Fort Collins, Colorado.

Palmer D. A. and R. A. Ryder. 1984. The first documented breeding of the boreal owl in Colorado. Condor 86: 215-217.

Solheim R. 1983a. Bygyny and biandry in the tengmalm's owl (*Aegolius funereus*). Ornis Scandinavica 14: 51-57.

Solheim R. 1983b. Breeding frequency of tengmalm's owl (*Aegolius funereus*) in three localities in 1974-1978. Proc. Nor. Cong. Ornithology, Kobnenhaven, Norway 3:79-84.

Spurr S. H. and B. V. Barnes. 1980. Forest Ecology. John Wiley and Sons, New York.

Stahlecker D. W. and J. W. Rawinski. 1990. First records for the boreal owl in New Mexico. Condor 92:517-519.

Takats, D. L. 1998. Barred owl habitat use and distribution in the Foothills Model Forest. Thesis, University of Alberta, Edmonton, Alberta.

Wardhaugh A. A. 1983. Owls of Britain and Europe. Blandford Press, Dorset.

Whelton B. D. 1989. Distribution of the boreal owl in eastern Washington and Oregon. Condor 91:712-716.

Wildlife Management Division. 1996. The status of Alberta wildlife. Alberta Environmental Protection, Natural Resources Service, Wildlife Management Division.