University of Alberta

Breeding habitat ecology of the barred owl (*Strix varia*) at three spatial scales in the boreal mixedwood forest of north-central Alberta

by

Benjamin Theodore Olsen ©

A thesis submitted to the Faculty of Graduate Studies and Research in partial fulfillment of the requirements for the degree Master of Science

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The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research for acceptance, a thesis entitled *Breeding habitat ecology of the barred owl* (Strix varia) *at three spatial scales in the boreal mixedwood forest of north-central Alberta* by *Benjamin Theodore Olsen* in partial fulfillment of the requirements for the degree of Master of Science in Environmental Biology and Ecology.

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December 4, 1998

Abstract

The objective of this study was to examine barred owl (*Strix varia*) habitat pattern at three spatial scales in north-central Alberta. Fifteen adult and five juvenile barred owls were radio-collared in order to (1) locate nesting sites, (2) determine home range characteristics, and (3) monitor the pre-dispersal movement of juveniles. Barred owl breeding home range size averaged 337.9 ha. Home ranges contained more old (100+ year) deciduous, old coniferous and old mixedwood forest, and less young forest (< 60 year) compared to the landscape. Although old forest was predominant within the owl home ranges, habitat use on a weekly basis was quite variable and most owls used old mixedwood less than expected, based the availability of this habitat type within the home ranges. However, within the home ranges owls used mature (60 – 100 year) deciduous forest non-randomly. Large diameter hollow trees (hereafter called owl cavity trees) were used for nesting and roosting. Ten owl cavity trees averaged 51.6 cm in diameter at breast height (dbh) (range 33.5 cm – 77.0 cm). Owl cavities occurred in balsam poplar (*Populus balsamifera*) and trembling aspen (*Populus tremuloides*) tree species. Vegetation structure within circular plots (30 m radius) centered on owl cavity trees was characterized by a higher density of large diameter snags (> 34cm dbh) compared to owl home ranges and areas of upland forest on the landscape. Owl cavity trees occurred in old (100+ year) and mature (60 – 100 year) forests. Based these findings, I discuss strategies for barred owl habitat provision and enhancement in the boreal mixedwood forest of north-central Alberta.

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In the fall of 1995, Dave Stepnisky, Rob Sissons, Carl Burgess and I were very eager to initiate a barred owl study in northern Alberta. We worked diligently that year to find logistical and financial support, and spent many weekends collecting field data on our own volition. I have appreciated working with these individuals over the years, and am grateful for their contribution to this project.

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Gordon Court collected most of the historical data on barred owls at Calling Lake, and his encouragement and direction throughout this project have been greatly appreciated. I especially thank Ray Cromie, John Moore and Trevor Roper for sharing their experience and companionship with me on several owling expeditions. Trevor Weins and the Federation of Alberta Naturalists provided the Breeding Bird Atlas data without reservation. Jocelyn Hudon, Curator of Ornithology at the Provincial Archives, granted me access to museum specimens. Tim Martin was a valuable resource in the GIS lab. Simon Dyer and Rob Anderson helped with the statistical analysis. I especially thank Cindy McCallum for her patience and assistance both in the field and in the lab.

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CHAPTER 1

Thesis introduction, overview and research objectives.

1.0 Thesis Introduction

Few studies have examined the ecology of the northern barred owl (*Strix varia varia* Barton) in detail, because the density of territories is typically low (Bosakowski *et al.* 1987), individuals inhabit remote woodlands (Devereux and Mosher 1984), and breeding evidence is difficult to ascertain (Frith *et al.* 1997). Some authors have noted their observations of the hunting activity (Takats 1996), habitat use (Leder and Walters 1980), and nesting behavior (Soucy 1976) of one or two individuals, but few have approached these topics quantitatively. However, significant advancements have been made regarding the knowledge of barred owl reproductive success (Postuplasky *et al.* 1997, Dunstan and Sample 1972, Johnson 1987), home range size (Elody and Sloan 1985, Nicholls and Fuller 1987), habitat selection (Mazur *et al.* 1998), nesting habitat use (Mazur *et al.* 1997, Devereux and Mosher 1984, Hanley 1997), breeding distribution (Dark *et al.* 1998) as well as interspecific competition (Sisco and Sharp 1986, Hamer 1988) and hybridization with the northern spotted owl (*Strix occidentalis caurina*) (Hamer *et al.* 1994). The focus of my research is to examine the ecology of the barred owl in north-central Alberta, primarily regarding its habitat during the breeding period.

Chapter 2 of this thesis is a review of the natural history of the barred owl. Although considerable effort has been made to document the range of this species in other regions of North America, little is known about the breeding distribution of the barred owl in Alberta (Boxall and Stepney 1982). Therefore, I felt it was necessary to examine the literature and consult local naturalists in order to update the current ornithological record of this species in Alberta. Boxall and Stepney (1982) confirmed eight nesting records for the province from 1949 to 1980. Twelve additional records were obtained from 1993 to 1998, and with one exception (Takats 1995), all are previously unpublished. As well as confirmed breeding locations, several observers have collected morphological data on barred owls from Fish and Wildlife specimens (G. Court, pers. comm.), banding records (R. Cromie, pers. comm.), and provincial archives (J. Hudon, pers. comm.). In this chapter I present the data obtained from these sources and compare them to other reports of barred owl morphology from the literature. Finally, I describe some aspects of the breeding behavior and nesting ecology of the barred owl, since the subsequent chapters are primarily concerned with this species during the breeding period.

Previous studies have examined barred owl habitat selection at various ecological scales. Mazur *et al.* 1998 quantified owl breeding habitat as 'old mixedwood forest' in the boreal ecoregion, and found that this particular habitat type was also predominant in nonbreeding home ranges. Nicholls and Warner (1972) examined barred owl home ranges and found that owl habitat preference and avoidance was highly significant, and that home range boundaries were consistent regardless of changes in seasonality, phenology and years.

Since the barred owl is presumed to be a habitat specialist in other regions, I attempted to quantify barred owl habitat selection in the boreal mixedwood forest of Alberta. Chapter 3 pertains to the radio telemetry study conducted at Calling Lake, Alberta (55° 15' N, 113° 19' W) from 1996 to 1997. Habitat composition within nine owl home ranges was compared to the study area (40 km x 20 km). Secondly, the proportion of owl locations within the each habitat type was compared to the home range composition. Two different scales of habitat selection were examined, since habitat use over an entire breeding season may differ from habitat selection on a weekly or daily basis. These two scales are analogous to second and third order habitat selection described by Johnson (1980). The main objective of the habitat selection analysis was to address the following questions:

1. Does the habitat composition within owl home ranges differ from the composition of the landscape in general?
2. Does owl habitat use within the home range differ from expected habitat use, based on the habitat availability within the home range?

Although habitat composition is important to consider, the spatial arrangement of habitat on the landscape cannot be ignored, since habitat configuration can (1) facilitate the movement of organisms between adjoining landscapes (Hansson 1992), (2) reduce potential edge effects (Angelstam 1992), and (3) possibly mitigate the implications of increasing habitat loss (Kareiva and Wennergren 1995). Habitat loss in eastern North America has had a deleterious effect on barred owl populations in some regions (Bosakowski *et al.* 1987). Furthermore, depredation by a competitive predator, the great horned owl (*Bubo virginianus*), is considered to be a negative edge effect for barred owl populations persisting in fragmented landscapes (Laidig and Dobkin 1995). Conversely, recent speculation regarding the relationship between barred and spotted owls suggests that barred owls are better adapted to fragmented forest habitats (Dunbar *et al.* 1991).

Although it is evident that the barred owl is responsive to changes in both habitat composition and configuration, it is uncertain whether increasing habitat loss and fragmentation will have negative implications for the barred owl in the boreal mixedwood forest. In Chapter 3, I examined barred owl habitat configuration at three spatial scales including owl foraging and roosting areas, breeding home ranges and simulated nonbreeding home ranges. Specifically, I have addressed the following questions in Chapter 3 with regard to owl habitat pattern:

1. Does habitat composition as well as patch size influence barred owl roosting and foraging habitat selection?
2. Does landscape configuration differ between owl home ranges, simulated nonbreeding home ranges and random areas on the landscape?
3. Does the landscape composition of the owls 'preferred habitat' differ between owl home ranges, simulated nonbreeding home ranges and random areas on the landscape?

Nest site availability is presumed to be a limiting factor in barred owl breeding habitat selection (Devereux and Mosher 1984), since owls do not construct their own nests (Johnsgard 1988), and individuals are too large to use cavities produced by primary cavity excavators, such as the pileated woodpecker (*Dryocopus pileatus*). The importance of large diameter hardwoods for nesting cavities has been well established (Soucy 1976), but few studies have examined the vegetation characteristics surrounding the nest site in relation to site fidelity and reproductive success (Hanley 1997). In Chapter 4, I examined the vegetation characteristics of barred owl cavity trees in relation to reference areas within owl home ranges and upland forest on the landscape. Specifically, the objectives of this chapter were to:

1. Compare the vegetation characteristics of owl cavity trees, and the surrounding forest, to references areas within owl home ranges and the landscape.

2. Determine the size and habitat composition of owl cavity tree patches.

3. Examine habitat composition at hierarchical spatial scales around barred owl cavity trees, using circular plots, increasing in dimension, overlaid on forest inventory data.

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Some aspects of the distribution, morphology, and breeding ecology of the northern barred owl (*Strix varia varia*).

2.0 North American Distribution

The northern race of the barred owl (*Strix varia varia* Barton) occurs throughout the eastern United States, from the Atlantic coast to the Great Plains (South Dakota, Nebraska, Kansas and Oklahoma), and from southern Texas to northern Minnesota (Johnsgard 1988). Its range extends into southern Canada through Ontario, Quebec and eastward into New Brunswick, Nova Scotia, Prince Edward Island and Labrador (Figure 2-1). In western North America, its distribution includes southern Manitoba, central Saskatchewan, northern Alberta and British Columbia, southern Alaska, Montana, Idaho and the Pacific Northwest (Washington, Oregon and northern California).

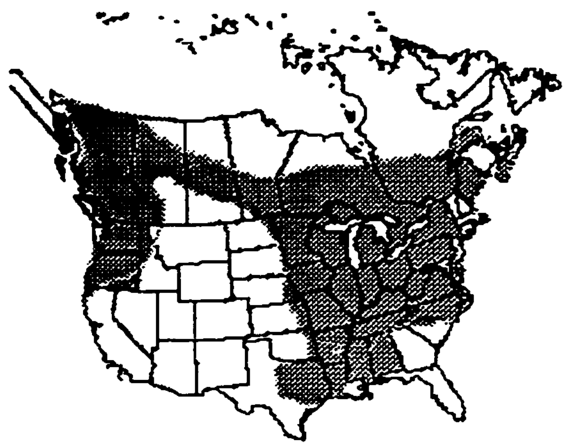


Figure 2-1: North American range of the barred owl according to Johnsgard (1988).

Range expansion of the barred owl from the northeast has been well documented in recent decades (Dark *et al.* 1998). Early evidence for the range expansion includes the first observations in British Columbia around 1940 (Grant 1966), Montana 1968-1970 (Shea 1974), Washington in 1965 (Rogers 1966) and Oregon in 1974 (Taylor and Forsman 1976). Breeding records have been obtained for Vancouver Island (Harrington-Tweit and Mattocks 1984), Washington (Leder and Walters 1980), and California (Evens and LeValley 1982), confirming that the northern race has become well established in the Pacific Coast region. The range expansion of the barred owl has resulted in considerable overlap with the distribution of the northern spotted owl (*Strix occidentalis caurina*), since both species have similar nesting habitat preference and forage primarily on nocturnal rodents (Taylor and Forsman 1976). In regions where both congeners occur, interspecific competition and hybridization (Hamer *et al.* 1994) has threatened the stability of spotted owl populations in some areas (Dark *et al.* 1998).

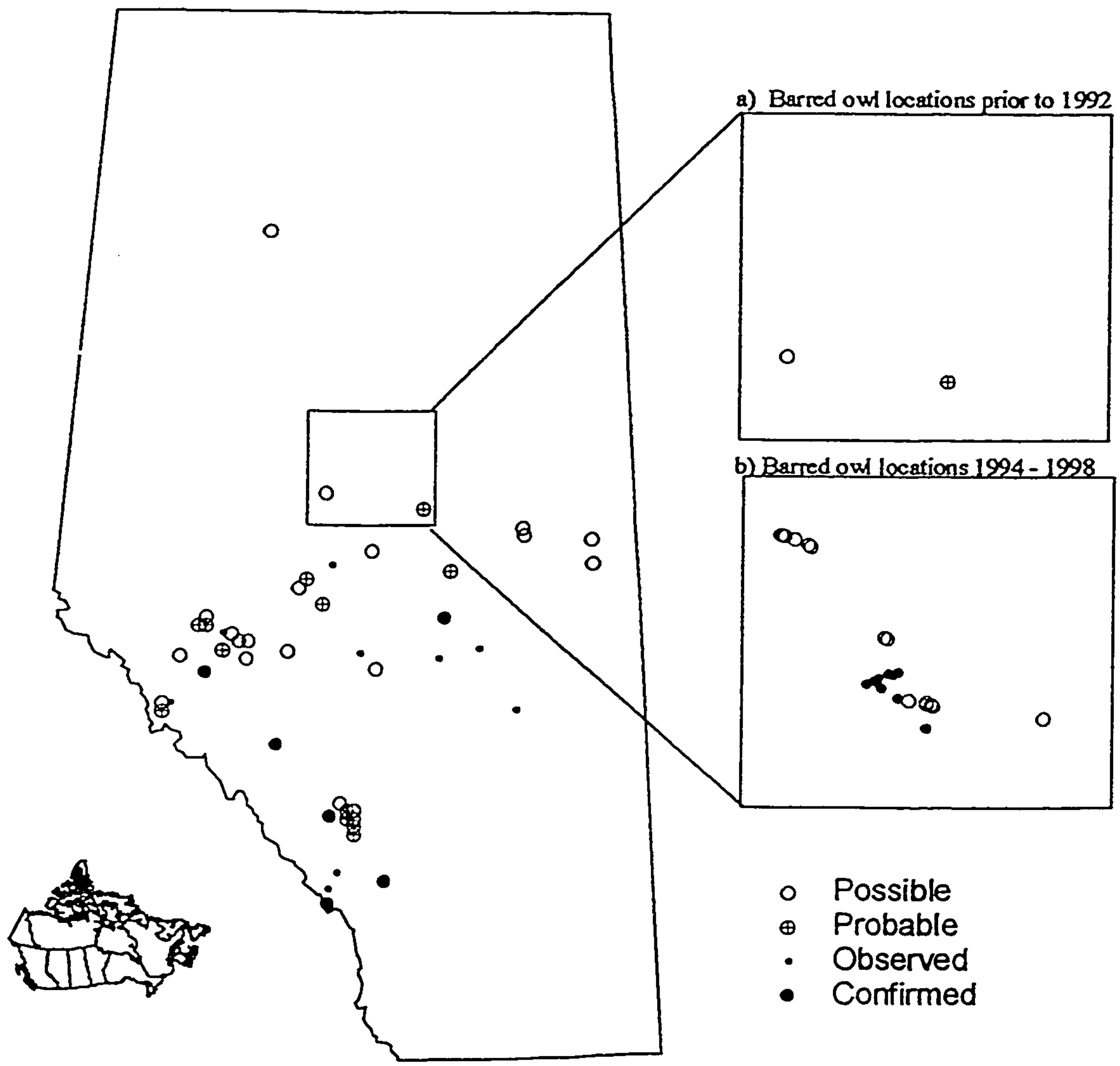
2.1 Provincial Distribution

2.1.1 Historical Observations

The barred owl has been well documented in western and central Alberta, but few accounts have been made of this species in northern regions (Figure 2-2). The barred owl has been recorded as far north as Fort Vermilion, AB [58°N, 116°W (Takats 1995)] and as far south as Beauvais Lake Provincial Park, AB [49°N, 114°W (Boxall and Stepney 1982)]. The barred owl escaped early observation in many regions of the province because of its tendency to inhabit remote woodlands away from human occupancy (Oeming and Jones 1955). An increase in the number of observations and breeding records over the past decade can be attributed to recent interest among researchers and naturalists to document the breeding range of the barred owl in Alberta, and not an expansion of its breeding range nor an increase in the number of owls for a particular region. As remote regions of the province are investigated, and trained observers enter the field, the ornithological record of this species in Alberta will undoubtedly continue to grow.

2.1.2 Provincial Breeding Records for Alberta

Evidence for a breeding population in Alberta was first obtained in 1949, when a family of barred owls was observed on the Prairie River near Slave Lake (Grant 1966). The first confirmed nesting site was not located until nearly two decades later in Edmonton, Alberta (Jones 1966). During the thirty years following the first breeding observation, Boxall and Stepney (1982) reported that only eight definite nesting sites had been recorded for the entire province. From 1988 to 1998, the number of confirmed nesting records more than doubled (Table 2-1). Three noteworthy records from Table 2-1 include the Bruderheim, Elk Island, and Sherwood Park observations. These records represent previously unpublished observations for the aspen parkland, an area believed to be uninhabited by the barred owl due to extensive habitat loss in this region (Boxall and Stepney 1982).



Historical records reproduced with permission from the Federation of Alberta Naturalists (1992) (T. Wiens, pers. comm.). Confirmation codes are: Observed (species identified but nonbreeding); Possible (species observed in suitable habitat); Probable (pair observed in nesting habitat and exhibit breeding behavior such as calling or nest building); Confirmed (occupied nest, nest with eggs, nest with young, fledglings observed but no nest found).

Figure 2-2: Historical barred owl observations for the province of Alberta, and the study area (Figure 2-2a) prior to 1992. Recent observations (Figure 2-2b) have resulted from detailed inventory work in this region.

Table 2-1: Alberta nesting records for the barred owl from 1949 to 1998.

Date	Location	Confirmation	Reference
1949, July 11	Slave Lake	1 adult and young	Grant 1966
1966, May 28	Edmonton	nest	Jones 1966
1968, April 1	Edmonton	nest	Boxall and Stepney (1982)
1976, Spring	Blue Lake	nest	Boxall and Stepney (1982)
1977, May	Jasper	nest	Boxall and Stepney (1982)
1977, Spring	Blue Lake	nest	Boxall and Stepney (1982)
1979, July	Miette River, Jasper National Park	1 adult and young	Boxall and Stepney (1982)
1980, July	Miette River, Jasper National Park	1 adult and young	Boxall and Stepney (1982)
1993, June 1	Peace River	adults and young	Takats (1995)
1994, June	Calling Lake, t72 r24†	young	G. Court (unpubl. data)
1995, May 15	Calling Lake, t73 r23†	adults and young	G. Court (unpubl. data)
1995, May 14	Calling Lake, t73 r24†	adults and young	G. Court (unpubl. data)
1988, Spring	Bruderheim	adults and young	R. Cromie (unpubl. data)
1993, Spring	Tawatina	adults and young	R. Cromie (unpubl. data)
1996, May 15	Calling Lake, t72 r25†	adults and young	B. Olsen (unpubl. data)
1996, Spring	Elk Island National Park	adults and young	H. Pletz (unpubl. data)
1997, May 28	Calling Lake, t71 r22†	adults and young	B. Olsen (unpubl. data)
1997, June 13	Lac La Biche	adults and young	B. Olsen (unpubl. data)
1998, May	Calling River East	adults and young	R. Cromie (unpubl. data)
1998, May	Sherwood Park	adults and young	R. Cromie (unpubl. data)
1998, May	Calling Lake, t73 r22†	adults and young	B. Olsen (unpubl. data)

†Legal land description of the township (t) and range (r) numbers, west of the 4th meridian.

2.2 Sexual Dimorphism and Body Size Characteristics

Several authors have reported on the morphology of barred owls in eastern north America (Johnsgard 1988), but few accounts have been made for northern latitudes. I sampled the Alberta population using measurements from the Provincial Archives ornithological database and banding records. Most specimens from the provincial database were sexed by dissection (J. Hudon, pers. comm.). In the case of the banding records, female owls were distinguished from male owls by vocalization (see section §2.3.1), breeding behavior, or the presence of a brood patch (R. Cromie, pers. comm.). Since most of the archival records did not provide an observation date, I was unable to account for the influence of seasonal variation on barred owl morphology.

Sexual dimorphism is pronounced in the barred owl, with females generally larger than the males (Table 2-2). In the Alberta sample, female owls were 21.2% heavier than male owls. This corroborates the findings of Hamer (1988) and Earhart and Johnson (1970) who found female barred owls to be on average 17.9% and 21.1% heavier than males, respectively. With the exception of body mass and footpad diameter, most other body measurements are similar between male and female owls. Hamer (1988) found that

Table 2-2: Male and female barred owl morphological characteristics (mean, range and sample size) from Baker Lake, Washington (Hamer 1998), Alberta banding records and museum specimens (Olsen, unpubl. data), the University of California Museum of Vertebrate Zoology (Earhart and Johnson 1970), and one other North American sample (Ridgway 1914).

	Female				Male			
	Hamer (1988)	Olsen (unpubl. data)	Earhart and Johnson (1970)	Ridgway (1914)	Hamer (1988)	Olsen (unpubl. data)	Earhart and Johnson (1970)	Ridgway (1914)
body mass (g)	805 n = 7	843.4[a] (602 - 1055) n = 18	800.9 (610 – 1051) n = 24		663 n = 8	664.2[a] (535 – 750) n = 15	631.9 (468 – 774) n = 20	
wing chord[b] (mm)	355 n = 7	339.3 (305 – 360) n = 18	310.7 (295 – 317) n = 25	338.3 (330 – 352) n = 7	327 n = 8	334.6 (318 – 345) n = 15	303.9 (295 – 309) n = 15	332.8 (320 – 340) n = 11
tail length[c] (mm)	250 n = 7	223.8 (150 – 240) n = 18		230.3 (224 – 257) n = 7	236 n = 8	217.1 (135 – 249) n = 15		225.4 (215 – 230) n = 11
body length[d] (mm)	474 n = 7	486.6 (480 – 495) n = 5			447 n = 8	480.8 (460 – 500) n = 6		
beak length[e] (mm)	44 n = 7				40 n = 8			
footpad diameter[f] (mm)	59 n = 7	63.1 (55 – 68) n = 4			51 n = 8	59.6 (47 – 67) n = 7		

[a] *Body mass was determined from a sample individuals in which the sex was known . Collection dates from the museum specimens (n = 11) were undetermined. Banding records (n = 22) were collected between 10 February and 08 August.*

[b] *Chord of the unflattened wing from the insertion of the alula to the end of the longest primary feather.*

[c] *Tail length is measured from the uropygial gland to the end of the middle retrix.*

[d] *Length of the body from the top of the head to the end of the retrices.*

[e] *Length of the upper mandible including the cere.*

[f] *Distance between the middle front toe and the hind toe of an extended foot, from the base of the talon.*

footpad diameter was 13.6% greater in female owls, which suggests that footpad diameter could be a characteristic that distinguishes male and female owls. Although there was a difference in male and female footpad diameter in the Alberta sample, the difference was subtle (5.9%) and overlap between male and female owls was considerable. Discriminant analysis using male (14) and female (19) owls of known sex from the Alberta sample, revealed that body mass significantly discriminated males and females, whereas footpad diameter, tail length, and wing chord only contributed to random variation (Wilk's Lambda = 0.473, $\chi^2 = 22.841$, $df = 1$, $p = 0.000$). The fit of the model was strong since 87.9% of the original cases were correctly classified by the first discriminant function, suggesting that body mass is a reliable predictor of barred owl sexual dimorphism.

2.3 Breeding Ecology

2.3.1 Territory Establishment and Courtship Behavior

The barred owl breeding season begins in the spring (March – April). During the early stages of territory establishment and courtship, the owls are highly vocal. The barred owl has an extensive repertoire of calls. These vocalizations are important for finding a mate, defending the territory and reaffirming the pair bond between resident owls. Sex can be determined when a pair of owls is heard calling simultaneously. The call of the male is typically deeper in pitch than that of the female. This difference is pronounced when the pair is calling together ('dueting'), and it is difficult to determine the sex when only a single individual is encountered. An experienced observer can learn to recognize the distinctive calls of a resident pair with practice. In my experience, the best way to become familiar with individual owl calls is to study recordings collected in the field. Figures 2-3 to 2-5 are vocalizations of a male barred owl collected on 14 February 1997 using a Sony professional analog recording device with a Sennheiser ME 80 directional microphone. The vocalizations were converted to digital audio files and displayed as spectrographs using Spectra Plus 4.0 software (Pioneer Hill Software, Poulsbo, WA).

The barred owl is more often encountered by sound than by sight. Its primary call involves a 4 syllable pattern (Type I song). A typical broadcast of the Type I call involves the main element, repeated two times, followed by a single note which dropping in pitch at the end. The main element consists of 4 notes or syllables, with the first and third syllable lower in pitch than the second and fourth. E. H. Forbush (1927) can be credited with the phrase "who cooks for you, who cooks for you, all" which is an accurate description of the Type I call (Figure 2-3).

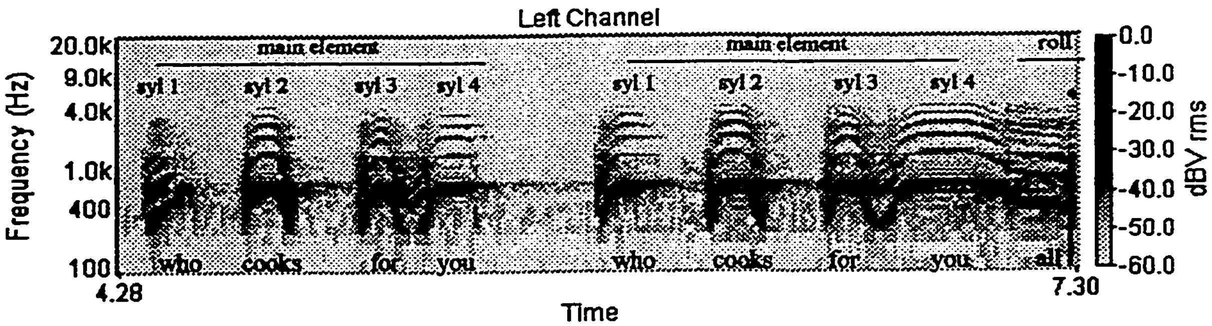


Figure 2-3. The Type I call of the barred owl. This call consists of the main element (repeated two times) and descending in pitch at the end. This is the most common vocalization, and has been paraphrased as "who cooks for you, who cooks for you, all".

The Type I call is commonly broadcast by a solitary individual. I believe unpaired owls use this song to advertise a vacant territory. Paired owls will also use the Type I song to establish territory boundaries. One member of the resident pair will usually circle the territory after sunset and broadcast a series of Type I calls. I believe this behavior corresponds with the time when most owls would begin their nightly hunting activities, and when a territorial intrusion by conspecifics would be most probable.

The behavioral response of a resident pair to a territorial intrusion is quite dynamic. The vocalizations of a resident pair can vary from one encounter to another. When one or both of the territorial owls becomes aggravated, the hooting changes in both pattern and volume. Aggravated hooting can be recognized by the repetition of the first syllable in the main element. The first syllable is repeated as many as 6 - 10 times, followed by the third and fourth syllables of the main element, and ending with the roll. This vocalization can be recognized on the spectrograph by the main element which is exaggerated because of the repetition of the first syllable (Figure 2-4). Since this vocalization is unique in terms of pattern and duration, I consider it to be the second distinctive call in the barred owl's repertoire (Type II call).

The type II call is commonly used to defend the territory from conspecific intruders. An excited pair will broadcast the type II call simultaneously, resulting in a loud raucous which has been described as 'caterwauling' by W. Brewster (Bent 1938).

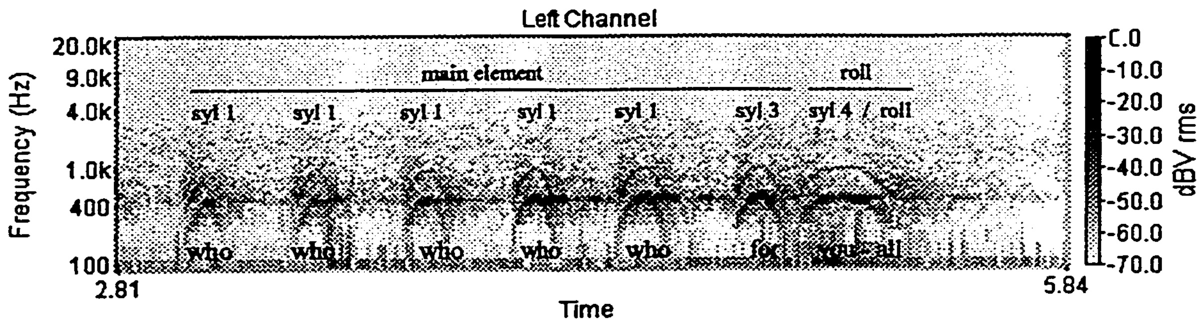


Figure 2-4. The Type II call of the barred owl. This call is characterized by the elongated main element that results from repetition of the first syllable.

Although it is difficult to paraphrase, the 'caterwauling' vocalization is worthy of examination because it can sometimes include the third distinctive call of the barred owl. The type III call results when the fourth syllable of the main element is slurred with the roll to produce a single, two-syllable note that has been described as 'who-ahhh' by many observers (Figure 2-5). This call signifies the climax of excitement during an encounter with a pair of territorial barred owls.

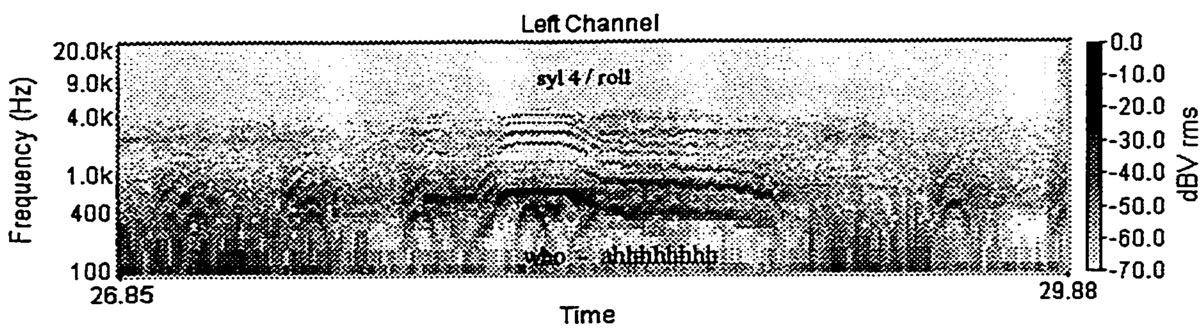


Figure 2-5. The Type III call of the barred owl. This call is characterized by a slurring of the fourth syllable of the main element with the roll.

2.3.2 Incubation and Brood Rearing

The incubation stage commences with the laying of the first egg [20 March, on average, in Maryland (Devereux and Mosher 1984)]. Clutch size can vary between 2 to 4 eggs (Murray 1976). Incubation begins before the last egg in the clutch has been laid, resulting in asynchronous hatching. After the first egg has been laid, females will incubate for 28 – 33 days (Johnsgard 1988). Brooding continues until the youngest chick is several weeks old. Devereux and Mosher (1984) reported the mean hatching date to be 10 April. Accurate estimates of barred owl laying and hatching dates have not been obtained for Alberta, and it is possible that egg dates are later in northern regions.

Once the chicks no longer require brooding, they remain in the nest for several weeks and are fed by the adults. During this time the nestlings lose most of their feathery white down and begin to grow primaries, secondaries and tail feathers. Although the nestlings do not fledge until 4 to 6 weeks of age, they may spend some of the time outside the cavity opening. This pre-fledging behavior is referred to as 'branching'. Once fledged, the young owls remain within the family group for up to 4 months prior to dispersal (Johnsgard 1988).

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Spatial pattern of barred owl (*Strix varia*) habitat at the stand and landscape scale in the boreal mixedwood forest.

3.0 Introduction

Previous studies of the barred owl (*Strix varia*) have shown consistent, and highly significant habitat preference and avoidance (Nicholls and Warner 1972, Mazur *et al.* 1998), but little is known about owl habitat pattern in forested landscapes. Habitat pattern refers to the composition as well as the spatial arrangement (*i.e.* configuration) of the habitat elements or 'patches' (Dunning *et al.* 1992). Habitat configuration is important to consider since many ecological relationships are influenced by landscape heterogeneity and connectivity at different ecological scales (Wiens and Milne 1989). Furthermore, some investigators postulate that the configuration of habitat on the landscape can mitigate the potential effects of habitat loss (Kareiva and Wennergren 1995). Albeit, others have cautioned that habitat configuration is often overemphasized, since the effects of habitat fragmentation are often negligible compared to the implications of habitat loss (Fahrig 1997).

In eastern North America, barred owl populations have declined due to habitat loss (Bosakowski *et al.* 1987) as well as increased competition and depredation by the great horned owl in 'fragmented' woodlots (Laidig and Dobkin 1995). Since the great horned owl is an edge specialist (Morrell and Yahner 1994), barred owls may select large patches of contiguous forest over small patches that are more fragmented (*i.e.* contain a higher proportion of edge habitat relative to the interior). The persistence of barred owls in extensive of tracts of unfragmented habitat in New Jersey (Laidig and Dobkin 1995) suggests that this species is an interior forest obligate. Conversely, the barred owl is not considered to be an interior forest obligate in the Pacific Northwest where it has been successful at colonizing recently fragmented old-growth forest habitats (Dark *et al.* 1998). Although there is strong evidence that the barred owl is responsive to changes in habitat composition and configuration, it is uncertain whether habitat loss and fragmentation will have a negative effect on barred owl populations in the boreal forest. Quantifying barred owl habitat pattern will play an integral role in the conservation and management of habitat for this species as industrial development proceeds in northern Alberta.

Several statistical methods have been proposed for evaluating resource selection in studies of wildlife habitat use (Alldredge and Ratti 1986, 1992). Previous studies have addressed habitat selection with respect to multiple spatial scales (Johnson 1980), the interdependence of habitat proportions, and the difference in habitat use among individual animals or groups of individuals within a population (Aebischer *et al.* 1993). Regardless of the method employed, evidence for habitat selection is generally determined by the relative abundance of each habitat type within a specified landscape. However, two landscapes with identical habitat composition may differ in terms of habitat quality if the configuration of habitat is unique to one of those areas.
For example, landscape configuration may influence habitat quality for organisms with a limited ability to disperse into adjoining landscapes (Hansson 1992) or species that are sensitive to edge effects (Angelstam 1992). Although the importance of habitat pattern in determining ecological processes has been well established (Addicott *et al.* 1987, Turner 1989, Turner 1990) few studies have addressed habitat selection in terms of landscape composition and configuration concurrently (Otis 1997).

I examined barred owl habitat pattern at various spatial scales in the boreal mixedwood forest of Alberta. The first objective was to determine the habitat composition of barred owl home ranges relative to the landscape. Secondly, I compared habitat selection within the home ranges by examining foraging and roosting locations. These scales are analogous to the third and second-order levels of habitat selection described by Johnson (1980). Finally, I examined third and second-order habitat pattern by measuring patch and landscape configuration of barred owl foraging and roosting areas, breeding season home ranges, and circular plots representing nonbreeding home ranges.

3.1 Methods

3.1.1 Study Area

The 800 km^2 study area (Figure 3-1) is located in the southern boreal forest around Calling Lake, Alberta (55° 15' N, 113° 19' W). The boreal mixedwood ecoregion

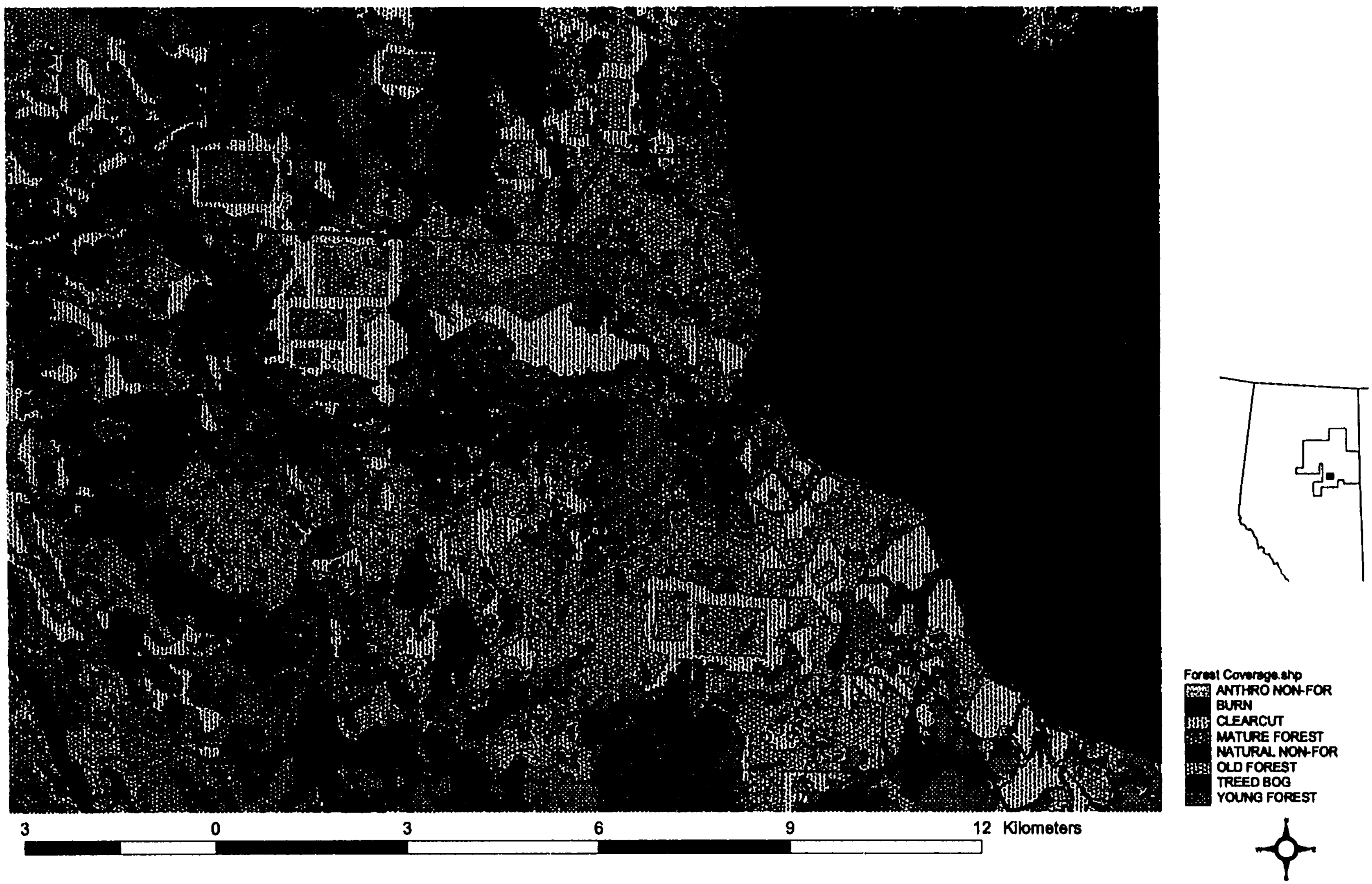

Figure 3-1: Forest composition of the study area located near Calling Lake Alberta (55° 15' N, 113° 19' W).

is the transition between the aspen parkland to the south and the boreal northlands (Strong and Leggat 1992). The study area is characterized by mixed and homogenous stands of trembling aspen (*Populus tremuloides*), balsam poplar (*Populus balsamifera*), jack pine (*Pinus banksiana*), white spruce (*Picea glauca*), and black spruce (*Picea mariana*) tree species. Less common are stands dominated by paper birch (*Betula papyrifera*), tamarack (*Larix lariciana*) and balsam fir (*Abies balsamea*), even though these species are widely distributed. The topographic relief is generally low lying with elevation ranging from 300m to 900m above sea level (Strong and Leggat 1992). January temperature averages -15.5°C and snowfall is approximately 60 mm (Strong and Leggat 1992). Mean July temperature is 16.2°C, and the total annual precipitation is approximately 400 mm (Strong and Leggat 1992).

3.1.2 Radio Telemetry

Barred owl territories were located during winter owl surveys from 1994 to 1996. We attempted to capture, band and radio-collar one member from each known territory within the study area. Capturing barred owls was accomplished by using three mist-nets and a barred owl decoy. The mist-nets were placed in a triangle around the decoy, with the owl tethered to a log on the ground. The mist-nets were fastened securely into the ground so that the trapping apparatus did not fall on the decoy when the resident owls attacked the nets. Once captured, barred owls were fitted with aluminum leg bands (U.S. Fish and Wildlife Service). A radio-telemetry device (Holohil Systems Ltd.) was fastened to the owl using a backpack harness (see Guetterman *et al.* 1991 for diagram). The Teflon harness was secured by sewing the neck and body loops together, near the breastbone of the owl. The joint was fastened with dental floss and sealed with epoxy.

Before releasing the owls, we collected morphological data which could be used to determine the sex and age each individual. We measured wing chord (mm), footpad diameter (0.1 mm), body mass (g), and tail length (mm). Wing chord was measured from the tip of the longest primary to the base of the alula. Tail length was measured from the uropygial gland to the tip of the retrices. Footpad diameter was measured from the base of the talon of the middle front toe to the hind toe. Sex was determined through a combination of behavior and morphological characteristics. Female barred owls are larger than the males by weight (see section §2.2 Sexual Dimorphism and Body Size Characteristics). Owls that were trapped from the nest while incubating or brooding young were assumed to be females. Owls captured by mist-netting were distinguished by their call. The call of the male barred owl is lower in pitch than the call of the female barred owl (see section §2.3.1 Territory Establishment and Courtship Behavior).

Fifteen adult and five juvenile barred owls were captured and marked with radio transmitters (Appendix 3-1). Radio tracking was accomplished using a Telonics TR-2 portable receiver and a three element hand held Yagi antenna. Owl locations were estimated by plotting the azimuth and the location of each reading on 1:20000 aerial photo field maps. Only error polygons less than one hectare were accepted. If the error polygon exceeded one hectare, the observer would find another geographic location from which to take subsequent readings or else wait until the owl had stopped moving. Owl locations were not estimated from the field maps due to the error associated with transferring locations from air photos to vegetation maps. Rather, the azimuth and the geographic coordinates from every reading were used to estimate animal locations using the home range analysis program Calhome (Kie *et al.* 1994). Breeding home ranges were estimated using biweekly locations taken between April and August 1995 to 1997 (Appendix 3-2). The minimum convex polygon (MCP) method was used to estimate home range size based on 10 – 30 relocations per individual. Mazur *et al.* (1998) found that 20 relocations was sufficient to estimate barred owl breeding season home ranges in Saskatchewan. Similarly, I found that home ranges could be estimated with 20 relocations per individual (Appendix 3-3). Owl locations and home ranges were exported from Calhome as text files for further analysis in Arc/Info® geographic information systems (ESRI, Inc. California, USA).

3.1.3 Habitat Classification

A map of the study area was produced from Alberta Vegetation Inventory (AVI) data using Arc/Info® geographic information systems (GIS). The landscape contained fifteen habitat cover types (Table 3-1). Habitat was classified according to stand origin and tree species composition since barred owl distributions are presumably influenced by forest age class (McGarigal and Fraser 1984) and cover type (Mazur *et al.* 1998). In order to reduce the number of cover types, I combined those which had few radio telemetry locations and represented a small proportion of the total area within barred owl home ranges. It was important to reduce the number of habitat categories since they out numbered the sample size of owls in this study. Three cover types (agri-open, anthro-open and burn) were deleted from the analysis since they represented <1% of the radio telemetry locations. Young deciduous, young mixedwood and young conifer habitats where combined into one class called young representing <3% of the total telemetry observations and <6% of the home ranges. The three cover types old treed-bog, mature treed-bog and young treed-bog were combined to a single category called trbog, representing <15% of MCP home ranges and <14% telemetry locations. Open water bodies larger 1000 ha were not included in the determination of available habitat.

Table 3-1: Criteria for reclassification of the Alberta Vegetation Inventory (AVI). The resulting coverage contained eighteen habitat categories based on age class and forest cover (Appendix 3-7 shows the proportional area of each forest cover type).

Reclass-Forest Cover	AVI Forest Cover†		Reclass-Age	AVI Forest Age Class††
Conifer	Sp1 = Sw, Ab, Lt, Pl, Pj	Pct ≥ 80		
	or			
	Sp1 = Sw, Ab, Lt, Pl, Pj Sp2 = Sw, Ab, Lt, Pl, Pj	Pct < 80		
Deciduous	Sp1 = Aw, Pb, Bw	Pct ≥ 80		
	or			
	Sp1 = Aw, Pb, Bw Sp2 = Aw, Pb, Bw	Pct < 80		
Mixedwood	Sp1 = Aw, Pb, Bw Sp2 = Sw, Ab, Lt, Pl, Pj, Sb	Pct < 80		
	or			
	Sp1 = Sw, Ab, Lt, Pl, Pj, Sb Sp2 = Aw, Pb, Bw	Pct < 80		
Treed bog	Sp1 = Sb	Pct ≥ 80		
Antropogenic	ANTHRO_NON_VEG			
Agriculture	ANTRO_VEG			
Wetland	NATURAL_NON_VEG NON_FORST_TYPE			
Burn	MOD_1_COND = BU			
Clearcut	MOD_1_COND = CC			
			Old (100+ y)	origin_yr_establ > 1891
			Mature (60 – 100 y)	origin_yr_establ 1931-1891
			Young (< 60 y)	origin_yr_establ < 1930

† Percent cover (Pct) of the dominant (Sp1) and sub-dominant (Sp2) overstory tree species. Tree species codes are *Picea glauca* (Sw), *Picea mariana* (Sb), *Abies balsamea* (Ab), *Larix lariciana* (Lt), *Pinus contorta* (Pl), *Pinus banksiana* (Pj), *Populus tremuloides* (Aw), *Populus basamifera* (Pb) and *Betula papyrifera* (Bw).
†† Forest age-class according to the AVI represents the estimated stand origin year (origin_yr_establ).

3.1.4 Habitat Selection

Habitat data that are expressed as a proportion 'used' versus 'available' can be tested using compositional analysis (Aebischer *et al.* 1993). The proportional use of each habitat type is normalized using a log-ratio transformation, avoiding the problem of interdependence between proportions of used and available habitat that sum to one (unit-sum constraint) (Aitchison 1986).

The proportion of radio telemetry locations in each habitat type was determined for nine individuals (Appendix 3-4a). The proportion of each habitat type within MCP summer home ranges was determined for each individual (Appendix 3-4b). In order to determine relative habitat availability, the proportion of each cover type in the study area was calculated (Appendix 3-4c). Since compositional analysis requires non zero values in the denominator, I replaced zero proportions with 0.01. Aebischer *et al.* 1993 suggests replacing zeros with a value less than the non-zero proportion.

Habitat proportions were transformed using log-ratios for the owl locations (Appendix 3-5a), MCP home ranges (Appendix 3-5b) and the landscape (Appendix 3-5c). Log ratios of used habitat are expresses as:

[1] $y = \ln (U_{i,n} / U_{j,n})$

Where U_i is the proportion of habitat i used by owl n, and U_j is the proportion of habitat j used by owl n. Log ratios of available habitat are:

[2] $y = \ln (A_{i,n} / A_{j,n})$

Where A_i is the proportion of habitat i available to owl n, and A_j is the proportion of habitat j available to owl n. Log ratios are calculated for each habitat category within the landscape (y_o) MCP home ranges (y_2) and the telemetry locations (y_1) for each individual. The log ratio differences (Appendix 3-6) represent the importance of each habitat relative to its availability. Therefore, we can compare the log ratio habitat proportions of the individual owl locations to that of the MCP home ranges by:

[3] $\mathrm{d} = \ln (\mathrm{U}_{i,n} / \mathrm{U}_{j,n}) - \ln (\mathrm{A}_{i,n} / \mathrm{A}_{j,n})$

or $d = y_1 - y_2$

Similarly, we can compare the log ratio habitat proportions of the MCP home ranges to the landscape by:

[4] $d = \ln (U_{i,n} / U_{j,n}) - \ln (A_{i,n} / A_{j,n})$

or $\quad d = y_2 - y_o$

The relative importance of each habitat class can be determined by inspection of *d*. Positive *d* values suggest preference and negative values suggest avoidance of a particular habitat type. To determine if habitat use differs from random, a matrix of arithmetic means of the log ratios for each habitat is established. A residual matrix of raw sums of squares and cross products calculated from *d* is used to test for non-random habitat use. Zar (1984) gives an example of how the residual matrix of raw sums of squares and cross products can be determined from *d* (difference in log-ratios):

$$R_2 = \begin{matrix} \Sigma X_1^2 & \Sigma X_1X_2 & \Sigma X_1X_3 & \cdots & \Sigma X_1X_M \\ \Sigma X_2X_1 & \Sigma X_2^2 & \Sigma X_2X_3 & \cdots & \Sigma X_2X_M \\ \Sigma X_3X_1 & \Sigma X_3X_2 & \Sigma X_3^2 & \cdots & \Sigma X_3X_M \\ \vdots & \vdots & \vdots & & \vdots \\ \Sigma X_MX_1 & \Sigma X_MX_2 & \Sigma X_MX_3 & \cdots & \Sigma X_M^2 \end{matrix}$$

Then, $\Lambda = | R_1 | / | R_2 |$ can be compared to a theoretical distribution of χ^2 at *n-1* degrees of freedom to obtain a p-value (whereby $| R_1 |$ is the determinant of the sums of squares and cross products matrices, and $| R_2 |$ is determinant of the mean corrected sums of squares and crossproducts). The mean corrected squares and products are determined by:

$$R_1 = \begin{matrix} \Sigma x_1^2 & \Sigma x_1x_2 & \Sigma x_1x_3 & \cdots & \Sigma x_1x_M \\ \Sigma x_2x_1 & \Sigma x_2^2 & \Sigma x_2x_3 & \cdots & \Sigma x_2x_M \\ \Sigma x_3x_1 & \Sigma x_3x_2 & \Sigma x_3^2 & \cdots & \Sigma x_3x_M \\ \vdots & \vdots & \vdots & & \vdots \\ \Sigma x_Mx_1 & \Sigma x_Mx_2 & \Sigma x_Mx_3 & \cdots & \Sigma x_M^2 \end{matrix}$$

whereby $\Sigma x_i^2 = [\Sigma X_i^2 - (\Sigma X_i)^2 / n]$ represents the mean corrected sums of squares and

$\sum x_i x_k = [\sum X_i X_k - (\sum X_i X_k) / n]$ represents the mean corrected sums of crossproducts for n number of habitat categories.

In order to determine which habitats contributed to the non-random habitat selection, a ranking matrix is established. The means and standard errors of each cell in the matrix is determined and compared to a theoretical distribution. Habitat types are then ranked according to the number of positive values in the each row. Significant differences delineate habitats that differ from random at $\alpha = 0.05$ based on the theoretical distribution of t (n – 1 degrees of freedom).

3.1.5 Habitat Configuration: Stand Level

Radio telemetry locations were used to compare patches used by barred owls for foraging and roosting with random patches on the landscape. Patches used by owls were described by area and cover type. I used the methods outlined by Otis (1997) to examine the proportional use of different sized patches within multiple habitat types. The size classes represented small (< 5.56 ha), medium (5.56 – 10 ha) and large (> 10 ha) sized patches. The distribution of patch sizes followed a reverse J-shaped curve. Therefore, I selected the break points for the size classes so that the number of observations in class would be proportional to the total. Based on these percentiles, the proportion of patches within in each size class was equal (small patches = 32%, medium patches = 33%, large patches = 35%).

I first tested the hypothesis that all patch sizes were used proportionately. Consider this as the patch size effect. The patch size effect (χ^2_{patch}) was tested by:

[1] $$\chi^2_{patch} = 2 \sum_{i=1}^{k} \sum_{j=1}^{n_i} y_{ij} \ln (y_{ij} / y_i \, \theta_{ij})$$

whereby $y_i = \sum_{j=1}^{n_i} y_{ij}$, $\theta_{ij} = p_{ij} / p_i$, and $p_i = \sum_{j=1}^{n_i} p_{ij}$. The degrees of freedom in this case are $df = \sum_{i=1}^{k} (n_i - 1)$ whereby n is the number of patch size classes in k number of different habitats.

To test the hypothesis of proportional habitat use within a given habitat type i:

[2] $$\chi^2_{patch\ i} = 2 \sum_{j=1}^{n_i} y_{ij} \ln (y_{ij} / y_i \theta_{ij})$$

whereby $y_i = \sum_{j=1}^{n_i} y_{ij}$, $\theta_{ij} = p_{ij} / p_i$, and $p_i = \sum_{j=1}^{n_i} p_{ij}$. The degrees of freedom are $n_i - 1$.

To test the proportional use of habitat type ($\chi^2_{habitat}$) independent of patch size:

[3] $$\chi^2_{habitat} = 2 \sum_{i=1}^{k} y_i \ln (y_i / y \theta_i)$$

whereby $\theta_i = p_i$, and the degrees of freedom are $k - 1$.

The test of overall proportional use (χ^2) is expressed is:

[4] $$\chi^2 = 2 \sum_{i=1}^{k} \sum_{j=1}^{n_i} y_i \ln (y_i / y \theta_{ij})$$

3.1.6 Habitat Configuration: Landscape Level

Habitat configuration was examined within breeding season home ranges, simulated nonbreeding home ranges and random areas on the landscape. Minimum convex polygon summer home ranges were used to represent breeding home ranges (hereafter called owl MCP). Concentric circles (1227 ha) centered on the owl MCPs simulated nonbreeding home ranges (hereafter called owl circles). In two cases where we could not estimate breeding home range size, the nest location was used as the geographic center of the nonbreeding home range circle. The owl circles provided another spatial scale to evaluate habitat pattern, and are not intended to represent actual nonbreeding home range geometry. Nine breeding home ranges, 11 nonbreeding season home ranges, and 46 random areas were used to examine landscape configuration.

Forest cover maps of the owl home ranges and circular areas were processed using the Fragstats program for landscape pattern analysis within Arc/Info® GIS. Fragstats calculates several measures of habitat composition and configuration at the landscape, class and patch level (McGarigal and Marks 1994). At the class level, the following variables describing habitat pattern were calculated for each cover type: patch density (PD), area (% LAND), largest patch index (LPI), mean patch size (MPS), patch size standard deviation (PSSD) and variation (PSCV), edge density (ED), shape index

(AWMSI and LSI), patch fractal dimension (AWMPFD), and interspersion/juxtaposition index (IJI). At the landscape level, three additional measures of habitat pattern were calculated: Shannon's diversity index (SHDI), Shannon's evenness index (SHEI), patch richness density (PRD). Within the owl home ranges and circular areas, each patch was described in terms of cover type, percent area (%LAND), perimeter (m), shape index (SHAPE) and fractal dimension (FRACT). Appendix 3-7 lists the landscape pattern indices at each level of analysis.

Analysis of variance (ANOVA) was used to compare the landscapes according to measures of habitat pattern. Owl MCPs, owl circles and random circles were compared using least significant difference (LSD) comparisons for multiple means. To meet the requirements of ANOVA, log and arc-sin transformations were used whenever appropriate (Narūsis 1994). At the class level, variables describing landscape pattern were reduced to a single orthogonal axis using principal component analysis (PCA). The principal component factors represented a linear combination of variables that accounted for the largest variation in the sample (Narūsis 1994). Principal components were appropriate in this case since many of the variables within each habitat class were highly correlated, if not completely redundant. Factors representing 67.9 - 70% of the total variance where retained for significance testing using analysis of variance procedures.

3.2 Results

3.2.1 Owl Home Ranges: Second-order Habitat Selection

Male home range size (mean = 365.26 ± 153.68 ha, n =5) did not differ from female home range size (303.78 ± 167.57; n = 4) ($U = 6.0$, $p = 0.327$). Overall, barred owl breeding home range size averaged 337.94 ± 152.93 ha (n = 9). This average included all owls, even those with fewer than 20 relocations. Average home range size based on individuals with >20 relocations did not differ substantially (327.18 ± 123.96 ha, n = 6).

Second-order habitat selection was determined by comparing the habitat composition of barred owl home ranges to the landscape. Second-order habitat selection differed from random ($\chi^2 = 15.507$, $df = 9$, $p < 0.005$). Relative habitat use was determined by the composition of the owl home ranges, compared to the composition of the study area (Figure 3-2). Relative habitat use varied between the individuals, and pooled values indicated which habitat types were, on average, used more than expected (*i.e.* preferred) and those which were used less than expected (*i.e.* avoided), based on the availability of each habitat type on the landscape (Figure 3-2). In order to rank habitats in terms of relative importance, and determine statistical differences between the ranks, a matrix of log ratio means and standard errors was established (Appendix 3-7). The matrix used to rank each habitat according to preference and avoidance can be summarized as follows:

OldMix < OldDec < OldCon < Wetland < MatMix < TreedBog < MatDec < MatCon < Clearcut < Young

Habitats that do not differ from one another are underlined (compared to t at $n - 1$ degrees of freedom). Young forest was less predominant within the owl home ranges compared to old conifer, old mixedwood and old deciduous forest. Young forest did not differ from mature conifer, mature mixedwood, mature deciduous, treed bog and clearcut and wetland habitats.

3.2.2 Owl Locations: Third-Order Habitat Selection

Owl habitat selection within the home ranges (third-order selection) was non-random ($\chi^2 = 26.124$, $df = 9, p < 0.001$). Relative habitat use varied between the individuals, and pooled values indicated which habitat types were, on average, used more than expected (*i.e.* preferred) and those which were used less than expected (*i.e.* avoided), based on the availability of each habitat type within the owl home ranges (Figure 3-3). In order to rank habitats and determine significance, a matrix of log ratio means and standard errors was established (Appendix 3-8). The matrix used to rank each habitat according to preference and avoidance can be summarized as follows:

MatDec < MatCon < TrBog < OldCon < Wetland < Clearcut < Young < MatMix < OldDec < OldMix

Habitats that do not differ from one another are underlined (compared to t at $n - 1$ degrees of freedom). Old mixedwood was used significantly less than mature deciduous, compared to the availability of old mixedwood with the home ranges.

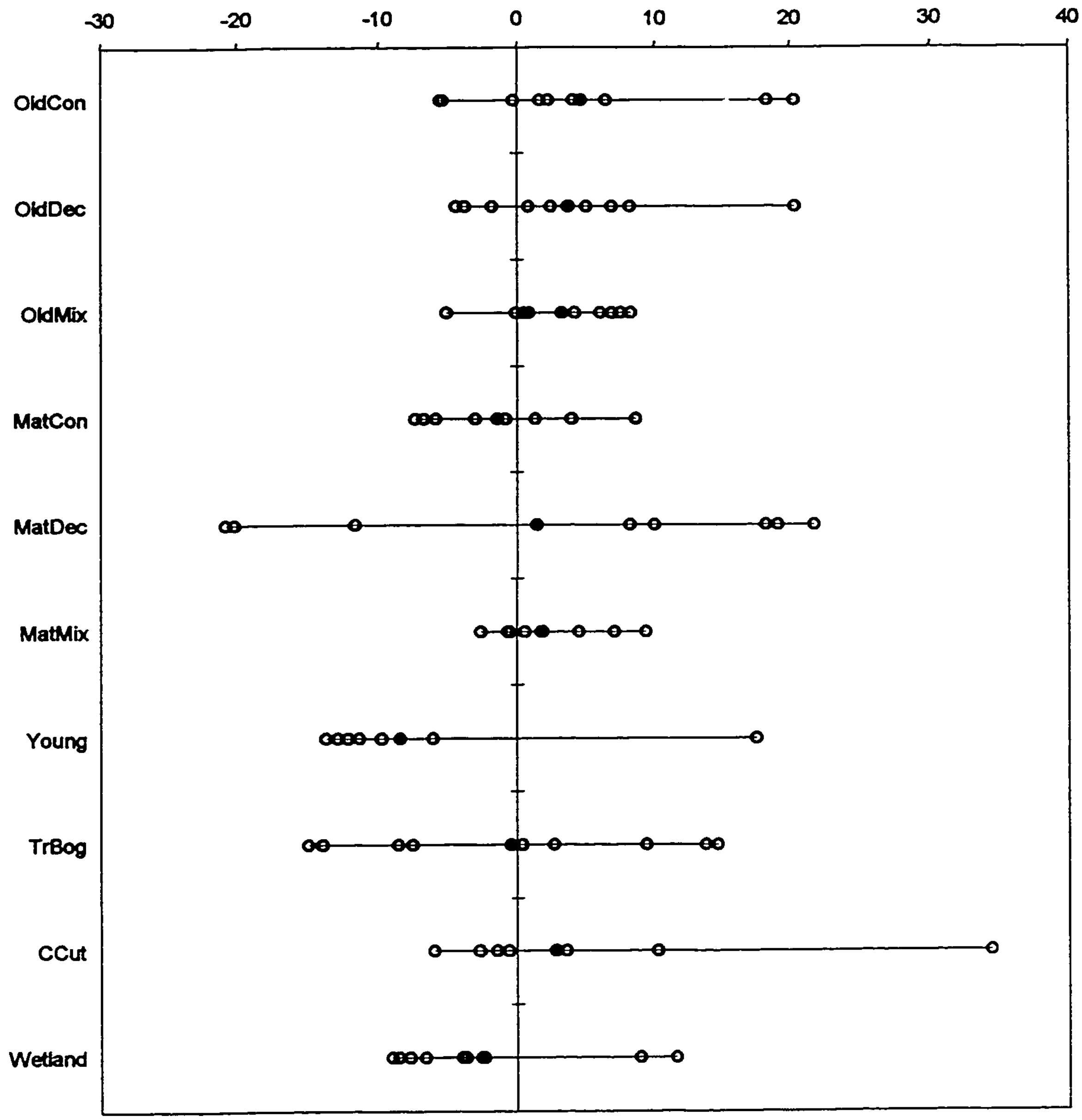

Figure 3-2. Second-order habitat use. Relative habitat selection for nine individuals (open circles) based upon the habitat composition of the home ranges (used habitat) and the composition of the study area (available habitat). Pooled values (dark circles) indicate which habitats were used, on average, more than expected (*i.e.* positive selection) and those which were used less than expected (*i.e.* negative selection), compared habitat availability within the landscape.

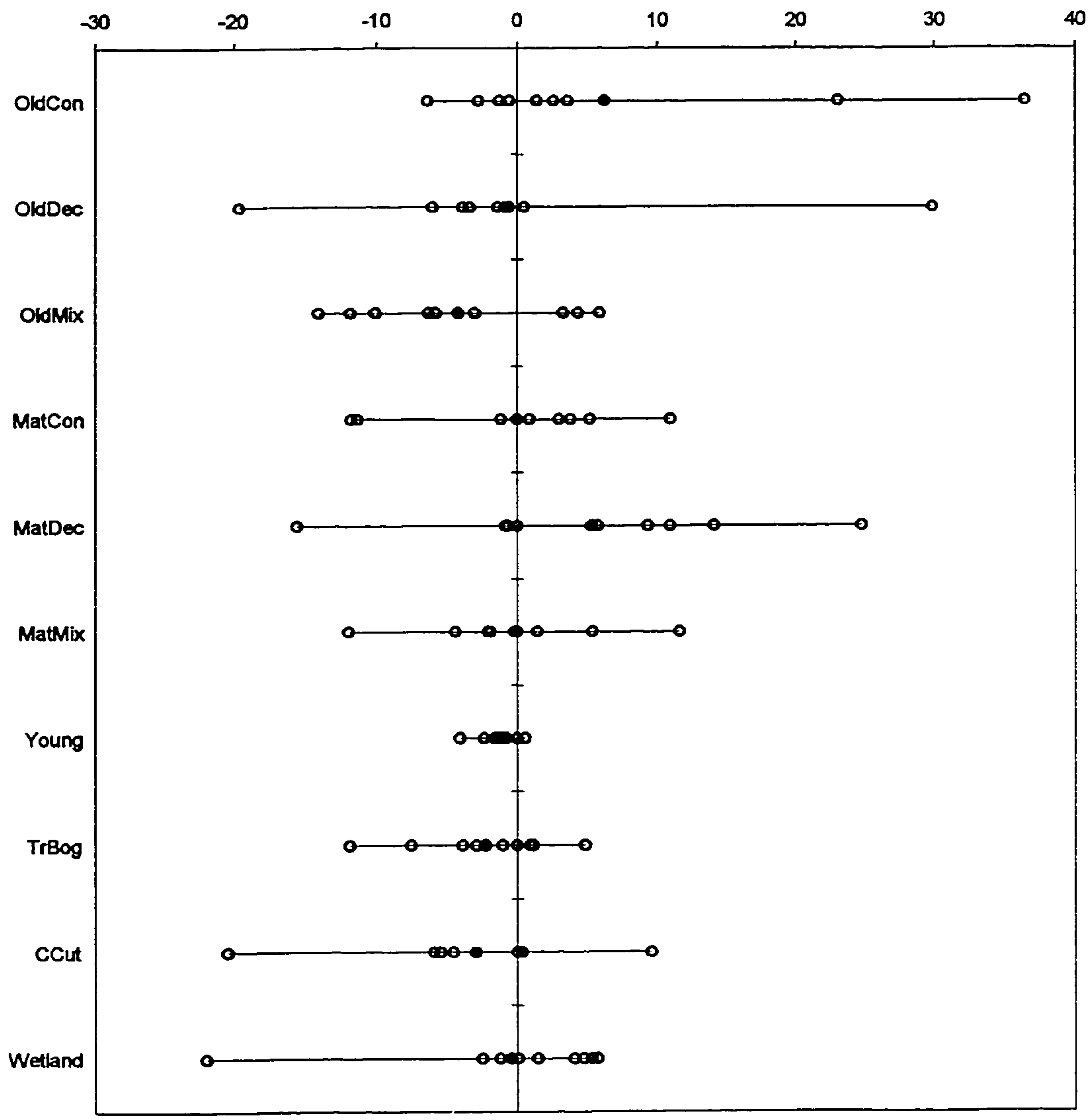

Figure 3-3: Third-order habitat use. Relative habitat selection for nine individuals (open circles) based upon the proportion of owl locations in each habitat type (used habitat) and the composition of the home ranges (available habitat). Pooled values indicate which habitats were used, on average, more than expected (*i.e.* positive selection) and those which were used less than expected (*i.e.* negative selection), compared to habitat availability within the owl home ranges.

3.2.3 Patch Level: Third-order Habitat Configuration

The proportion of large (> 10 ha), medium (5.56 – 10 ha), and small (< 5.56 ha) patches on the landscape was equal (Figure 3-4a). Owl habitat use of small, medium, and large sized patches (Figure 3-4b) was non-random (Table 3-2a). Owls used large patches of mature forest disproportionately. Large patches of non-forest were also used non-randomly. Habitat use was random between small, medium and large patches of old forest habitat. Habitat use among the patch size classes of young forest was also random. Owls used old, mature, young and non-forest disproportionately, irrespective of patch size (Table 3-2b). Overall, both cover type and patch area contributed to differential habitat use by barred owls (Table 3-2c).

3.2.4 Landscape Level: Second-order Habitat Configuration

Eight of thirteen variables describing landscape pattern were significant in discriminating between owl MCPs, owl circles and random circles (Table 3-3). Breeding home ranges were characterized by a greater number of patches (PD); patches that were smaller in size (MPS); patches that were less variable in size (PSSD and PSCV); patches that contained more edge (ED); patches that were more 'irregular' in shape (LSI and MSI); and had greater heterogeneity (PRD) compared to random areas on the landscape. The owl circles were characterized by a greater number of patches (PD); and patches that were smaller (MPS) but less variable in size (PSSD) compared to the landscape.

At the class level, the habitat pattern indices for three cover types (old conifer, old mixedwood, old deciduous) were reduced to a single orthogonal axis using principal components. The cover types were chosen based upon their rankings from the compositional analysis at the second-order (home range level) of habitat selection. Only one of the principal component factors for the habitat classes significantly discriminated the groups. The factor representing old conifer habitat was significant ($F = 3.919$, *sig.* = 0.029, $df = 2$) while factor scores for old mixedwood ($F = 20.236$, *sig.* = 0.791, $df = 2$) and old deciduous ($F = 0.319$, *sig.* = 0.729, $df = 2$) contributed to random group separation.

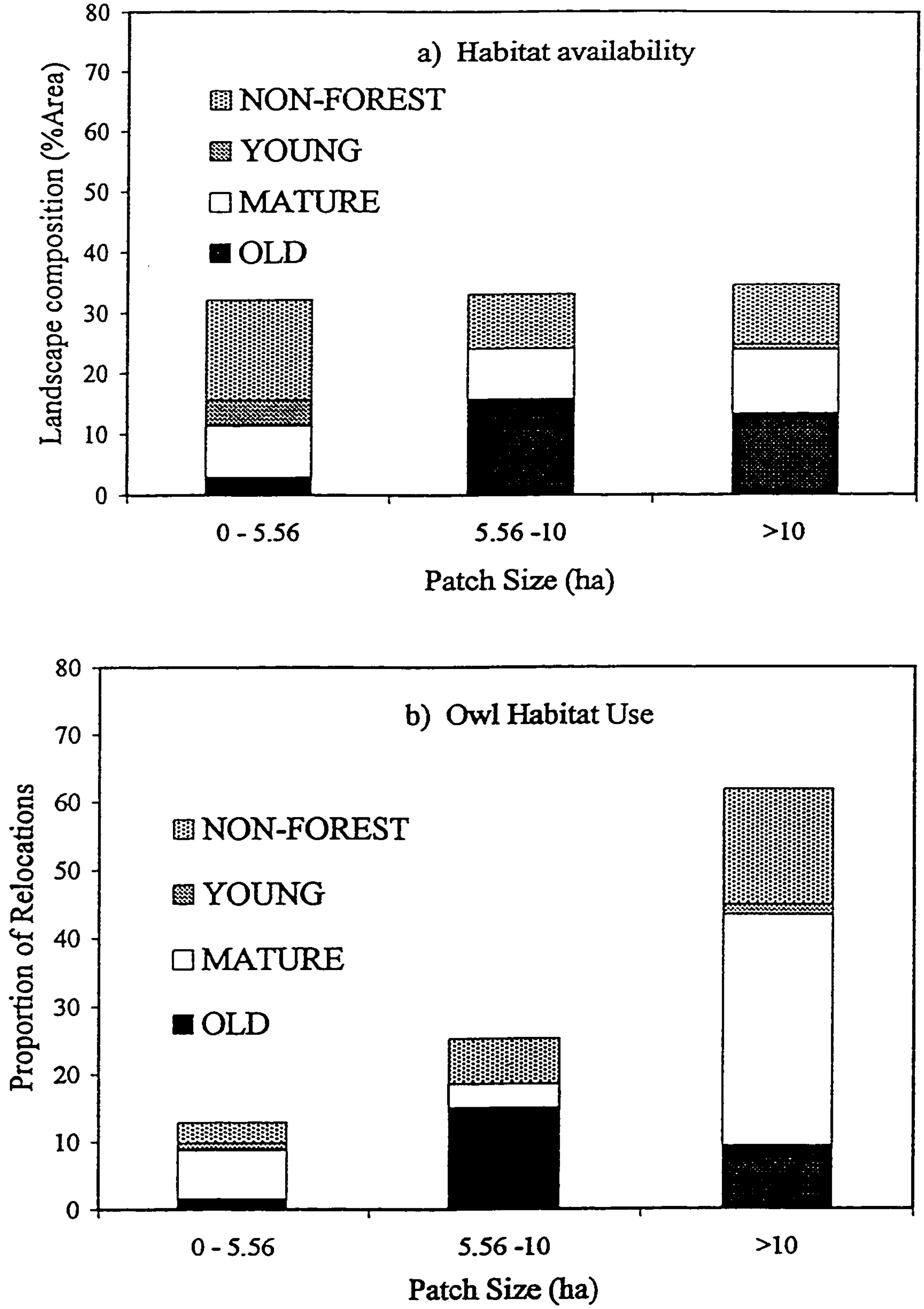

Figure 3-4: Owl habitat use vs. availability within the study area based on patch size and cover type.

Table 3-2: Summary of proportions (use vs availability), test statistics and significance values for quantifying differential habitat use based on patch size and cover type using the Otis (1997) method.

	Habitat Type i												
	Old			Mature			Young			Non-Forest			p_j [d]
Patch Size j	y_{ij} [a]	n_{ij} [b]	p_{ij} [c]	y_{ij}	n_{ij}	p_{ij}	y_{ij}	n_{ij}	p_{ij}	y_{ij}	n_{ij}	p_{ij}	
Small (< 5.56 ha)	3	44	0.03	14	128	0.08	2	64	0.04	6	253	0.17	0.32
Medium (5.56 - 10 ha)	29	238	0.16	7	127	0.08	0	0	0	13	138	0.09	0.33
Large (> 10 ha)	18	201	0.13	66	160	0.11	3	13	0.01	33	151	0.1	0.35
y_i [e]	50			87			5			52			
p_i [f]			0.32			0.27			0.05			0.36	

$\chi^2_{patch\ i}$	Test Statistic	Critical Value	df	*significance*
Old	1.58	2.273	2	$0.5 < p < 0.25$
Mature	46.72	13.186	2	$p < 0.001$
Young	3.82	4.605	2	$0.5 < p < 0.25$
Non-Forest	37.62	13.186	2	$p < 0.001$
a) Patch effect				
χ^2_{patch}	89.74	26.124	8	$p < 0.001$
b) Habitat effect				
$\chi^2_{habitat}$	29.34	16.266	3	$p < 0.001$
c) Overall				
χ^2	119.08	31.264	11	$p < 0.001$

[a] y_{ij} = No. of radio telemetry locations in patch size j of habitat i
[b] n_{ij} = No. of patches in size class j of habitat i
[c] p_{ij} = Proportion of the study area in patch size j of habitat i
[d] $p_j = \Sigma p_i$ for patch size j
[e] $y_i = \Sigma y_{ij}$
[f] $p_i = \Sigma p_{ij}$

Table 3-3: Results of the multivariate analysis of landscape pattern within owl breeding season home ranges (owl MCP), non-breeding season home ranges (owl circle) and the landscape (random).

Landscape Pattern	Descriptive statistics[b]						Multi-variate Analysis[c]					
	owl circle		owl MCP		random		ANOVA				Multiple comparison of means	
Variable[a]	mean	SE	mean	SE	mean	SE	*df*	*F*	*Sig*	*Power*	LSD	*Sig*
Patch Density (#/100ha)	14.22	0.83	20.84	1.48	11.32	0.51	2	20.344	0.000	1.000	RAND < CIRCLE	0.011
											CIRCLE < MCP	0.003
											RAND < MCP	0.000
Largest Patch (%)	15.47	1.95	19.26	2.34	20.57	1.83	2	0.883	0.419	0.196		
Mean Patch Size (ha)	7.38	0.61	5.01	0.37	9.69	0.45	2	18.767	0.000	1.000	MCP < CIRCLE	0.006
											MCP < RAND	0.000
											CIRCLE < RAND	0.011
Patch Size Standard Deviation (ha)	19.79	2.27	9.96	1.00	28.97	2.28	2	18.167	0.000	1.000	MCP < CIRCLE	0.002
											MCP < RAND	0.000
											CIRCLE < RAND	0.037
Patch Size Coefficient of Variation (%)	266.42	18.96	198.89	14.48	290.55	13.74	2	6.125	0.004	0.874	MCP < CIRCLE	0.025
											MCP < RAND	0.001
Edge Density (m/ha)	106.51	4.73	113.43	7.04	95.43	2.78	2	3.777	0.028	0.669	RAND < MCP	0.020
Mean Shape Index	2.93	0.12	2.45	0.15	3.18	0.09	2	7.777	0.001	0.941	MCP < CIRCLE	0.030
											MCP < RAND	0.000
Landscape Shape Index	11.50	0.46	6.96	0.58	10.44	0.27	2	20.623	0.000	1.000	MCP < CIRCLE	0.000
Patch Fractal Dimension	1.36	0.01	1.35	0.01	1.36	0.00	2	0.452	0.639	0.120		
Patch Richness Density (#/100ha)	1.21	0.02	4.15	0.60	1.15	0.02	2	154.873	0.000	1.000	MCP > CIRCLE	0.000
											MCP > RAND	0.000
Shannon's Diversity Index	2.12	0.06	1.92	0.09	1.98	0.03	2	2.146	0.125	0.424		
Shannon's Evenness Index	0.79	0.02	0.78	0.03	0.75	0.01	2	1.505	0.230	0.309		
Interspersion Juxtaposition Index	73.42	1.69	71.43	1.99	71.95	0.67	2	0.519	0.597	0.132		

[a] Mean Shape Index and Patch Fractal Dimension are the Average Weighted (AW) values, whereby large patches are weighted more than smaller patches.
[b] Mean and standard error for owl MCPs (n = 9), owl circles (n = 11) and random circles (n= 46).
[c] Multi-variate ANOVA results with Least Dignificant Difference (LSD) comparisons for multiple mean values.

Table 3-4: Results of the multivariate analysis of old conifer habitat pattern within owl breeding season home ranges (owl MCP), non-breeding season home ranges (owl circle) and the landscape (random).

Old Conifer Habitat	Descriptive statistics[b]						Multi-variate Analysis[c]					
	owl circle		owl MCP		random		ANOVA				Multiple comparisons	
Variable[a]	mean	SE	mean	SE	mean	SE	*df*	*F*	*Sig*	*Power*	LSD	*Sig*
Area (%)	12.722	2.397	11.270	3.074	7.230	1.010	2	3.185	0.048	0.589	RAND < CIRCLE	0.022
Patch Density (#/100 ha)	1.656	0.223	3.088	0.420	1.132	0.107	2	15.943	2.692E-06	0.999	RAND < MCP RAND < CIRCLE CIRCLE < MCP	0.000 0.046 0.004
Largest Patch (%)	5.705	1.723	5.856	2.016	2.842	0.476	2	3.864	0.026	0.679	RAND < CIRCLE	0.024
Mean Patch Size (ha)	8.334	1.583	3.442	0.967	6.070	0.529	2	5.432	0.007	0.829	MCP < CIRCLE MCP < RAND	0.002 0.015
Patch Size Standard Deviation (ha)	16.878	4.505	6.122	2.839	9.055	1.208	2	5.681	0.005	0.846	MCP < CIRCLE RAND < CIRCLE	0.002 0.015
Patch Size Coefficient of Variation (%)	191.255	14.201	136.372	23.114	132.500	8.793	2	4.240	0.019	0.722	MCP < CIRCLE RAND < CIRCLE	0.038 0.006
Edge Density (m/ha)	28.372	3.383	28.442	5.194	18.258	2.138	2	4.182	0.020	0.715	RAND < CIRCLE	0.016
Mean Shape Index	3.096	0.213	2.314	0.118	2.483	0.114	2	4.233	0.019	0.721	MCP < CIRCLE RAND < CIRCLE	0.017 0.008
Lanscape Shape Index	3.808	0.333	2.672	0.346	2.813	0.212	2	3.420	0.039	0.622	MCP < CIRCLE RAND < CIRCLE	0.050 0.013
Patch Fractal Dimension	1.378	0.009	1.378	0.008	1.367	0.005	2	0.984	0.379	0.214		
Interspersion Juxtaposition Index (%)	72.845	2.964	63.119	4.502	65.924	2.002	2	1.699	0.191	0.344		

[a] Mean Shape Index and Patch Fractal are the Average Weighted (AW) values, whereby large patches are weighted more than smaller ones .
[b] Mean and standard error for owl MCPs (n = 9), owl circles (n = 11) and random circles (n= 46).
[c] Multi-variate ANOVA results with Least Dignificant Difference (LSD) comparisons for multiple mean values.

Nine of eleven variables describing old conifer habitat pattern were significant in discriminating the owl home ranges, nonbreeding home ranges and random plots (Table 3-4). Owl home ranges contained more old conifer patches (PD); old conifer patches that were smaller (MPS) but more variable in size (PSSD and PSCV); and old conifer patches that were more irregular in shape (MSI and LSI) compared to random areas on the landscape. Within the owl circles, old conifer patches were more abundant in terms of area (%LAND) and patch density (PD); patches were more variable in size (PSSD and PSCV); and more complex in geometry compared to random areas on the landscape.

3.3 Discussion

3.3.1 Home Range Size

Several studies have examined barred owl home range size. In this study, breeding home range size was similar to that reported by Hamer (1988) in Baker Lake, Washington, USA. In the Washington example, and in this study, breeding home range size was twice as large as the breeding home range size of barred owls in Saskatchewan (Mazur 1997). Breeding home range size of barred owls in Saskatchewan was similar to that reported by Elody and Sloan (1985) in Michigan.

Barred owl home ranges are known to increase substantially during the months following the breeding period. Nonbreeding home ranges averaged 644 ha in Washington, 565 ha in Minnesota (Nicholls and Warner 1972), 282 ha in Michigan (Elody and Sloan 1985), and 1234 in Saskatchewan (Mazur 1997). Regardless of seasonal changes in home range size, barred owls do not migrate (Hamer 1988) nor do they venture far from their breeding territories, since nonbreeding home ranges overlap breeding home ranges entirely for most owls (Mazur 1997). Barred owls will defend their nesting areas tenaciously, even during the nonbreeding period, since nesting resources are typically scarce and may limit the distribution of barred owls in some regions (Devereux and Mosher 1984).

Although we were unable to conduct intensive radio telemetry surveillance during the nonbreeding period, we did confirm that most residents could be found in close proximity to their breeding areas in the winter. In two years of radio-tracking, only one owl left the study area indefinitely during the nonbreeding period. However, this owl did not have a breeding territory the previous summer, and was likely dispersing through the study area in search of a vacant territory. Based on our observations, barred owls in this study exhibited high territory fidelity, which is consistent with other investigations of this species (Nicholls and Warner 1972, Nicholls and Fuller 1987).

3.3.2 Habitat Selection

Barred owl home ranges contained a greater diversity of habitat types than expected. Generally, old forest was predominant within the home ranges, along with clearcuts, mature forest and treed bogs. Although old deciduous, old mixedwood and old conifer forest obtained the highest rankings, none of the top three habitat types were selected preferentially over one another at this scale. Since young forest was strongly selected against, preference for mature and old forest was nearly inevitable. At the home range scale, barred owl habitat selection could be a function of habitat avoidance. Since young stands have lower structural diversity than mature and old forest types (Lee *et al.* 1995), barred owls would have greater difficulty finding a suitable nesting cavity in young forest stands. Barred owls nest almost exclusively in rotten snags, which have a tendency to blow over or become uprooted (Mazur *et al.* 1997, Olsen unpubl. data). Therefore, individuals may select areas with the highest density of potential nest trees in order to ensure a suitable nest site from year to year. In the boreal region, old mixedwood forests have a high density of large diameter snags (Lee *et al.* 1995; Chapter 4) and this habitat type is an important source natural nesting structures for the barred owl.

At the stand level, Mazur *et al.* (1998) found that barred owl roosting and foraging habitat selection partially explained the predominance of old mixedwood forest within the breeding home ranges. Based on the individual owl locations, barred owls in this study did not use old mixedwood forest in proportion to its availability within the home ranges. Barred owls selected old conifer, mature conifer, mature deciduous, treed bog; and avoided old deciduous, old mixedwood, mature mixedwood and young forests. Since the barred owl is a generalist predator (Johnsgard 1988), habitat selection could be influenced by prey availability (Zabel *et al.* 1995) rather than a strong affinity for any particular habitat type at this scale. Although old mixedwood forest provides the best diversity of prey for the barred owl (Mazur *et al.* 1998), owls in this study did not restrict their foraging and roosting activities to any particular habitat type.

There are several reasons for the discrepancy in habitat use between this study, and the study conducted by Mazur (1997) in Saskatchewan. Differences in stand composition and age structure between the study areas could have two implications for barred owl habitat selection. First, the Alberta population may be better adapted to a diversity of forest types due to large scale and frequent natural disturbances in this region. An alternative explanation is that habitat use is consistent between the two populations, but our ability to observe these similarities is limited by some unknown factor. This would be true, for example, if owl habitat use was similar between the two study areas, but habitat composition (*i.e.* availability) differed considerably between the two landscapes.

The forest classification data in this study differed from the forest classification data used by Mazur (1997). Therefore, some of the discrepancies in habitat selection between the two may be attributed to differences in habitat classification, and not to differences in habitat use *per se*. In this study, old forest was defined as stands with an estimated origin of 100+ y, representing 17.5% of the landscape, compared to old forest (80+ y) in Saskatchewan which represented 27.9% of the study area (Mazur *et al.* 1998). Mazur *et al.* (1998) defined old forest as greater than 80 years of age, which is intended to represent forest stands that are beyond "current harvest rotations". I used a more conservative definition of old forest (stands greater 100 years), which was based on two assumptions. First, aspen canopies begin to open at 70 – 100 years (Lee *et al.* 1995), creating conditions which lead to complex structure in late-successional boreal forests. Second, aspen stands between the ages of 90 – 130 years can support unique communities of vertebrate fauna compared to rotational-aged stands (Alberta Environmental Centre 1995). Therefore, forested stands 100+ y, are likely unique in terms of physiognomic and floristic characteristics, compared to mature (60 – 100y) and young (< 60 y) forests in this region. Although a definition of old forest similar to that provided by Mazur *et al.* (1998) could have yielded results that are more comparable, this would have resulted in an over-estimate of habitats presumed to contain 'old-growth' characteristics.

The importance of edge forest and open habitat within barred owl foraging areas has likely been underestimated in many investigations of this species. Since barred owls may hunt in forest clearings, and retreat into the interior forest to consume their prey, many studies of habitat selection have underestimated the significance of open habitat to the foraging activities of this species. Although anecdotal, I have noted the prevalence of barred owls along edge habitats, especially in the spring (April – May). During the 1996 field season, we noticed an increase in the abundance of barred owls along roadways and cutlines which seemed to correlate with the beginning of the calling period for wood frogs (*Rana sylvatica*) and boreal chorus frogs (*Pseudacris trisariata*). Barred owls were observed along ephemeral ponds, presumably hunting amphibians, more often at night than during the day. The importance of ephemeral streams could not be evaluated since these landscape features do not exist on forest inventories at the appropriate spatial required for a detailed habitat analysis.

Our ability to detect differences in habitat use could have been limited by the small sample of owls in this study. A larger sample size would have provided increased statistical power, as well as ensuring a representative sample of the population. Given the number of territories within the study area, increasing the sample size would have meant radio-collaring both members of each resident pair. Although this was logistically possible, it introduces problems of pseudoreplication (Hurlbert 1984) and spatial autocorrelation (Legendre 1993), given the lack of independence between resident owls.

3.3.3 Foraging and Roosting Habitat Configuration

Several authors have suggested that the barred owl is sensitive to anthropogenic disturbance (Bosakowski *et al.* 1987) and requires extensive tracts of undisturbed forest (Laidig and Dobkin 1995). I tested the hypothesis that individual owls select forest patches based on habitat type and patch size, and concluded that barred owls did not select patches based exclusively on habitat type. However, barred owls selected large patches (>10 ha) more often than expected. The barred owl may select large patches in order to avoid competition and depredation by the great horned owl, an edge specialist (Morrell and Yahner 1994) and predator of barred owl adults and young (Bosakowski et al 1989). However, since we only tested for habitat selection among patches that differed in area, it would be misleading to assume that large patches have inherently less edge compared to smaller forest patches. It is more likely that barred owls select large patches based on the amount of habitat that is available, rather than the configuration of the patch itself. Future studies should discriminate between patches based on the ratio of patch edge to area in order to determine if the barred owl is an interior forest obligate or averse to habitats that are more fragmented.

3.3.4 Home Range Habitat Configuration

In any landscape, the degree of fragmentation (*i.e.* extent to which the habitat elements are spatially separated), increases as the number of habitat elements becomes larger (Fahrig 1997). For example, two landscapes with identical habitat composition (% area), may differ in terms of the degree of fragmentation if the number of habitat patches is significantly greater within one of the landscapes. Similarly, two landscapes with a different number of patches, are not necessarily different in terms of the degree of fragmentation if the total area of habitat is not held constant.

Overall, barred owl home ranges had the highest density of patches compared to the owl circles and the landscape. Furthermore, the diversity of habitat types within barred owl home ranges suggests that not only were these areas more fragmented, but also more heterogeneous compared to random areas on the landscape. In terms of geometry, patches within owl home ranges were typically smaller, more complex in shape, and contained more edge compared to random areas.

Of the three habitat types that were predominant within barred owl home ranges, the spatial configuration of old conifer forest proved to be significant in discriminating between owl home ranges and the landscape. Since the total area of old conifer habitat was equal between owl home ranges and owl circles, the difference in the number of old conifer patches within home ranges suggests that this habitat type was in fact more fragmented, compared to the owl circles.

One explanation for the difference in habitat configuration between owl home ranges and the landscape could be the influence of habitat composition. Owl home ranges contain a higher proportion of old conifer, old mixedwood, and old deciduous forest. These habitat types often occur in small patches with complex geometry compared to treed bogs, mature and young forests which have a tendency to be more contiguous in shape and dimension. The pattern of old forest habitat on the landscape is influenced by defoliating insect outbreaks, forest fire and windfall. These processes have produced a 'mosaic' of habitats differing in species composition, stage of succession and physical structure (Bonan and Shugart 1989). If the barred owl is well adapted to this naturally fragmented mosaic, it seems unlikely that habitat configuration will be jeopardized by current forest management practices which attempt to emulate natural disturbances through irregular cut block shape and dimension. However, habitat availability could be affected if harvest operations fail to provide sustainable levels of old, mature and young forest within this system. Short harvesting rotations can affect the abundance of old and mature forest on the landscape. Management practices that maintain the 'natural' distribution and abundance of old, mature and young stands will be important for preserving habitat within early, mid and late-successional forests in the boreal mixedwood ecoregion.

3.4 Management Implications and Directions for Further Research

Logging will have a deleterious effect on barred owl habitat if forest management practices fail to preserve the natural composition and spatial arrangement of habitats which have been maintained historically by large-scale disturbances such as fire. The effect of habitat loss will likely be more severe than the changes in habitat configuration that will result as logging proceeds in the boreal mixedwood region. Stand-level management recommendations regarding cut-block design and proximity will only influence barred owl habitat selection in the short term. Therefore, it seems appropriate to manage barred owl habitat at the landscape scale, if the long term objective is to provide suitable habitat for the barred owl. Maintaining barred owl populations will be accomplished if forest managers are successful at preserving the natural forest age distribution of the landscape. Long term monitoring of barred owl populations will be necessary in order evaluate our progress towards accomplishing this goal.

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CHAPTER 4

Barred owl (*Strix varia*) cavity tree and breeding habitat patch characteristics

4.0 Introduction

The barred owl (*Strix varia*) is presumed to be an indicator of old-growth biological communities in the boreal ecoregion because of its association with late-successional forest (James 1993, Mazur *et al.* 1998). As a result, recent studies have quantified its breeding habitat in order to provide recommendations for forest management (Van Ael 1996, Takats 1997, Mazur 1997). In Alberta, the boreal mixedwood forest constitutes 40% of the forested landbase (Rowe 1972), and little is known about the breeding habitat requirements of owls in this region (Court and Hannon 1995). Most of the merchantable forest in northern Alberta has been allocated for commercial timber harvesting, and concern has now focused towards determining the implications for many endemic wildlife species (Cumming *et al.* 1994), including the barred owl.

The availability of large diameter trees and snags is an important factor in determining barred owl nest site selection, since barred owls do not construct their own nests (Johnsgard 1988). Secondly, the large body size of the barred owl prevents it from using cavities produced by primary cavity excavators, unlike smaller cavity nesting species. In the boreal mixedwood forest, hardwood trees that become hollow from heart-rot disease provide suitable barred owl nesting cavities. Since old mixedwood stands have a high density of large diameter hardwood snags (Lee *et al.* 1995, Lee 1998) these areas represent an important source of natural nesting sites for the barred owl.

Previous studies have quantified barred owl nest tree dimensions, but only a few have examined nesting habitat relative to the surrounding forest (Hanley 1997, Mazur *et al.* 1997). Since owls may perceive suitable habitat in terms of the 'nest-patch' instead of the 'nest-tree', it is important to consider vegetation structure at various spatial scales. The distinction between 'nest-tree' and 'nest-patch' characteristics has significant implications for management because owls may avoid suitable nesting sites that are located in sub-optimal habitats.

The objective of this study was to characterize barred owl nesting habitat at several spatial scales in the boreal mixedwood forest. I examined the vegetation characteristics of barred owl cavity trees and the surrounding forest (0.28 ha) in relation to reference areas within owl home ranges and the landscape. Secondly, I examined habitat composition and patch dimension of owl cavity tree areas using forest inventory data and geographic information systems (GIS). The results provided information regarding nesting habitat composition and configuration which can be used to manage barred owl habitat in the boreal mixedwood forest.

4.1 Methods

4.1.1 Study Area Location and Site Description

This study was conducted near Calling Lake, Alberta (55° 15' N, 113° 19' W). The study area is approximately 40 km x 20 km and is located in the boreal mixedwood ecoregion. The boreal mixedwood ecoregion is the transition between the aspen parkland to the south and the boreal northlands (Strong and Leggat 1992). It covers 290 000 km^2 of aspen (*Populus tremuloides*), poplar (*Populus balsamifera*), white spruce (*Picea glauca*), jack pine (*Pinus banksiana*), and black spruce (*Picea mariana*) and mixedwood forest types. These distinct vegetation communities constitute 95% of the forested land base in the boreal mixedwood region (Cumming *et al.* 1994).

The boreal mixedwood ecoregion is characterized by a heterogeneous arrangement of forest stands differing in age and species composition. This heterogeneity is the result of catastrophic fires and defoliating insect outbreaks (Bonan and Shugart 1989). Disturbances such as fire produce optimal conditions for pioneer species such as aspen to predominate in the early seral stages. Primary succession by aspen and poplar on mesic sites is followed by white spruce / mixedwood predominance in old-growth areas (Strong and Leggat 1992). Lowlands are predominantly black spruce and jack pine is typical on xeric upland sites (Strong and Leggat 1992).

4.1.2 Radio Telemetry

Barred owl nests were located during the breeding season (April –May) by walking-in on radio-collared individuals (see section §3.1.2). At three of the nest locations, I radio-collared five juveniles after fledging. In 1997, the juveniles were located once as week from June to August (1997) in order to monitor their pre-dispersal movements. Nest locations and juvenile positions were determined using a Trimble *Geo*Explorer® geographic positioning system (GPS). All GPS locations were differentially corrected using PFINDER software (Trimble Navigation Ltd.). The GPS positions were differentially corrected in order to ensure that the accuracy of each location was within 2-5 m (P. Gallupe, pers. comm.).

4.1.3 Microhabitat Vegetation Sampling

Vegetation was sampled at each owl cavity tree and at three reference areas within the home range. Three reference plots were located at least 200 m apart along a transect starting from the owl cavity tree. The direction of the transect was randomly chosen, but the reference plots had to be suitable or potential cavity trees (> 34 cm dbh) that were unoccupied by owls. At each location, four 0.04 ha plots were used to sample the vegetation. One plot was centered on the cavity tree and the others were placed 30m away at 120°, 240° and 360°. The following characteristics of the cavity trees were measured: diameter at breast height (dbh), tree height, cavity entrance height, and percent lean. Within the 0.04 ha plots, I recorded the number of live trees, standing dead trees (snags) and fallen dead trees (coarse woody debris). Standing trees were recorded as the total number of each species in four diameter classes (8-15, 15-23, 23-38, >38cm). Basal area of trees was calculated using the median radii for each diameter class (5.75, 9.5, 15.25 and 21.5cm) in the equation:

[1] $$BA = \Sigma (N_i \bullet r_i^2 \bullet \pi)$$

whereby N_i is the number of stems in diameter class i, and r_i is the median radius of diameter class i. For snags (>12 cm dbh) I recorded tree species, dbh, height and percent lean. For coarse woody debris (fallen trees >11 cm dbh) we recorded tree species and length. Tree, snag and coarse woody debris densities were calculated for each site by dividing by the total plot area (0.16046ha). Shrubs were sampled in a 0.008 ha sub-plot nested within each 0.04 ha plot. Species and numbers of saplings (<2.5 cm) and poles (2.5-8 cm) were recorded. Shrub densities were calculated for each site by dividing by the total sub-plot area (0.0314159 ha). The physical stratum was estimated for each site by measuring the tallest shrub height, subcanopy height and canopy height using a clinomenter. Canopy cover was determined, using a spherical densiometer, as the average of four readings in each cardinal direction. Physical stratum and canopy cover were determined for each site based on readings from the centre plot.

Differences in vegetation characteristics between owl cavity trees and reference trees were initially explored using non-parametric measures of central tendency (Mann Whitney *U*). Multivariate analysis was used to determine which habitat characteristics could discriminate owl cavities from reference areas. The original list of vegetation descriptors was reduced to eight variables that were not serially correlated ($r < 0.8$). Logistic regression was used because the dependent variable was dichotomous (1 or 0) and no assumptions had been made about the distribution of the predictor variables. In order to assess the contribution of each vegetation descriptor to the multivariate model, Wald's chi-square statistics were examined. Model significance was determined by the log-likelihood chi-square statistic, presence/absence classification accuracy (logistic cut point of 0.5), and the Hosmer-Lemeshow goodness-of-fit test (Rabe *et al.* 1998). Positive regression coefficients suggest that an increase in the descriptor variable represents an increase in likelihood of owl cavity presence. Conversely, negative values suggest a decrease in the variable represents a decrease in the probability of owl occupancy (Rabe *et al.* 1998). For each independent variable, the probability of entering the logistic model was set at α 0.05 and variables were removed at α 0.1.

Landscape vegetation data was collected during a previous study (M. Norton pers. comm.). The landscape vegetation plots ($n = 36$) were located in upland areas of predominantly old (100+ y) and mature (60-100 y) forest. Sampling procedures were consistent with the protocol established for our study area (Schmiegelow and Hannon 1993; see previous section §4.1.3 Microhabitat vegetation sampling). In the owl study an additional vegetation plot was added at the owl nest tree. Since only 3 vegetation plots per site were used in the landscape study, the centre plot was removed from the owl data to compare the cavity tree areas and home range reference areas with the landscape plots. First I calculated snag frequency within each diameter class at owl nest locations, home ranges, and the landscape. Second, I compared the density of potential nest trees (snags > 34cm dbh) at each of the spatial scales using single-factor ANOVA, and detected pair-wise differences with multiple *t-tests*.

4.1.4 Landscape Pattern Analysis

A landscape classification was produced from digital forest inventory data using Arc/Info® GIS. The landscape classification contained fifteen habitat categories (see section §3.1.3). Forest cover was then classified to the level of stand age (old, mature, young) and cover type (coniferous, mixedwood, deciduous, treed bog, and clearcut). Old forest defined as stands greater than 100 y (stand origin <1891), mature forest defined stands between 60 and 100 y (stand origin 1890–1931), and young forest included all stands less than 60 y (origin >1931). Four concentric circles (12.5, 78.15, 312.57, 1227.82 ha) representing hierarchical spatial scales, centered on the cavity tree locations (n = 8), were overlaid on forest cover data. The circles represent average nonbreeding home range size (1234 ha) (Mazur 1997), average breeding home range size (314 ha), largest nest patch size (50-70 ha), and mean nest patch size (9 ha) (Olsen unpubl. data).

4.2 Results

4.2.1 Cavity Tree Characteristics

Ten owl cavity trees were located, eight in balsam poplar (*Populus balsamifera*) and two in trembling aspen (*Populus tremuloides*). Live trees (60%) were distinguished from dead trees (40%) by the presence of new growth. With the exception of one stick-nest, owls selected hollow tree cavities exclusively. Five nests were located in side-entrance window cavities, and four in top-entrance chimney cavities. Window cavities described holes which were created from broken branches, and chimneys occurred in hollow trunks of topless trees. On average, owl cavity trees were larger in diameter than reference cavity trees within the home range (Table 4-1).

Several variables were used to describe microhabitat within 0.04 ha vegetation plots at owl cavity trees and reference cavity trees (Table 4-1). Owl cavity trees were characterized by a higher density of large diameter (>34 cm) snags, greater snag basal area, and taller shrubs compared to the reference areas. A multivariate model was used to predict cavity occupancy based on eight variables describing vegetation pattern (Table 4-2). Only two vegetation descriptors were significant predictors of owl cavity occupancy. The number of large diameter snags and shrub height distinguished owl cavities from random cavities. This model accurately classified 90% of the reference sites and 40%

Table 4-1: Mean ± SE and range of the microhabitat vegetation characteristics at barred owl cavity trees and random areas within owl home ranges. Variables retained for subsequent multivariate analysis are indicated in **bold type**.

	Barred owl cavity tree		Reference cavity tree		*Statistics* ††	
	mean ± SE	range	mean ± SE	range	*U*	*P*
Cavity Tree						
Cavity tree dbh (cm)	51.6 (4.3)	33.5 - 77	42.1 (1.3)	31.0 – 60.0	86.5	0.046
Cavity height (m)	10.4 (2.1)	5.8 - 26.8	8.9 (0.9)	3.0 – 20.0	115.0	0.678
Tree height (m)	16.0 (2.6)	6.5 - 29.2	10.8 (1.3)	3.0 - 29.2	90.5	0.062
Tree lean (%)	3.8 (2.0)	0.0 – 21.0	4.1 (1.9)	0.0 - 53.0	124.5	0.432
Overstory Floristic†						
Decid basal area (m^2/ha)	22.8 (2.5)	5.6 - 30.8	19.2 (2.0)	1.5 – 41.0	111.0	0.233
Conif basal area (m^2/ha)	6.5 (3.0)	0.0 - 26.8	10.8 (2.1)	0.0 - 37.4	129.5	0.528
Small *Populus* stems/ha	216.3 (69.2)	0.0 - 604.5	281.5 (48.4)	0.0 - 916.1	122.0	0.396
Large *Populus* stems/ha	181.4 (27.0)	24.9 - 311.6	148.1 (19.0)	6.2 - 411.3	111.0	0.233
Small *Picea* stems/ha	66.7 (33.5)	0.0 - 324.1	138.4 (31.6)	0.0 - 722.9	113.0	0.259
Large *Picea* stems/ha	45.5 (24.9)	0.0 - 236.8	73.7 (16.0)	0.0 - 286.7	145.5	0.890
Small *Abies* stems/ha	26.2 (16.8)	0.0 - 155.8	63.2 (27.8)	0.0 - 604.5	146.0	0.914
Large *Abies* stems/ha	7.5 (5.3)	0.0 - 49.9	2.3 (1.1)	0.0 - 24.9	140.5	0.770
Understory Strata¥						
Shrubs (10^3/ha)	3.9 (0.7)	1.1 - 9.1	3.5 (0.4)	0.5 - 8.8	136.5	0.678
Saplings (10^3/ha)	3.0 (0.7)	0.9 - 8.3	2.8 (0.3)	0.3 - 8.6	148.0	0.963
Poles (10^3/ha)	0.9 (0.2)	0.2 - 2.6	0.8 (0.2)	0.0 - 3.7	126.0	0.469
Shrub height (m)	4.4 (1.02)	0.0 - 9.2	2.5 (0.6)	0.0 - 9.8	95.5	0.089
Coarse woody (m^3/ha)	22.4 (6.2)	3.1 - 66.4	18.6 (2.7)	0.9 - 59.5	134.0	0.634
Overstory Strata‡						
Canopy cover (%)	68.4 (4.7)	39.0 - 86	65.2 (3.4)	22.0 - 87.0	138.0	0.837
Canopy height (m)	24.9 (0.9)	20.4 - 29.2	24.6 (0.9)	16.0 - 35.2	136.0	0.678
Sub-canopy height (m)	8.5 (2.6)	0.0 -19.6	9.1 (1.5)	0.0 - 22.8	142.0	0.818
Snag basal area (m^2/ha)	7.0 (1.2)	1.8 - 14.7	4.7 (0.4)	0.1 - 8.9	98.0	0.109
Large snags/ha	25.6 (6.1)	0.0 - 56.1	9.6 (2.0)	0.0 - 43.6	68.5	0.009
Small snags/ha	72.9 (20.7)	6.2 - 236.8	97.4 (11.0)	6.2 - 236.8	106.0	0.177

† Small stems are > 8 cm and ≤ 23 cm dbh, large stems are > 23 cm dbh.
‡ Small snags are > 12 cm and ≤ 34 cm dbh, large snags are > 34 cm dbh.
¥ Saplings < 2.5 cm and poles are 2.5 - 8 cm dbh. Shrub density is the sum of saplings and poles.
†† Comparison of central tendency using the Mann Whitney U test statistic.

Table 4-2: Multivariate regression analysis of the microhabitat vegetation characteristics at barred owl cavity trees and random areas within owl home ranges.

(a) Microhabitat vegetation descriptors entering the model

Variable	**B**	**S.E.**	**Wald χ^2**	**Significance**	**R**
Shrub height (m)	0.2583	0.1392	3.4446	0.0635	0.1792
Large snags (no./ha)	0.0823	0.0309	7.0869	0.0078	0.3363
constant	-3.4054	1.0307	10.9151	0.0010	

(a)) Microhabitat vegetation descriptors not entering the model

Variable	**Score**	**Significance**
Cavity tree dbh (m)	1.1441	0.2848
Coarse woody debris (m^3/ha)	0.1456	0.7028
Large *Abies balsamea* (stems/ha)	0.8894	0.3456
Large *Picea glauca* (stems/ha)	0.0151	0.9023
Large *Populus* (stems/ha)	1.1392	0.2858
Snag basal area (m^2/ha)	0.18	0.8585

of the owl nests (overall model accuracy = 77.5%). The fit of the data to the logistic model was strong according the log likelihood ratio ($\chi^2 = 12.12$, $df = 2$, $p = 0.0023$).

In order to determine nest site availability at three spatial scales, I examined the density and abundance of snags at owl cavity plots, reference plots within owl home ranges, and the landscape. The size class distribution of snags followed a reversed-J shaped curve (Figure 4-1). Owl cavity tree plots had fewer small diameter snags, and a greater number of large diameter snags compared to the owl home ranges and the landscape. Assuming that the minimum diameter for a barred owl nest tree is 34 cm, the density of potential nest trees was greater at owl cavity trees than at reference areas within owl home ranges ($t = 3.87$, $df = 34$, $p < 0.001$) (Figure 4-2). The density of potential nest trees was also greater at owl cavity trees sites than at random locations in upland forest on the landscape ($t = 2.73$, $df = 43$, $p < 0.009$). The density of potential nest trees was greater within owl home ranges than within random areas of upland forest on the landscape ($t = 2.91$, $df = 61$, $p < 0.005$).

4.2.2 Cavity Tree Patches and the Surrounding Landscape

Although some nests were located far from recent clearcuts, most were within 200m and some less than 50m (Table 4-3). Owl nest patches were variable in size, but most were less than 10 ha. Owls nested in old and mature forest stands, and no nests were located in young forest stands. The age class of stands used by owls for nesting was random ($x^2 = 3.94$, $p > 0.05$, $df = 2$). Owl nested in predominately mixedwood and deciduous stands. Stand cover type was also random ($x^2 = 2.0$, p > 0.05, $df = 3$).

Landscape composition around owl nesting sites was examined at four hierarchical spatial scales. Habitat composition changed considerably as distance from nest site increased (Figure 4-3). Old forest was the most abundant cover type within 12.5 ha circles centered on the owl nest sites (Figure 4-3). The abundance of old forest habitat decreased with increasing distance from the nest. Conversely, young forest, mature forest, and treed bog increased in abundance with increasing circle dimension. Even at the largest spatial scale, old and mature forest were the predominant habitat types surrounding the owl nests, representing 25% and 30% of the total landscape area respectively (Figure 4-3).

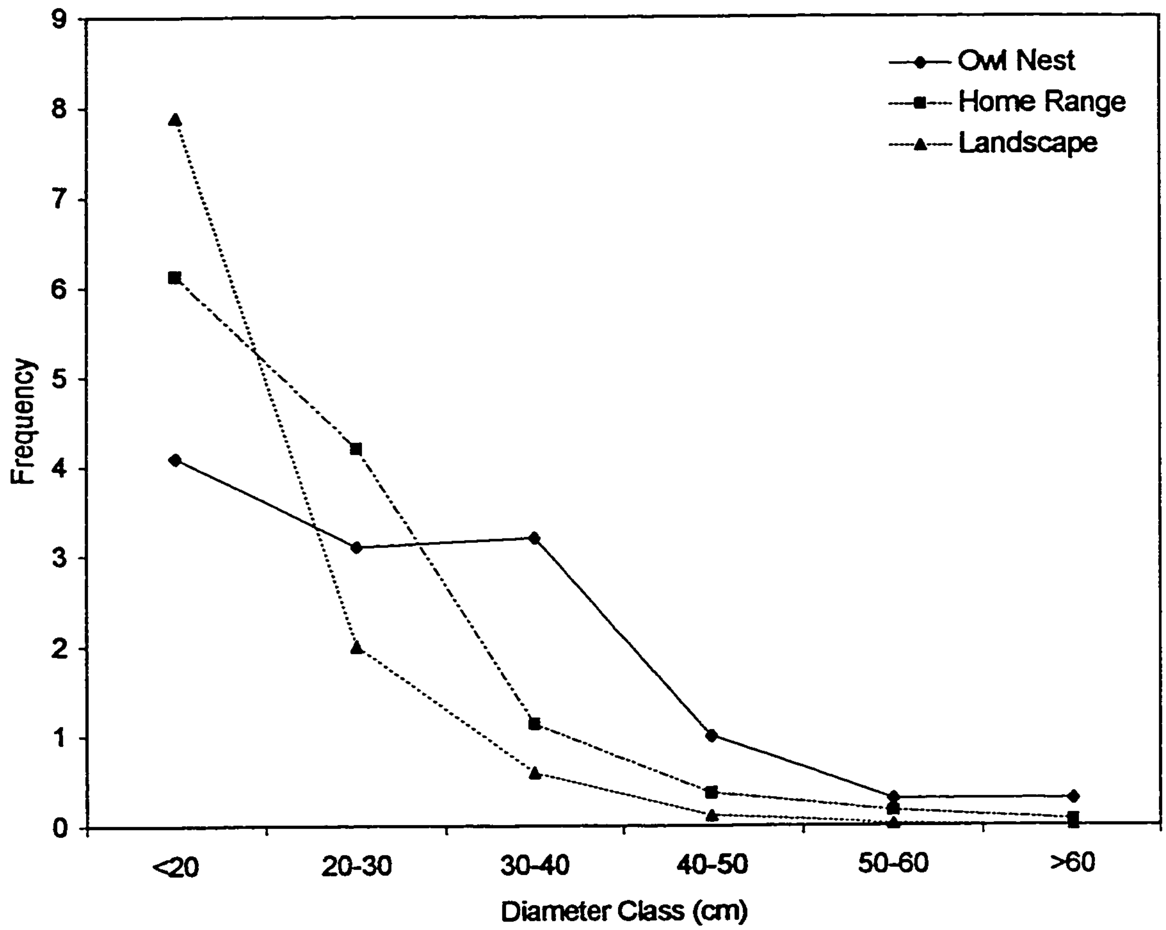

Figure 4-1: Mean size class distribution of standing dead trees (>12 cm dbh, all species combined) within four 0.04 ha plots centered on owl cavity trees (n = 9), reference areas within owl home ranges (n = 27), and upland areas on the landscape (n = 36).

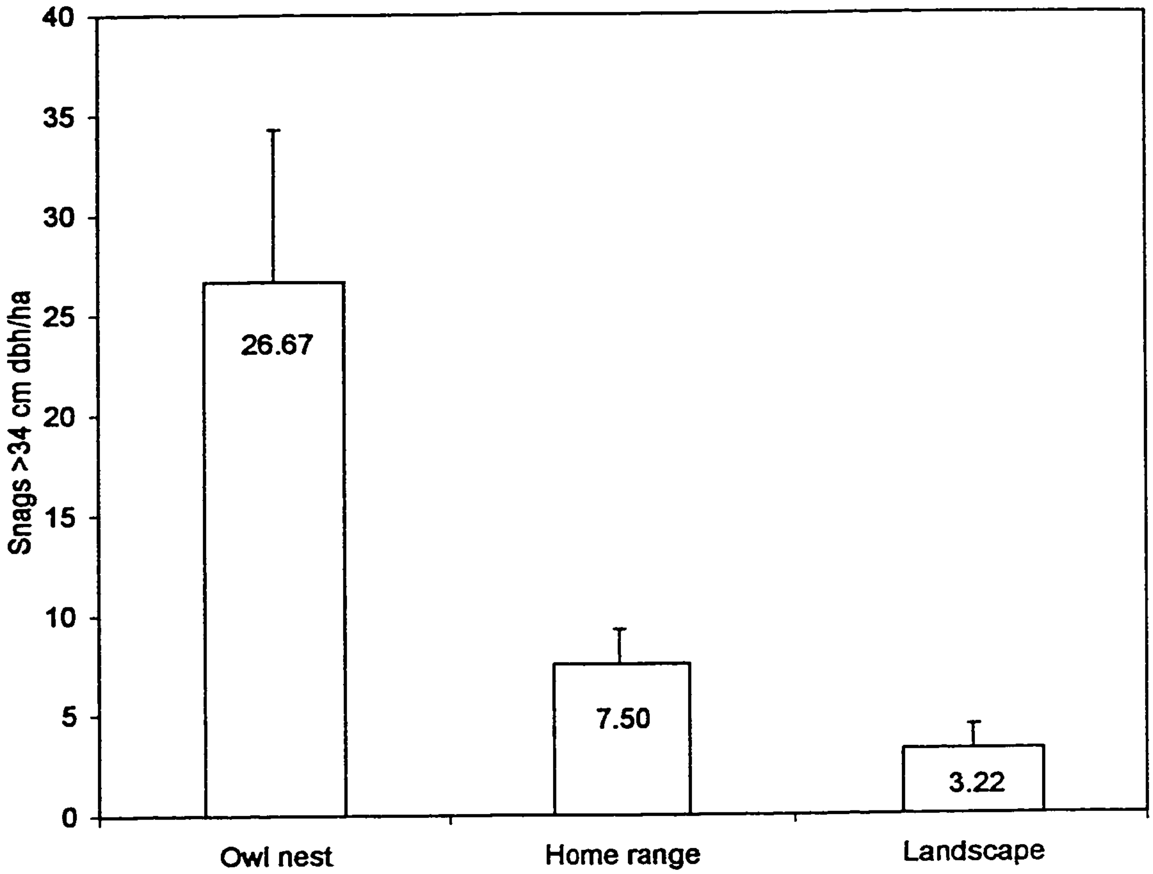

Figure 4-2: Mean + SE of 'potential nest tree' density (snags > 34cm dbh/ha) within owl cavity tree areas (n = 9), owl home ranges (n = 27) and the landscape (n = 36).

Table 4-3: Patch characteristics of owl cavity tree areas (n = 8). Age class, cover type, patch area, patch edge, patch edge / area, and distance to the nearest clearcut were calculated from owl cavity tree GPS locations overlaid on forest inventory data.

Nest ID	Age Class[a]	Cover Type	Area (ha)	Edge (m)	Edge/Area (m/ha)	Distance to CC[b] (m)
Nest #9502	Old	Mixedwood	2.2	820.7	368.0	42.5[††]
Nest #9606	Old	Mixedwood	3.4	1091.6	318.3	139.6[†]
Nest #9703	Old	Coniferous	33.7	4689.6	139.2	146.9[†]
Nest #9713	Old	Mixedwood	15.0	2801.2	186.6	37.3[‡]
Nest #9815	Old	Deciduous	9.1	1496.8	164.1	1376.0[†]
Nest #9407	Mature	Deciduous	1.7	517.3	300.8	35.0[†]
Nest #9501	Mature	Deciduous	2.8	1044.4	145.9	561.1[†]
Nest #9705	Mature	Mixedwood	44.5	7869.9	176.9	0.0[‡‡]
Median			3.6	1068.0	271.1	91.1
Mean			9.0	1672.4	261.4	292.3
Std Dev			11.0	1402.6	91.8	473.6

[a] Forest inventory stand age classes include old (> 100 y), mature (60 – 100 y), and young (< 60 y) forest.
[b] Shortest distance, in any direction, to the nearest clearcut (CC) edge. Superscripts denote the type of clearcut as follows: recent (<5 y old) aspen cutover (†), recent (< 5 y old) conifer cutover (††), historical cutover (MOF, 15 y old) (‡) and recent partial cutover (10 – 30% overstory retention) (‡‡).

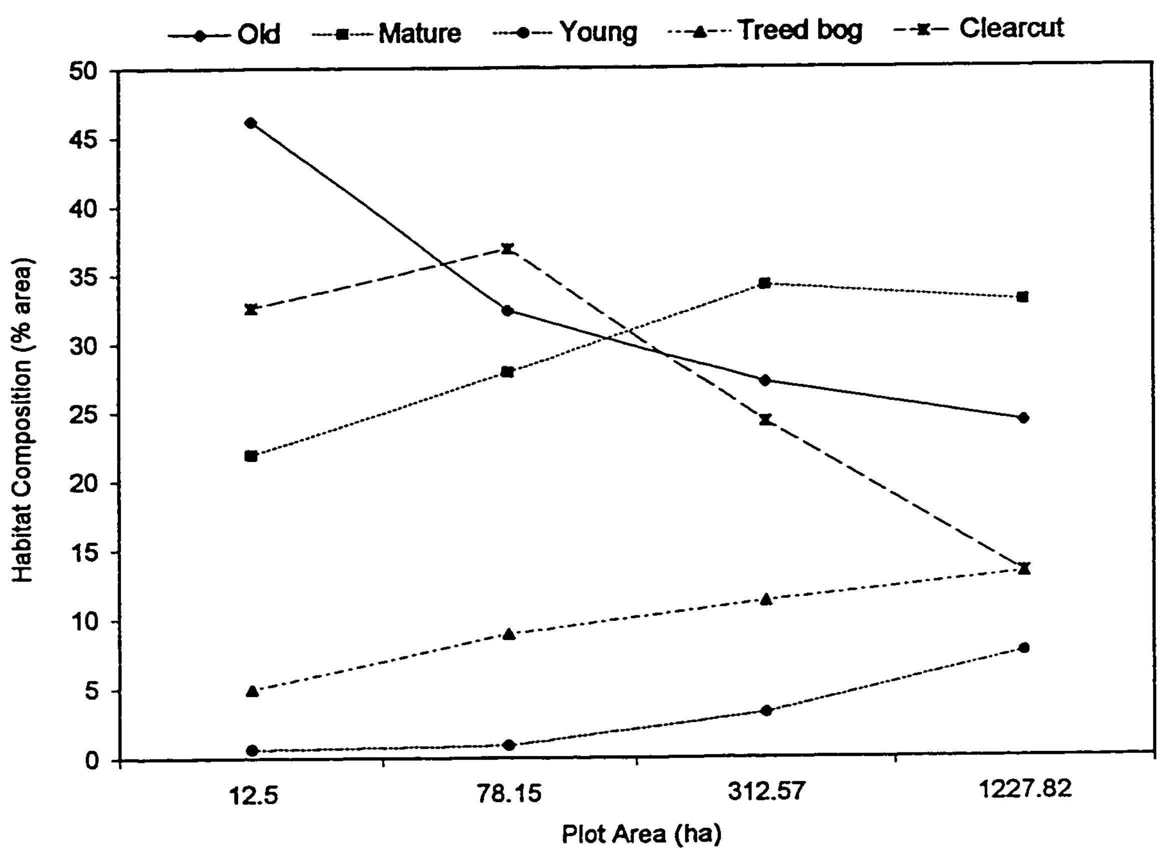

Figure 4-3: Landscape composition of old forest (100+ y), mature forest (60 – 100 y), young forest (< 60 y), treed bog and clearcut habitat within circular plots, representing four spatial scales, centered on owl cavity tree locations.

4.2.3 Pre-dispesal Movement of Juveniles

I radio-collared five nestlings at three different locations in 1997 and found that the juveniles remained close to their natal areas after fledging. At nest #9713, the average distance between weekly locations, over a ten week period, was 227.2 m (Figure 4-4). From June to August the juveniles at nest #9713 remained within the nest patch and avoided adjacent clearcut areas. Pre-dispersal home ranges averaged 19.9 ha during this period (Figure 4-4). At nest #9714, the distance between weekly locations averaged 140.6m, and the pre-dispersal home ranges (mean = 2.83 ha) were considerably smaller

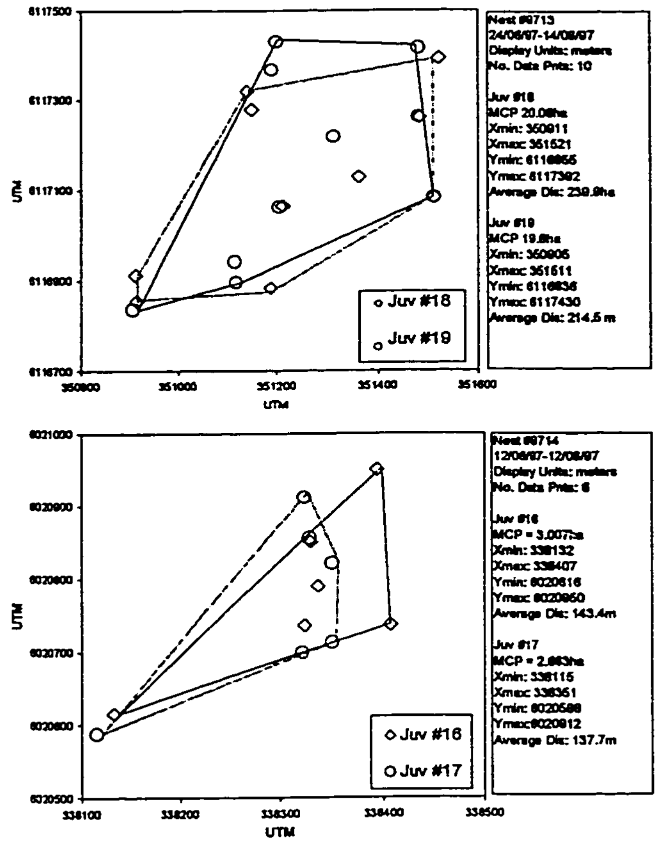

Figure 4-4: Pre-dispersal movement of juveniles at nest #9713 (top figure) and nest #9714 (bottom figure).

(Figure 4-4). We were unable to obtain geographic coordinates for the juvenile locations at the third nest, preventing any estimates of weekly movement distances and pre-dispersal home range size. However, one radio-collared young and its unmarked sibling were located within the nest patch periodically from June-August (G. Tondellier pers. comm.), confirming that barred owl juveniles consistently utilize their natal areas after fledging.

4.3 Discussion

4.3.1 Vegetation Structure

In this study, barred owls nested in trembling aspen and balsam poplar trees exclusively. Similarly, Takats (1997) reported six cases of barred owls occupying balsam poplar trees in west-central Alberta. Although poplars are the predominant nest tree for barred owls in the boreal forest, Mazur *et al.* (1997) found that white spruce and paper birch sometimes provide suitable nesting sites. Barred owls use poplar trees because hardwoods have a tendency to decay quickly and remain standing when rotten. Conifer trees live longer and often become uprooted (Peterson and Peterson 1992) instead of breaking and becoming snags, and seldom form cavities from broken branches. Furthermore, aspen and poplar are the predominant snag species in the boreal mixedwood forest, representing 69-91% depending on age of the stand (Lee 1998).

The habitat immediately surrounding barred owl nesting areas was characterized by a high density of large diameter snags. The density of potential nest trees (snags > 34 cm dbh) was considerably lower within the home ranges, suggesting that barred owls select breeding areas within the home range based on snag availability. Furthermore, the low density of potential nest trees on the landscape implies that suitable nesting sites are typically scarce in this region. Our findings corroborate those of Hanley (1997), who reported that large (>43 cm) snag density and snag basal area discriminated barred owl breeding areas from nonbreeding sites.

Hanley (1997) concluded that barred owls select areas with the highest density of large diameter snags in order to "localize reproductive effort within a small subset of the owl's home range". Barred owls select nesting areas based on snag density for two reasons. First, barred owl snags are susceptible to blowdown (Olsen unpubl. data). In Saskatchewan Mazur *et al.* (1997) reported as many as 20% of the barred owl nests had fallen over during the three year study period. In this study, one barred owl nested in a snag which was so weak it fell over before the nestlings had a chance to evacuate. Stands with the highest density of large diameter snags provide the greatest potential for a suitable nesting site from year to year. The second reason for the barred owl's preference of stands with high structural diversity can be attributed to predator avoidance. Areas with a high density of potential nesting sites may offer protection from nest predators (Martin and Roper 1998) since nest predators are less effective in areas with more spatial heterogeneity (Bowman and Harris 1980). In smaller owl species, such as the Tengmalm's owl, mammalian nest predation can be reduced be nest relocation (Sonerud 1989).

If cavity trees are limited, barred owls may locate an alternative site for nesting. Records of barred owls using abandoned hawk and squirrel nests are prevalent (Bent 1938, Mazur *et al.* 1997), but less common are instances of ground nesting (Robertson 1959) and one report of a natural hole in an earthen bank (Shakelford 1996). On one occasion in this study, a stick-nest was used after the cavity tree was destroyed by logging. The presence of barred owls in platform-type nests suggests that cavities may be preferred by the owls, but are not essential for breeding. However, recent evidence provided by Postuplasky *et al.* (1997) has shown that reproductive success from cavities is considerably greater than platform nesting sites. The barred owl can be considered an obligate cavity nester because it requires cavity type structures for successful breeding, and the presence of barred owls in platform-nests is one indication that natural tree cavities are in short supply (Postpalsky *et al.* 1997).

Suitable cavity trees are likely limited due to several factors. First, territorial behavior reduces the number of suitable nesting sites available to non-territorial individuals which would otherwise be capable of breeding (Newton 1979). Because barred owls procure large areas of suitable habitat within their breeding home ranges, and exclude conspecifics through territorial interactions, natural nesting sites may be limited through intraspecific competition. Second, forest harvesting practices can have both direct and indirect effects on nest site availability. Habitat loss results as the number of suitable and potential nest trees are removed during forest harvesting operations. The indirect effect of habitat loss results from competition with other cavity nesters including tree climbing mammals, woodpeckers, and other owls species capable of colonizing fragmented woodlands after harvesting. Because barred owl cavities are naturally rare, and are limited through territorial behavior, forest harvesting will have a negative effect on nest site availability unless suitable and potential cavity trees are provided in adequate numbers and dispersion for breeding owls within landscapes managed for timber production. However, not all large diameter trees form suitable cavities. Measures of cavity production and recruitment will be necessary in order to predict cavity tree availability at various stages of forest succession.

4.3.2 Habitat Pattern

Several authors have suggested that the barred owl is sensitive to anthropogenic disturbance (Bosakowski *et al.* 1987) and requires extensive tracts of undisturbed forest (Laidig and Dobkin 1995). Therefore, I predicted that barred owls would nest in large patches far from disturbed areas and forest clearings. Although some nests were far from clearcuts, most were within 200m. One nest was located immediately adjacent to a partial-cut where large diameter trees and snags had been left after harvesting. Devereux and Mosher (1984) reported that barred owl nests were closer to forest clearings than random sites. In Saskatchewan, some barred owl nests were located as close as 25m to roads, while others were as far as 2km.

Previous studies have described barred owl nest trees qualitatively (Leder and Walters 1980) and quantified cavity tree dimensions, but few have considered the patch in which the nest was located. The distinction between nest tree selection and nest patch occupation is an important one, since barred owls may avoid suitable nest trees if they are located in sub-optimal habitats. For example, some woodpecker species will inhabit cavity trees that are left in cut-blocks after logging. However, I found no evidence of this in the literature pertaining to barred owl nesting habitat.

Patches used by barred owls for nesting were typically small (< 50 ha), with a minimum patch size of 1.7 ha. The smallest patch used for nesting was a 'habitat island' of mature deciduous forest, isolated from adjacent habitat by at least 200m through experimental logging (Schmiegelow and Hannon 1993). In another case, clearcut logging isolated a 15 ha patch that was also used for nesting. In both these examples the owls nested successfully, but the nest patches were abandoned the following year. Since our estimates of nest patch size were derived from forest inventory data, the patches do not necessarily represent habitat from the owls perspective, and may underestimate the actual size of patches selected for nesting. However, the two previous examples suggest that these estimates of minimum, mean and maximum nest patch size have a great deal of interpretive value when considering nesting areas surrounded by clearcutting.

Generally, barred owls avoid single, isolated stems and prefer clumps of over-story trees and snags for nesting (Devereux and Mosher 1984). Since the young are flightless when they leave the nest, owlettes will climb adjacent trees using their beaks and talons. Small sticks leaning against larger trees (*i.e.* 'leaners') often provide a means for the young owls to reach an elevated perch. Once atop its perch, a young owl can practice flying by jumping from the branch and climbing up again. However, I have only noticed this behavior on one occasion, and it is more typical for a young owls to remain in the same tree, close to the trunk, under branches and concealed from view. I have noticed that barred owl fledglings use large diameter white spruce trees because these trees have many lower branches which make them easier to climb. Furthermore, white spruce provides suitable shade and cover under the dense branches, which may be important for predator avoidance. Once they have found a suitable roost, young owls will remain there, sometimes for several days, until their flight feathers have developed.

Barred owl young leave the nest at an early age (28-35 days, Bent 1938), but remain within the natal area during the pre-dispersal stage of development. Even after the young can fly, the adults continue to feed and protect them for several months (Dunstan and Sample 1972, Bird and Wright 1977). Barred owl young maintain relatively small pre-dispersal home ranges, and individuals remain close to one another for most of the summer. Although, old-growth forest has been well established as an important source of natural nesting sites for the barred owl (Hanley 1997, Mazur *et al.* 1997), this particular habitat type may also provide suitable prey and cover required by juveniles prior to dispersal. Future studies should examine barred owl reproductive success, juvenile mortality and foraging behavior in relation to prey availability, habitat composition and patch/landscape configuration in order to determine the influence of habitat pattern on barred owl breeding ecology.

4.4 Conclusion

The predominance of old-growth forest surrounding barred owl nest sites is consistent with other investigations of this species at similar spatial scales (Hanley 1997, Mazur *et al.* 1997). In the boreal mixedwood forest of Alberta, snag density increases proportionately with stand age (Lee 1998). Therefore the association between barred owls and old-growth forest can be explained, in part, by its preference for areas with a high density of large diameter snags, and not an affinity for old-growth forest per se. For example, barred owls will readily occupy young forest stands when nest boxes are provided (Elderkin 1987). However, because old mixedwood stands are an important source of natural nesting structures in the boreal forest, these areas represent critical barred owl habitat during the breeding period (Mazur *et al.* 1998).

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5.0 Thesis Conclusions

In this study, barred owls maintained relatively large (100-600 ha) breeding season home ranges, which was consistent with other investigations of this species (Mazur *et al.* 1998, Nicholls and Fuller 1987, Elody and Sloan 1985). Habitat composition within the home ranges was variable, but most owls selected old (100+ y) deciduous, mixedwood and conifer forest, and avoided young (< 60 y) forest. Mazur *et al.* (1998) concluded that specifically 'old mixedwood forest' characterized barred owl breeding habitat in the boreal forest of Saskatchewan. However, there was no indication that mixedwood forest was selected over deciduous, and conifer types, at the home range scale in this study. Within the home ranges, owls used a variety of habitat types for foraging and roosting. Only mature deciduous forest was used greater than expected, while old mixedwood forest was used less than expected based the availability of these habitat types within the home ranges. Barred owl habitat composition can be described generally as mature (60-80 y) and old (100+ y) upland forest within our study area. Furthermore, owl habitat selection is likely a function of physiognomic stand characteristics (age, structural complexity and overstory density) rather than floristic stand characteristics such as tree species composition (*i.e.* % deciduous, mixedwood and conifer).

Since previous studies have indicated the importance of large, contiguous tracts of forested habitat (Bosakowski *et al.* 1987), I tested the hypothesis that barred owls selected foraging and roosting patches based on patch size and composition. The results corroborated my previous findings that owls used mature forest disproportionately compared to old, young and non-forest which were used randomly at this scale. However, a strong patch size effect was observed, suggesting that foraging and roosting habitat use was primarily influenced by extent (*i.e.* patch size) rather than patch composition (*i.e.* habitat type). Since owls selected large patches (10+ ha) over smaller patches, one is tempted to presume that owls are selecting for interior forest habitats. However, patch size alone does not indicate whether patches contain more or less edge, since large patches may be more fragmented if the amount of edge habitat is not held constant. Therefore, it is likely that owls were selecting patches based on the amount of habitat available, and no assumptions can be made about patch configuration or degree of fragmentation based on the results at this scale.

Breeding habitat selection is a function of availability, since owls do not construct their own nesting sites. Barred owls in this study selected large diameter cavity trees within patches of predominantly old and mature forest. Cavity tree patches were characterized by a higher density of large diameter snags, compared to random areas within home ranges and reference areas on the landscape. If suitable nesting sites are limited, barred owls would benefit from maintaining exclusive breeding territories with a high density of large diameter trees and snags for two reasons. First, areas with a high density of suitable cavity trees offer the greatest probability of a suitable nest site from year to year, if snag recruitment rates are low. Secondly, nest depredation can be lower areas with greater structural diversity, resulting in increased reproductive success. Since old forest stands are structurally diverse (Lee 1998), and contain a high density of suitable nesting sites, these areas represent critical breeding habitat for the barred owl.

The landscape in this study was predominantly forested, and less than 6% of the total area has been removed by logging (Appendix 3-7) to date. Therefore, the results from this study might not be representative of a forested landscape which is managed for timber production. However, after the second pass, mature and old forest stands adjacent to current cutblocks will be removed, creating a mosaic of young cutovers (< 9 years old) interspersed with recent clearcuts. Forest composition after the second pass of harvesting will be very different than the pre-harvest boreal mixedwood mosaic. After the second pass, forest stand age distribution and species composition will be more representative of a landscape managed for timber production compared to the current first pass condition. Following the second pass of harvesting, changes in habitat composition will be substantial, and continued effort should be made to monitor owl populations during this period.

5.1 Management Implications and Research Directives

Management recommendations pertaining to barred owl habitat have indicated the importance of large diameter trees and snags that contain cavities, as well as the retention of mature trees in harvested areas (Forsman and Bull 1989). Petersen (1985) advocated selectively cutting hardwoods in order to provide potential barred owl nest sites in intensively managed areas as forest regeneration proceeds. However, partial cutting with 10-50% overstory retention increases habitat suitability for the great horned owl (Bosakowski *et al.* 1987), which can result in increased depredation of barred owl adults and young (Laidig and Dobkin 1995). Therefore, these and other silvicultural practices must evaluated before prescribing management guidelines for the barred owl. Furthermore, information regarding the seral stage of owl recolonization should be addressed in order determine the effectiveness of partial cutting and other silvicultural practices. The importance of large diameter trees and snags was been well established, however further research is need to determine if nest site availability is a limiting factor in the breeding ecology of the barred owl. For example, barred owls are known to use platform nests when cavities are unavailable, however productivity from these sites is often negligible compared to natural tree cavities (Postupalsky *et al.* 1997).

The emphasis of barred owl habitat preservation and enhancement has primarily focused on the retention of large diameter trees, and little consideration has been directed towards the importance of habitat patches. Patches of old-growth character trees within the managed forest could advance the recolonization process (Bosakowski 1991) if owls perceive these areas as suitable nesting habitat soon after harvesting. Furthermore, patches of young and mature forest must be provided in order allow snag recruitment processes to occur as regeneration proceeds in the managed forest. Future research should consider the spatial arrangement of young, mature, and old forest patches in relation to nesting habitat suitability, reproductive success, and cavity tree production. Long-term studies of snag production and recruitment at various stages of forest succession should also consider cavity tree demographics because not all large diameter trees and snags become suitable for secondary-cavity nesting owls. Estimates of cavity production, recruitment, and blowdown will be necessary in order to predict cavity tree availability at various stages of forest succession and under different harvesting regimes and silvicultural practices.

The barred owl is considered to be a management indicator species in eastern North America (USDA 1985, 1986) and western Canada (James *et al.* 1995). Given its affinity for mature and old growth forest, this species could be used to determine the minimum area requirements of old-growth biological communities in the boreal ecoregion (James 1993). Since barred owl home range size can vary from 600 ha in the breeding season to 2000+ ha in the nonbreeding period (Mazur 1997), large areas of old forest will be important for maintaining barred owl habitat on the landscape. Recognizing the inherent variability of stand age and species composition in the boreal region, a system of floating reserves (Cumming *et al.* 1996) seems appropriate for managing wildlife species associated with later-successional forests. If these areas are harvested on an extended rotation (120 y), rather than a fiber-maximization period (60-80 y), habitat suitability for old-growth obligate species will be maintained. Finally, habitat management for the barred owl, or any other endemic wildlife species cannot occur in isolation. Longer term monitoring of the barred owl, and other potentially sensitive avifauna will provide a benchmark for which to evaluate our management practices in the boreal mixedwood region.

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Appendices

Appendix 3-1: Barred owl radio-collaring and tracking information.

Fifteen adult and five juvenile barred owls were captured and marked with radio-transmitter devices (Table 1). One female barred owl (#9402) was tracked from 19 June to 18 August, 1994. Owl #9402 was depredated by a great horned owl sometime between 10 October 1994 and 4 February 1995. Another female (#9504) replaced this owl in the spring of 1995. Owl #9504 was trapped from the nest cavity on 20 May 1995. Owl #9504 was depredated by a great horned owl shortly after the bird was radio-collared. Radio tracking continued on a less intensive basis form November 1995 to March 1996. During this period we monitored the winter movements of owls #9501 and #9503.

From May to August, 1996 we tracked five male (#9501, #9606, #9607, #9609, #9610) and three female (#9503, #9605, #9608) barred owls. Owl #9608 was depredated by a great horned owl early in the radio-tracking period. Owl #9606 shed its radio-collar two weeks into the tracking period, shortly after leading us to the nest site that contained at least one chick on 31 May 1996.

Owls #9611, #9712, #9713, #1915 were tracked from May to August 1997. In the 1997 breeding season we focused our attention on the pre-dispersal movements of five juvenile barred owls at three different nesting sites. During this period we obtained locations from juveniles at Tawatina (#9716, #9717), Calling Lake (#9718, #9719), and Lac La Biche (#9720).

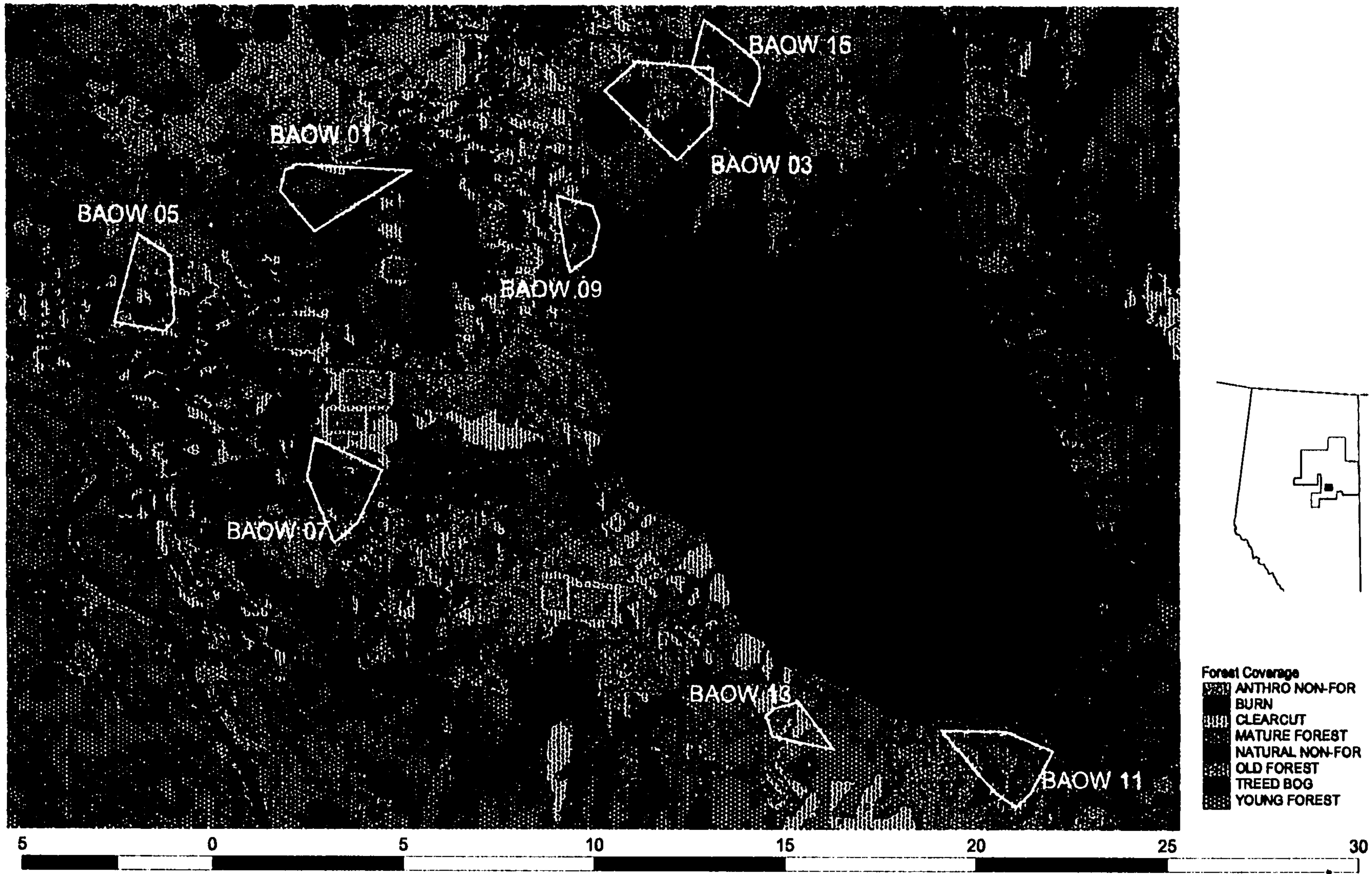
Table 1. Record of radio-collared barred owls in this study.

Owl-ID[a]	Sex[b]	Location	Status	Date Captured	Method[c]	# relocations
#9501	M	BOG ROAD		14-4-95	MN	30
#9402	F	GROUSE ROAD	depredated	17-6-94	DL	23
#9503	F	TOWER ROAD		12-6-95	DL	28
#9504	F	GROUSE ROAD	depredated	20-4-95	HN	
#9605	F	QUINN CREEK		10-2-96	HN	31
#9606	M	WEST ROAD		12-5-96	DL	12
#9607	M	LONG LAKE		16-5-96	MN	27
#9608	F	SOUTH CAMP	depredated	28-5-96	MN	7
#9609	M	WOLF ROAD	depredated	28-6-96	MN	24
#9610	M	TOWER ROAD		3-7-96	DL	29
#9611	M	PARK		8-8-96	MN	17
#9712	M	HUSKY ROAD		3-4-97	MN	11
#9713	F	1000 ROAD		14-4-97	MN	10
#9714	F	TAWATINA		13-5-97	HN	
#9715	F	PELICAN CRK		5-6-97	MN	23
#9716	J	TAWATINA		27-5-97		6
#9717	J	TAWATINA		27-5-97		6
#9718	J	1000 ROAD		12-6-97		10
#9719	J	1000 ROAD		12-6-97		10
#9720	J	LAC LA BICHE		13-6-97		12

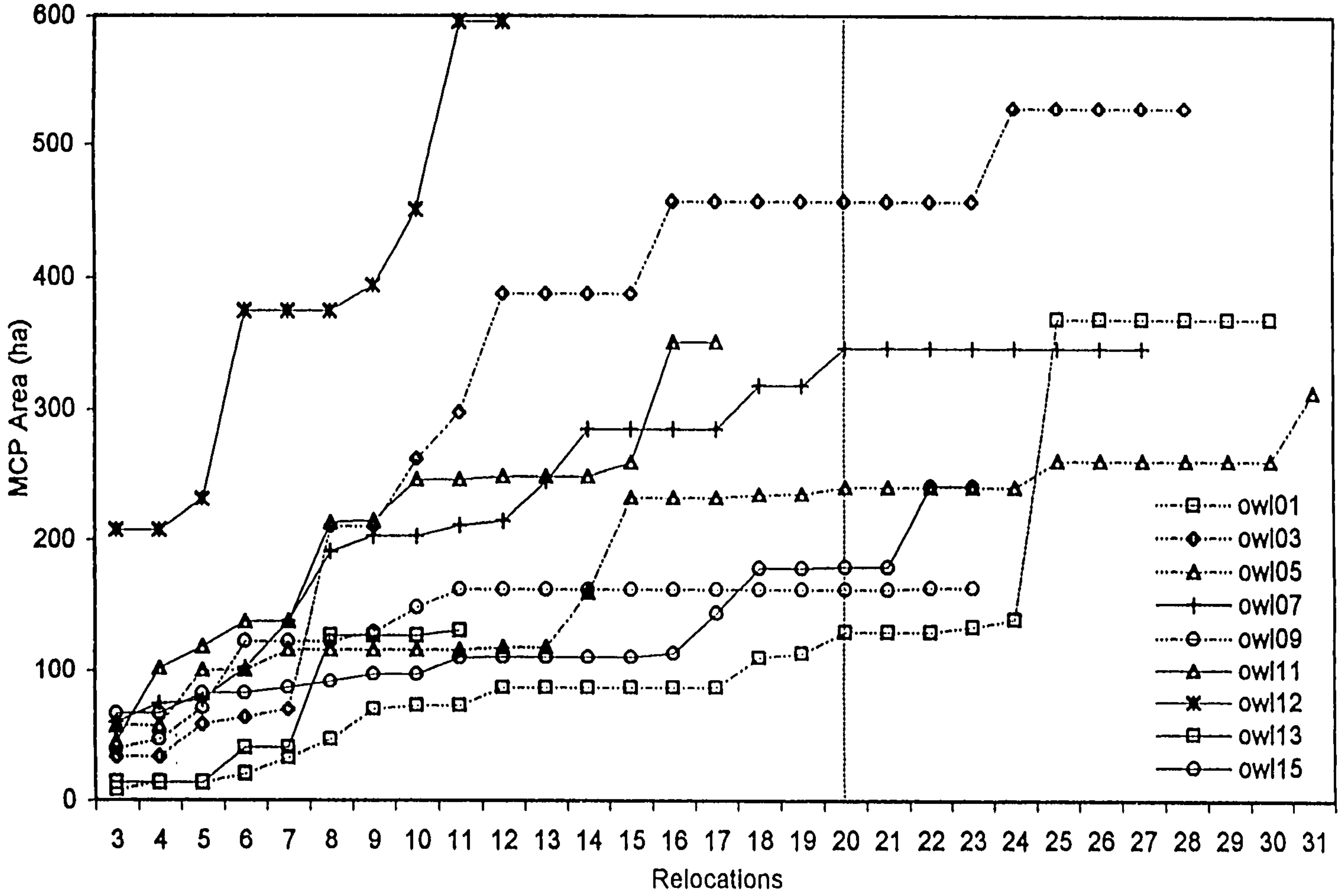
[a] first two digits in the owl-id correspond to the year that the bird was captured

[b] (M)ale, (F)emale and (J)uvenile

[c] Mist net (MN), modified Swedish goshawk drop trap (DL), hand net (HN)



Appendix 3-2: Barred Owl minimum convex polygon (MCP) home ranges within the Calling Lake study area.



Appendix 3-3: Minimum Convex Polygon (MCP) home range size relative to the number of relocations per individual.

Appendix 3-4: Habitat composition of the landscape (3-4c), owl home ranges (3-4b) and the proportion of relocations in each habitat type (3-4a).

a). % of the owl relocations in each habitat type.

OWL-ID	OldCon	OldDec	OldMix	MatCon	MatDec	MatMix	Young	TrBog	CCut	Wetland
BAOW01	0.00	0.00	6.67	0.00	40.00	0.00	0.00	30.00	0.00	23.33
BAOW03	22.22	3.70	0.00	7.41	18.52	14.81	0.00	25.93	3.70	3.70
BAOW05	9.68	0.00	9.68	3.23	48.39	0.00	0.00	0.00	25.81	3.23
BAOW07	3.70	0.00	11.11	7.41	55.56	11.11	0.00	7.41	3.70	0.00
BAOW09	8.33	12.50	16.67	4.17	8.33	12.50	8.33	16.67	0.00	8.33
BAOW11	47.06	5.88	0.00	5.88	23.53	0.00	0.00	5.88	0.00	11.76
BAOW12	50.00	12.50	0.00	12.50	0.00	0.00	0.00	12.50	0.00	12.50
BAOW13	0.00	40.00	0.00	0.00	0.00	0.00	30.00	0.00	20.00	0.00
BAOW15	16.67	0.00	0.00	12.50	54.17	0.00	0.00	12.50	0.00	4.17

b). % of the MCP home ranges.

MCP-ID	OldCon	OldDec	OldMix	MatCon	MatDec	MatMix	Young	TrBog	CCut	Wetland
MCP01	1.27	1.37	0.77	11.34	29.04	1.94	0.83	28.85	5.4	19.18
MCP03	24.97	7.55	14.06	4.37	9.15	3.17	0.01	29.77	3.33	3.63
MCP05	8.26	0.72	12.68	4.37	42.6	4.38	1.58	7.46	16.21	1.73
MCP07	1.07	3.32	6.7	6.53	30.86	9.67	4.00	6.42	9.54	21.87
MCP09	8.9	11.98	13.33	15.96	9.14	7.12	7.72	17.70	4.5	2.56
MCP11	10.65	25.48	5.72	0.66	39.13	0.01	2.33	1.02	0.01	6.36
MCP12	26.95	13.31	11.84	1.51	0.67	11.96	0.01	24.38	0.01	7.71
MCP13	6.33	10.12	10.05	0.01	0.01	0.01	31.34	0.01	40.39	1.20
MCP15	13.03	5.93	6.25	8.65	40.01	2.07	0.01	15.36	0.01	6.60

c). % of the landscape

	OldCon	OldDec	OldMix	MatCon	MatDec	MatMix	Young	TrBog	CCut	Wetland
landscape	6.61	5.11	5.83	7.36	20.86	2.64	13.78	15.01	6.00	10.27

Appendix 3-5: Log ratio transformations of landscape habitat composition (3-5c), home range composition (3-5b) and the proportion of telemetry locations in each habitat type (3-5a).

a). Owl telemetry locations: $y_1 = \ln(U_{i,n} / U_{j,n})^a$

OWL-ID	OldCon /Wetl	OldDec /Wetl	OldMix /Wetl	MatCon /Wetl	MatDec /Wetl	MatMix /Wetl	Young /Wetl	TrBog /Wetl	CCut /Wetl	Wetland /Wetl
BAOW01	-7.76	-7.76	-1.25	-7.76	0.54	-7.76	-7.76	0.25	-7.76	0.00
BAOW03	1.79	0.00	-5.91	0.69	1.61	1.39	-5.91	1.95	0.00	0.00
BAOW05	1.10	-5.78	1.10	0.00	2.71	-5.78	-5.78	-5.78	2.08	0.00
BAOW07	5.91	0.00	7.01	6.61	8.62	7.01	0.00	6.61	5.91	0.00
BAOW09	0.00	0.41	0.69	-0.69	0.00	0.41	0.00	0.69	-6.73	0.00
BAOW11	1.39	-0.69	-7.07	-0.69	0.69	-7.07	-7.07	-0.69	-7.07	0.00
BAOW12	1.39	0.00	-7.13	0.00	-7.13	-7.13	-7.13	0.00	-7.13	0.00
BAOW13	0.00	8.29	0.00	0.00	0.00	0.00	8.01	0.00	7.60	0.00
BAOW15	1.39	-6.03	-6.03	1.10	2.56	-6.03	-6.03	1.10	-6.03	0.00

[a] habitat type Wetland was used in the denominator for $U_{j,n}$.

b). MCP summer home ranges: $y_2 = \ln(U_{i,n} / U_{j,n})^a$

MCP-ID	OldCon /Wetl	OldDec /Wetl	OldMix /Wetl	MatCon /Wetl	MatDec /Wetl	MatMix /Wetl	Young /Wetl	TrBog /Wetl	CCut /Wetl	Wetland /Wetl
MCP01	-2.71	-2.64	-3.22	-0.53	0.41	-2.29	-3.14	0.41	-1.27	0.00
MCP03	1.93	0.73	1.35	0.19	0.92	-0.14	-5.89	2.10	-0.09	0.00
MCP05	1.56	-0.88	1.99	0.93	3.20	0.93	-0.09	1.46	2.24	0.00
MCP07	-3.02	-1.89	-1.18	-1.21	0.34	-0.82	-1.70	-1.23	-0.83	0.00
MCP09	1.25	1.54	1.65	1.83	1.27	1.02	1.10	1.93	0.56	0.00
MCP11	0.52	1.39	-0.11	-2.27	1.82	-6.46	-1.00	-1.83	-6.46	0.00
MCP12	1.25	0.55	0.43	-1.63	-2.44	0.44	-6.65	1.15	-6.65	0.00
MCP13	1.66	2.13	2.13	-4.79	-4.79	-4.79	3.26	-4.79	3.52	0.00
MCP15	0.68	-0.11	-0.05	0.27	1.80	-1.16	-6.49	0.84	-6.49	0.00

[a] habitat type Wetland was used in the denominator for $U_{j,n}$

c). Landscape: $y_0 = \ln(U_{i,n} / U_{j,n})^a$

	OldCon /Wetl	OldDec /Wetl	OldMix /Wetl	MatCon /Wetl	MatDec /Wetl	MatMix /Wetl	Young /Wetl	TrBog /Wetl	CCut /Wetl	Wetland /Wetl
Landscape	-0.44	-0.70	-0.57	-0.33	0.71	-1.36	0.29	0.38	-0.54	0.00

[a] habitat type Wetland was used in the denominator for $U_{j,n}$

Appendix 3-6: Log ratio differences scores of owl telemetry locations vs. MCP summer home ranges (d_1); and MCP summer home ranges vs. the landscape (d_2).

a) Owl telemetry locations vs MCP summer home ranges: $d_1 = y_1 - y_2$

d_1	OldCon /Wetl	OldDec /Wetl	OldMix /Wetl	MatCon /Wetl	MatDec /Wetl	MatMix /Wetl	Young /Wetl	TrBog /Wetl	CCut /Wetl	Wetland /Wetl
BAOW01	-5.04	-5.12	1.96	-7.23	0.12	-5.46	-4.61	-0.16	-6.49	0.00
BAOW03	-0.14	-0.73	-7.27	0.51	0.68	1.52	-0.02	-0.16	0.09	0.00
BAOW05	-0.46	-4.90	-0.89	-0.93	-0.50	-6.71	-5.69	-7.24	-0.16	0.00
BAOW07	8.93	1.89	8.20	7.82	8.28	7.83	1.70	7.83	6.74	0.00
BAOW09	-1.25	-1.14	-0.96	-2.52	-1.27	-0.62	-1.10	-1.24	-7.29	0.00
BAOW11	0.87	-2.08	-6.96	1.57	-1.12	-0.62	-6.07	1.14	-0.62	0.00
BAOW12	0.13	-0.55	-7.56	1.63	-4.69	-7.57	-0.48	-1.15	-0.48	0.00
BAOW13	-1.66	6.16	-2.13	4.79	4.79	4.79	4.74	4.79	4.08	0.00
BAOW15	0.71	-5.93	-5.98	0.83	0.76	-4.87	0.46	0.25	0.46	0.00

b) MCP summer home ranges vs the landscape: $d_2 = y_2 - y_0$

d_2	OldCon /Wetl	OldDec /Wetl	OldMix /Wetl	MatCon /Wetl	MatDec /Wetl	MatMix /Wetl	Young /Wetl	TrBog /Wetl	CCut /Wetl	Wetland /Wetl
MCP01	-2.27	-1.94	-2.65	-0.19	-0.29	-0.93	-3.43	0.03	-0.73	0.00
MCP03	2.37	1.43	1.92	0.52	0.22	1.22	-6.19	1.72	0.45	0.00
MCP05	2.00	-0.18	2.56	1.26	2.49	2.29	-0.38	1.08	2.78	0.00
MCP07	-2.58	-1.19	-0.62	-0.88	-0.36	0.54	-1.99	-1.61	-0.29	0.00
MCP09	1.69	2.24	2.22	2.16	0.56	2.38	0.81	1.55	1.10	0.00
MCP11	0.96	2.09	0.46	-1.93	1.11	-5.10	-1.30	-2.21	-5.92	0.00
MCP12	1.69	1.24	0.99	-1.30	-3.15	1.80	-6.94	0.77	-6.11	0.00
MCP13	2.10	2.83	2.69	-4.45	-5.50	-3.43	2.97	-5.17	4.05	0.00
MCP15	1.12	0.59	0.51	0.60	1.09	0.20	-6.79	0.47	-5.95	0.00

Appendix 3-7: Landscape, class and patch level habitat pattern indices.

SCALE	LANDSCAPE PATTERN METRICS	Forest Coverage[a]		% of Area
LANDSCAPE				
	MPS – mean patch size (ha)			
	PSSD – patch size SD (ha)			
	PSCV – patch size cv (%)			
	LPI – largest patch index (%)			
	ED – edge density			
	LSI – landscape shape index			
	AWMSI – edge:area			
	AWMPFD – fractal dimension			
	SHDI – shannons diversity index			
	SHEI – shannons evenness index (0>1)			
	PD – patch density			
	PRD – patch richness density			
	IJI – interspersion and juxtaposition (%)			
CLASS				
	AREA			
	LAND (% AREA)	OLD origin > 1891	OLDCON – Sw, Ab, Lt, Pl, Pj	6.6
	MPS – mean patch size (ha)			
	PSSD – patch size SD (ha)		OLDDEC – Aw, Pb, Bw	5.1
	PSCV – patch size cv (%)			
	LPI – largest patch index (%)		OLDMIX – Sw, Ab, Lt, Pl, Pj, Aw, Pb, Bw	5.8
	ED – edge density			
	LSI – landscape shape index			
	AWMSI – edge:area	MATURE		
	AWMPFD – fractal dimension	origin 1890 – 1931	MATCON - Sw, Ab, Lt, Pl, Pj	7.4
	SHDI – shannons diversity index			
	SHEI – shannons evenness index		MATDEC - Aw, Pb, Bw	20.9
	PD – patch density			
	IJI – interspersion and juxtaposition (%)		MATMIX - Sw, Ab, Lt, Pl, Pj, Aw, Pb, Bw	2.6
		YOUNG origin > 1891	YNGCON - Sw, Ab, Lt, Pl, Pj	3.1
			YNGDEC - Aw, Pb, Bw	9.6
			YNGMIX - Sw, Ab, Lt, Pl, Pj, Aw, Pb, Bw	1.1
		TRBOG >70% Sb	OLDTRB - origin > 1891	3.1
			MATTRB - origin 1890 – 1931	8.4
			YNGTRB - origin > 1891	3.6
		REGENCUT	REGCUT – vegetated clearcut	6.0
		REGENBURN	REGENBURN – vegetated burn	5.4
		NONFOR-NATURL	WATER – non-forest natural	3.2
			MARSH – non-forest natural	7.1
		NONFOR-ANTHRO	AGRI – non-forest vegetated	0.5
			ANTHRO – non-forest unvegetated	0.6
PATCH				
	CLASS TYPE			
	AREA			
	LAND (% AREA)			
	PERIMETER			
	SHAPE INDEX			
	FRACTAL DIMENSION			

[a] Species codes for overstory trees are *Picea glauca* (Sw), *Picea mariana* (Sb), *Abies balsamea* (Ab), *Larix laricina* (Lt), *Pinus contorta* (Pl), *Pinus banksiana* (Pj), *Populus tremuloides* (Aw), *Populus basamifera* (Pb), *Betula papyrifera* (Bw). Clearcuts include recent (<5 y old) aspen cutovers, recent (< 5 y old) conifer cutovers, historical cutovers (MOF, 15 y old) and recent partial cutovers (10 – 30% overstory retention).

Appendix 3-8: Second-order habitat selection. Log ratio means, standard errors and simplified ranking matrix for the owl home ranges vs. the landscape. Habitats are ranked according to the log ratio scores. Significant differences between ranks are indicated by + signs in the ranking matrix.

a) log ratio mean / SE

OWL-ID	OldCon	OldDec	OldMix	MatCon	MatDec	MatMix	Young	TrBog	CCut	Wetland
OldCon		-0.010	-0.382	1.400	1.130	0.889	2.588	1.275	1.414	1.258
OldDec	0.010		-0.273	1.300	1.080	0.793	2.961	1.128	1.409	1.467
OldMix	0.382	0.273		1.563	1.253	1.069	3.127	1.336	1.736	1.557
MatCon	-1.400	-1.300	-1.563		-0.083	-0.612	1.406	-0.299	0.487	-0.713
MatDec	-1.130	-1.080	-1.253	0.083		-0.309	1.388	-0.077	0.459	-0.523
MatMix	-0.889	-0.793	-1.069	0.612	0.309		1.470	0.491	0.737	-0.132
Young	-2.588	-2.961	-3.127	-1.406	-1.388	-1.470		-1.286	-1.418	-2.197
TrBog	-1.275	-1.128	-1.336	0.299	0.077	-0.491	1.286		0.499	-0.498
CCut	-1.414	-1.409	-1.736	-0.487	-0.459	-0.737	1.418	-0.499		-0.908
Wetland	-1.258	-1.467	-1.557	0.713	0.523	0.132	2.197	0.498	0.908	

b) ranking matrix

OWL-ID	OldCon	OldDec	OldMix	MatCon	MatDec	MatMix	Young	TrBog	CCut	Wetland	Rank
OldCon		-	-	+	+	+	+++	+	+	+	7
OldDec	+		-	+	+	+	+++	+	+	+	8
OldMix	+	+		+	+	+	+++	+	+	+	9
MatCon	-	-	-		-	-	+	-	+	-	2
MatDec	-	-	-	+		-	+	-	+	-	3
MatMix	-	-	-	+	+		+	+	+	-	5
Young	—	—	—	-	-	-		-	-	-	0
TrBog	-	-	-	+	+	-	+		+	-	4
CCut	-	-	-	-	-	-	+	-		-	1
Wetland	-	-	-	+	+	+	+	+	+		6

Significance determined by comparing to $t = 2.306$ at df (n-1) = 8 and alpha < 0.05. Triple signs represent a significant deviation from random.

Appendix 3-9: Third-order habitat selection. Log ratio means, standard errors and simplified ranking matrix for the owl telemetry locations vs. the landscape. Habitats are ranked according to the log ratio scores. Significant differences between ranks are indicated by + signs in the ranking matrix.

a) log ratio mean / SE

OWL-ID	OldCon	OldDec	OldMix	MatCon	MatDec	MatMix	Young	TrBog	CCut	Wetland
OldCon		1.077	1.564	-0.580	-0.483	1.040	1.013	-0.174	0.624	0.188
OldDec	-1.077		0.517	-1.928	-1.729	-0.065	-0.161	-1.669	-0.736	-1.084
OldMix	-1.564	-0.517		-1.498	-2.560	-0.595	-0.584	-1.647	-0.971	-1.373
MatCon	0.580	1.928	1.498		-0.055	1.523	1.670	0.226	1.961	0.506
MatDec	0.483	1.729	2.560	0.055		2.080	1.719	0.354	1.074	0.629
MatMix	-1.040	0.065	0.595	-1.523	-2.080		-0.049	-1.722	-0.593	-0.731
Young	-1.013	0.161	0.584	-1.670	-1.719	0.049		-1.531	-0.633	-1.024
TrBog	0.174	1.669	1.647	-0.226	-0.354	1.722	1.531		0.650	0.325
CCut	-0.624	0.736	0.971	-1.961	-1.074	0.593	0.633	-0.650		-0.275
Wetland	-0.188	1.084	1.373	-0.506	-0.629	0.731	1.024	-0.325	0.275	

b) ranking matrix

OWL-ID	OldCon	OldDec	OldMix	MatCon	MatDec	MatMix	Young	TrBog	CCut	Wetland	Rank
OldCon		+	+	-	-	+	+	-	+	+	6
OldDec	-		+	-	-	-	-	-	-	-	1
OldMix	-	-		-	---	-	-	-	-	-	0
MatCon	+	+	+		-	+	+	+	+	+	8
MatDec	+	+	+++	+		+	+	+	+	+	9
MatMix	-	+	+	-	-		-	-	-	-	2
Young	-	+	+	-	-	+		-	-	-	3
TrBog	+	+	+	-	-	+	+		+	+	7
CCut	-	+	+	-	-	+	+	-		-	4
Wetland	-	+	+	-	-	+	+	-	+		5

Significance determined by comparing to $t = 2.306$ at df (n-1) = 8 and alpha < 0.05. Triple signs represent a significant deviation from random.