Spatial Habitat Selection by Barred Owls *(Strix varia)* in the Boreal Forest of Saskatchewan, Canada

A Thesis

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The Barred Owl (*Strix varia*) is a forest owl with relatively narrow habitat requirements. Its space use and habitat selection in the boreal forest, the northern portion of its range, are poorly understood. This study examined home range size and habitat selection of Barred Owls in the boreal forest of central Saskatchewan from 1993 to 1995. Fifteen adult Barred Owls (11-♀, 4-♂) were fitted with radio-transmitters. Locations of these owls were determined throughout the year to estimate home range size and habitat use. Breeding and non-breeding home range size, calculated with the 95% Minimum Convex Polygon estimator, averaged 148.6 hectares (SD=111.6), and 1234.0 hectares (SD=630.7) respectively. The large home range size during the non-breeding period was thought to occur as a result of a decrease in prey availability. Breeding and non-breeding home ranges overlapped entirely for all but two of the owls.

Habitat selection was investigated at two levels: home range selection and owl habitat use. Mann-Whitney *U*-tests and Log-ratio Compositional Analysis were used to examine habitat selection based on home range placement. Barred Owl breeding home ranges contained more old mixedwood forest than expected from random, and non-breeding home ranges contained more mature and old mixedwood, and mature and old deciduous forest than expected randomly. Both breeding and non-breeding home ranges contained low proportions of young forest and treed muskeg. Breeding home ranges were found to contain higher proportions of old mixedwood than non-breeding home ranges. Habitat composition of home range core areas, of both breeding and non-breeding home ranges, did not differ from habitat composition of total

home ranges. Different

revealed that habitat use by Barred Owls for foraging and roosting differed from the proportions of habitat available within the study area. During the breeding period, Barred Owls selected mature and old mixedwood, and mature deciduous forests. Similarly, in the non-breeding period, mature and old mixedwood, and mature and old deciduous forests were selected. Barred Owls are highly territorial, restricting their movements to within and defending their entire home range. During the breeding period, owls used habitat in proportion to its availability within their home range, with the exception of young mixedwood forest which was selected against. Owls selected old mixedwood within their non-breeding home ranges and avoided young and coniferous forests, treed muskeg and open areas. Barred Owl habitat use in the breeding and non-breeding periods did not differ. The results show that Barred Owls in the boreal forest of Saskatchewan were not using habitat at random, but selected certain habitats. Mature and old mixedwood forests were most strongly selected followed by mature and old deciduous forest. The existence of old mixedwood forests is often at odds with the objectives of commercial forestry management. Proper management of forest harvesting is necessary to ensure representation of all forest types, ensuring the retention of forest biodiversity. The Barred Owl, with its relatively narrow habitat needs, is a potential candidate as a good forest management indicator of old mixedwood forest in the boreal forest. This study provides important baseline data in order for the Barred Owl to be used as a forest management tool in the boreal forest of Saskatchewan.

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1 INTRODUCTION

The patterns of space use by animals are the result of morphological, physiological and behavioural adaptations to sectors of the environment (Ford and Krumme 1979). Adaptations to certain environmental features result in selection of those specific environmental features or habitats, and therefore a non-random distribution of animals (Lack 1933). Habitat selection is thought to be universal amongst animals (Cody 1985, Orians and Wittenberger 1991). The theory of habitat selection predicts that habitat selection occurs in order to maximize individual fitness (Orians and Wittenberger 1991). Adaptations to certain habitats enable animals to better exploit resources within those habitats, therefore increasing their reproductive and survival rates. Knowledge of animal habitat and space requirements is therefore, also an important factor in conservation planning.

The simple abundance of individuals in certain habitat types is not neccessarily a good indicator of habitat quality (McCallum 1994). Individuals may be abundant in a habitat, and yet the survival and reproductive rates in that habitat may be insufficient to maintain the population without immigration. This type of habitat is termed "sink habitat" (McCallum 1994). Conversely, "source habitat" is that in which reproductive and survival rates result in a net increase in the number of individuals, leading to emigration (McCallum 1994). Competition between conspecific individuals within a preferred habitat may decrease reproductive and survival rates, or force new arrivals into suboptimal or sink habitat (Fretwell and Lucas 1970, Pulliam and Danielson 1991).

Habitat selection is said to occur when a habitat is used in greater or lesser

amounts relative to its availability. Habitat selection choices occur at a series of levels, reliant on the spatial and temporal heterogeneity of the environment. Habitat selection can therefore be viewed as a series of choices, each relying on the choice of the previous level (Morris 1987). Within large scale habitat types (grassland, forest, marsh etc.), animals make an additional selection often referred to as macrohabitat (Morris 1987). Macrohabitat selection occurs at the home range or territory level, referring to where the animals chose to live (Morris 1987). This level of habitat selection relies on general habitat features (Orians and Wittenberger 1991). Conversely, microhabitat refers to specific chemical or physical features of the environment, and choices at this level often rely on the choices already made at the macrohabitat level (Morris 1987).

Habitat selection occurs in order to obtain one or a number of specific resources. For example, nest sites and foraging sites are two major resources involved in habitat selection (Cody 1985, Alcock 1989). Often habitat selection studies focus on only one dimension of habitat selection (nests, food, roosts). Animals may select a habitat that is suboptimal for one dimension, but is optimal for another (McCallum 1994). Therefore it must be emphasized that habitat selection does not necessarily indicate requirement of certain habitats, but only that occupancy rates are significantly different from random. Ultimately knowledge of animal habitat requirements is best. However, specific information on individual fitness and microhabitat features are often difficult to obtain.

The use of space by many animals is confined to a home range or territory. The area within which an animal's normal day-to-day activities occur is referred to as its "home range" (Burt 1943). To be considered a "territory", the area must be an

exclusive, actively defended area (Noble 1939, Pitelka 1959). Home ranges or territories are established and maintained for a variety of reasons. They vary from very small territories used to attract mates or breed to large annual territories used to secure all resources necessary (Schoener 1968, Alcock 1989). Many organisms establish summer breeding territories on an annual basis. In contrast, others maintain territories throughout the year. The differences lie within the purpose of the territory or home range. Some breeding territories are exclusively maintained for a nest site, with adjacent areas used for foraging. In other species both food and nest sites are found within the breeding territory. Territories that are maintained year-round typically include all of the resources necessary for survival (Schoener 1968).

The size of home ranges and territories varies both with the function of the territory and the availability of resources (Alcock 1989). Territories and home ranges that are exclusively used for nesting are usually considerably smaller than those used for feeding (Schoener 1968). In general, home range size also tends to increase with body size of the animal (McNab 1963). Larger animals have greater energy requirements and therefore must often range over a wider area to secure these resources. Aphids (*Pemphigus* spp.) have very small feeding territories (Whitham 1986), whereas feeding territories of birds of prey are immensely larger (Schoener 1968). Additionally, home ranges and territories of predatory species tend to be larger than those of herbivores (McNab 1963, Schoener 1968). Predators tend to obtain most or all of their food within their territory. Species with territories that include both a nest site and foraging site tend to be larger than those including only one critical resource.

When settling on a territory, animals are often required to assess the future availability of food (Orians and Wittenberger 1991). For some organisms this may be difficult as they establish territories prior to prey emergence, as in the Yellow-headed Blackbird (*Xanthocephalus xanthocephalus*), which preys on emerging aquatic insects (Orians and Wittenberger 1991). Viitala *et al.* (1995) found that Kestrels (*Falco tinnunculus*) in northern Europe were able to detect vole urine and faeces that were highly reflective of ultraviolet light. Kestrels were therefore able to assess the potential prey abundance in a given area. The size of a feeding territory is correlated with the abundance of prey, which in turn is influenced by the habitat. Therefore, home range or territory size is often a reflection of habitat quality (Schoener 1968, Alcock 1989).

Animals should benefit by being able to assess the quality of habitat in a given area prior to establishing a territory (Orians and Wittenberger 1991). For birds, nest site availability is a major factor influencing habitat selection and the location of a breeding territory (Hilden 1965, Seeley 1977, Newton 1979, Orians and Wittenberger 1991). Within species that rely on secondary tree cavities as nest sites, nest site availability is thought to be the major factor influencing habitat selection and territory maintenance (Hilden 1965, Lundberg 1979, McDonald 1995). Such a resource could be thought of as a super-stimulus, and may drive habitat selection (Hilden 1965).

The conservation of birds often includes understanding habitat relationships (Newton 1979, Pettingill 1985). Bird populations are ultimately limited by two major resources: nest sites and food (Newton 1979). Both of these are considered important factors influencing habitat selection (Lack 1933, Orians and Wittenberger 1991). This

naturally extends to understanding the nature of nest sites and food availability within habitat. Conservation efforts therefore often focus on habitat relationships and the factors of habitat that appear to be important. Due to their charismatic appeal, and relative ease of observation, birds are often the focus of conservation efforts. Owls as a group have further been the focus of conservation-oriented attention. Owls tend to have large area, and often specific, habitat requirements, which can make them sensitive to relatively small habitat changes. Although primarily nocturnal, owls are relatively easy to census, because they are very vocal during the breeding period. The conservation of large areas of habitat for owls often results in habitat for a wide variety of other species being conserved. Therefore, owls are often used as habitat indicators for habitat management (Bosakowski 1994, Hayward and Verner 1994).

Owl habitat relationships have been investigated throughout the world. Within the northern hemisphere, a large component of research on owls has focused on forest-dwelling species (Nero *et al.* 1987, Hayward and Verner 1994). Forest owls use habitat in a variety of ways and for a number of specific resources. For example, throughout its circumpolar, distribution the Great Gray Owl (*Strix nebulosa*) relies on two major types of habitat, open areas in the form of bogs, muskeg and grassy meadows for foraging, and upland forest for nesting (Mikkola 1983, Korpimäki 1986, Servos 1987, Duncan and Hayward 1994). The Great Gray Owl is considered a prey specialist, feeding almost exclusively on small rodents (Mikkola 1983, Duncan and Hayward 1994). This large owl is not as discriminating in its choice of nest sites, and it will use a variety of structures (Hildén and Solonen 1987, Duncan and Hayward 1994).

Adequate prey is thought to be the key factor in habitat selection by Great Gray Owls (Hildén and Solonen 1987, Servos 1987). However, adequate foraging habitat must be adjacent to upland forest likely to contain a nest site (Hildén and Solonen 1987). Great Gray Owls do not space their territories evenly, but exhibit more of a clumped distribution in areas with abundant prey, where their territories exhibit large areas of overlap between neighbouring pairs (Servos 1987). As prey specialists, Great Gray Owls become nomadic when rodent populations crash, moving to areas with higher prey availability (Korpimäki 1986, Duncan 1987).

The Boreal Owl (or Tengmalm's Owl) (*Aegolius funereus*) also exhibits a preference for specific habitat types (Korpimäki 1981, Hayward *et al.* 1993). It has been shown to select mature and old coniferous or mixedwood forest both in Eurasia and North America (Korpimäki 1981, Hayward *et al.* 1993). The Boreal Owl finds both food and nest sites within its home range (Hayward *et al.* 1993). It is considered a prey specialist, feeding primarily on voles and nests in secondary tree cavities, which are considered scarce (Johnsgard 1988, Hayward *et al.* 1993). However, its prey undergoes 3-4 year population cycles, therefore the Boreal Owl is under conflicting pressures. The scarcity of nest sites favours site tenacity, but its diet speciality favours nomadism during vole population crashes (Lundberg 1979, Korpimäki 1987). The Boreal Owl is therefore forced to undertake a nomadic strategy during prey crashes, abandoning its nesting area.

Owls that rely on scarce nest sites (ie secondary tree cavities or snags) would be expected to benefit from year-round site tenacity, thereby defending the scarce

resource (Lundberg 1979). The Ural Owl (*Strix uralensis*), Tawny Owl (*S. aluco*), and Spotted Owl (*S. occidentalis*) are three examples of nest-site-limited owls that are site tenacious throughout the year (Southern and Lowe 1968, Lundberg 1979, Forsman *et al.* 1984). Habitats selected are ones containing suitable nest sites. All three owl species are considered generalist predators, consuming a range of prey species (Southern 1954, Lundberg 1976, Forsman *et al.* 1984). They tend to prey largely on mammals, but when populations of favoured mammalian prey decline, they can exploit alternate prey (Lundberg 1979, Forsman *et al.* 1984). Because of their ability to switch prey they are able to maintain year-round territories defending the scarce nest site (Lundberg 1979). Habitat quality measures would thus need to include the availability of a nest, as well as the abundance of prey. Home range size is thought to be a reflection of prey availability; therefore, home ranges with lower quality habitat should tend to be larger (Carey and Peeler 1995). Carey *et al.* (1990) and Redpath (1995) found an inverse relationship between preferred habitat patch size and home range size for Spotted and Tawny Owls. Spotted Owl home ranges increased in size as size of old-growth patches decreased and Tawny Owl home ranges size increased as wood size decreased (Carey *et al.* 1990, Redpath 1995). In other words, the fragmentation of preferred habitat results in an increase in home range size for both species. Owls may have had to move greater distances to reach high quality patches for foraging (Carey and Peeler 1995). These owl species tend to have territories that exhibit little overlap with conspecific neighbours (Lundberg 1981, Forsman *et al.* 1984, Redpath 1995), implying that spacing is important for resource partitioning. Similar to the Ural, Tawny,

and Spotted Owl, the Barred Owl (*Strix varia*) relies on scarce nest sites and is considered a prey generalist (Johnsgard 1988). It also should benefit by maintaining year-round territories to defend its nest site. However, little is known about the specific habitat and area requirements of the Barred Owl.

The Barred Owl is widely distributed in North America (Fig. 1). During the 20th century this species is believed to have expanded its range into the boreal forest of Canada to the western montane forests of Canada and the United States from its earlier distribution in the eastern forests of the United States (Houston 1959, Taylor and Forsman 1976, Boxall and Stepney 1982, Sharp 1989). Many published "first records" of the Barred Owl in western Canada and the United States are from the 1940's to 1960's (Grant 1966, Rogers 1966), which lead to the belief that this owl only recently extended its range. However, early records show that the Barred Owl was present in Manitoba as early as 1899 (Seton 1909) and in Colorado in 1897 (Bent 1961). Manitoba and Colorado lie at opposite extremes of the believed range extension, suggesting that the Barred Owl was present in this region at least one century ago. In Washington, the Barred Owl has come into contact with the congeneric Spotted Owl of the western United States, where hybridization has occurred (Hamer *et al.* 1994).

Barred Owl habitat selection has not been studied extensively, with studies largely focussed in the northeastern portion of United States (Nicholls and Warner 1972, Devereux and Mosher 1984, Elody and Sloan 1985, Bosakowski *et al.* 1987, Laidig and Dobkin 1995). In this region, Barred Owls select large contiguous tracts of mature to old-growth hardwood and mixed hardwood/softwood forests. Some authors

Figure 1. Distribution of the Barred Owl in North America (shaded area). The Barred Owl is a year-round resident throughout its range.

have also reported a need for swamps and association with water (Bent 1961, Bosakowski *et al.* 1987, Laidig and Dobkin 1995). Recent research in the boreal forest of northwestern Ontario and west-central Alberta have found similar habitat selection patterns (Van Ael 1996, Takats, 1997).

In Minnesota, Nicholls and Warner (1972) radio-marked 10 adult Barred Owls and found them to strongly select mixedwood and oak forests, and avoid open fields, marshes, and alder swamps. Similarly, in Michigan seven radio-marked Barred Owls selected old-growth hemlock and hemlock/maple forest (Elody and Sloan 1985). Additional habitat associations have been documented through surveys. Bosakowski *et al.* (1987) found Barred Owls in New Jersey associated with mature oak, northern hardwoods and hemlock, as well as an association with water and swamps. Also in New Jersey, Laidig and Dobkin (1995) found Barred Owls strongly associated with cedar swamp-pitch pine lowlands, as well as with mature hardwood swamp forests. In Virginia, Barred Owls were located significantly more often in old versus young forests and were found more often in contiguous forest versus forest highly fragmented by farmland (McGarigal and Fraser 1984). In the boreal forest of northwestern Ontario, Van Ael (1996) found Barred Owls associated with tall, unfragmented mixedwood forests while avoiding conifer and young stands. Similarly, Takats (1997) found Barred Owls in Alberta to select old mixedwood forest for nesting, roosting and foraging.

Barred Owls are highly territorial, defending a territory throughout the year (Nicholls and Fuller 1987, Johnsgard 1988). Their home ranges are defended against neighbouring Barred Owls, and therefore can be considered territories (Nicholls and

Fuller 1987). Information on Barred Owl home range size is limited to a few studies. In Michigan, Elody and Sloan (1985) found Barred Owl breeding home ranges to average 118 hectares, and annual home ranges to be 282 hectares. Similarly, in Minnesota Nicholls and Fuller (1987) found Barred Owls to have an average home range of 274 hectares, with no discrimination made between breeding and non-breeding periods. Barred Owls in Washington had considerably larger home ranges, with breeding season home ranges averaging 321 hectares, and annual home ranges averaging 644 hectares (Hamer 1988). Individual Barred Owls appear to maintain home ranges with little or no overlap with others except for their mate (Nicholls and Fuller 1987, Hamer 1988). Spacing between Barred Owl pairs would likely function in partitioning resources.

Nest sites are considered to be the major factor determining habitat selection by Barred Owls (Devereux and Mosher 1984, Elody and Sloan 1985). The owls nest primarily in tree cavities in the form of a hollow in the top of a broken-off tree (snag) or in a cavity formed by disease, and less often use old stick nests (Devereux and Mosher 1984). Barred Owl nest sites in Maryland were found to be in taller trees and larger (>50 cm dbh) trees than expected at random (Devereux and Mosher 1984). This requirement of large diameter trees which provides a suitable nest site is thought to be a major factor influencing habitat selection by Barred Owls (Bent 1961, Dunstan and Sample 1972, Devereux and Mosher 1984).

As a strategy to enable site tenacity in order to defend scarce nest sites, Lundberg (1979) suggested that nest site specialists should adopt a catholic diet

enabling them to use a large range of prey and maintain year-round territories. The diet of the Barred Owl includes a wide range of prey, including squirrels, voles, mice, grouse, passerines, amphibians, invertebrates, and fish (Bent 1961, Marti 1974, Marks *et al.* 1984, Elderkin 1987, Bosakowski and Smith 1992). Their diet varies seasonally as well as with the abundance of specific prey species, implying that the Barred Owl is a true generalist. However, a large portion of the Barred Owl's diet is typically composed of small mammals, with birds taken less frequently and amphibians and invertebrates taken only during the summer. Barred Owls are under pressure to remain on their territory to protect their nest site, but must be able to secure adequate food within their territory. As a generalist predator, they should be able to select habitat for a nest site and maintain their territory surrounding the nest site throughout the year. Long-term residency of a home range allows greater familiarity with the habitat, enabling more efficient exploitation of prey, especially in periods of low prey availability (Lundberg 1979). Others have suggested that old forest, where nest sites are typically found, provides easier hunting due to lower tree densities, and numerous perches in large trees (Nicholls and Warner 1972). If Barred Owls required old forest solely for a nest site, one might predict that foraging would not necessarily be limited to old forest.

Habitat loss is the greatest threat to wildlife populations today (Newton 1979). Understanding the habitat relationships of species is essential in order to conserve wildlife populations. Within the boreal forest of Canada, forest of mixed deciduous and coniferous species which is considered old (> 80 years) is a highly species-diverse ecological community (Stelfox 1995b). Conservation of this forest type is often at odds

with the economic goals of the forestry industry. The Barred Owl in the boreal forest, from previous records and known habitat selection in portions of its range, likely relies on such old mixedwood forest. If so, conservation of this species in the boreal forest requires an understanding of its area requirements and specific habitat preference in the boreal forest. The conservation of sufficient habitat to support a stable population of Barred Owls will ultimately benefit many species that also inhabit this diverse forest type. Therefore, the Barred Owl is a likely candidate for use as a forest management indicator.

I first wanted to determine the amount of area adult Barred Owls use during both the breeding and non-breeding periods. I predicted that in the boreal forest of Saskatchewan Barred Owl home ranges would be larger than those found in other portions of its range. Prey availability is probably lower in the boreal forest than in southern regions, and this is likely the main reason for larger home ranges, especially in the winter when many potential prey species either migrate or are not accessible.

Secondly I wished to test the hypothesis that Barred Owls do not use habitat at random. I specifically wanted to determine which types of habitat Barred Owls selected in the boreal forest. I tested this at two levels. First, I compared the habitat found within owl home ranges to habitat found in surrogate home ranges placed in the study area at random. Placement of a home range or territory is considered second-order habitat selection (Johnson 1980). Second, I compared habitat used by individual owls to habitat found at random in the study area and habitat found within their home ranges. I predicted that Barred Owls would select old forest, specifically old mixedwood forest

during both the breeding and non-breeding periods based on home range placement and owl habitat use. In the boreal forest, old mixedwood forest is likely the only forest type with enough large diameter trees suitable for nest sites, and an abundance of prey (Stelfox 1995b). Such knowledge of Barred Owl home range size and habitat selection is important for the conservation of this species, and may aid in the management of its habitat ultimately benefiting all species that rely on that habitat type.

2 METHODS

2.1 Study Site

The research was conducted from May 1993 to April 1995 within the southern boreal forest of Saskatchewan, Canada (53°35'-54°15'N, 105°05'-106°45'W) (Fig. 2). The 400,000-ha study area encompassed the Prince Albert Model Forest, including a portion of Prince Albert National Park. The dominant tree species in the study area include trembling aspen (*Populus tremuloides*), balsam poplar (*Populus balsamifera*), white birch (*Betula papyrifera*), white spruce (*Picea glauca*), black spruce (*Picea mariana*), tamarack (*Larix laricina*), jack pine (*Pinus banksiana*), and balsam fir (*Abies balsamea*). The habitat includes pure deciduous, mixed coniferous/deciduous, and pure coniferous forest, muskeg, and shrub lands. Elevation ranges from 490 to 698m. The topography is gently rolling, interspersed with numerous lakes and creeks. The climate is boreal continental, with an average annual precipitation of 401 mm: 281 mm as rain and 120 mm as snow. July and January temperatures average 17.6°C and -19.7°C respectively, with annual extreme temperatures of 36.1°C and -48.3°C

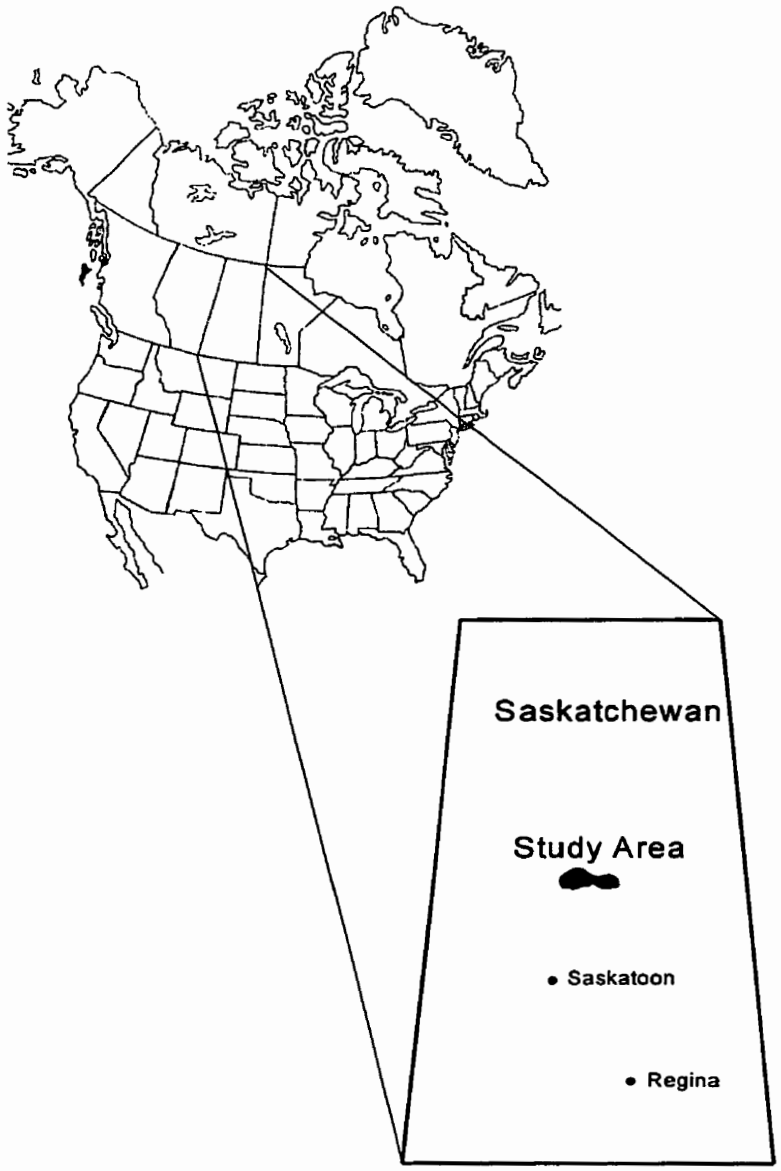


Figure 2. Study area in central Saskatchewan, Canada.

(Environment Canada Parks 1986). Approximately half of the study area is currently being commercially harvested for wood pulp and timber.

2.2 Radio-telemetry

2.2.1 Owl Capture and Radio-marking

Barred Owls were captured throughout the year, with most (78%) being caught during the breeding period (April - August). A variety of capture techniques were used including: mist nets with a movable mounted Barred Owl, mist nets and laboratory mice in a wire cage, free-ranging live laboratory mice and a hand-held net, and a noose pole. Two-shelved mist nets (AFO Mist Nets, Manomet, MA), 12 metres long with 121 mm mesh were supported between 1.27 cm diameter 3.0 m long electrical conduit poles. Two mist nets were set in a "V", with either the mounted owl or mice in a bal-chatri (small wire cage with fishing line nooses on outside) placed between the mist nets in the middle of the "V" (Elody and Sloan 1984). Owls were lured to the set-up location by broadcasting a tape recorded call of a pair of Barred Owls. Owls became entangled in the mist net when diving to drive off the "intruding" owl or attempting to capture the mouse. Observers hid 10 - 20 m away and removed the owls as soon as they were seen to be caught in the net. These two methods were employed at night. In the case of the hand-held net, a Barred Owl located during the day was approached and a live laboratory mouse was set out on a piece of styrofoam (approximately 20 cm x 20 cm). The person with the net sat immediately beside the mouse and as the owl stooped for the mouse, it was netted. Owls located near their nests were often bold, allowing one

to approach quite closely. Once immediately below the tree the owl was perched in, a wire noose at the end of a 6.1 m extension pole could be slipped around the owl's neck and the owl could be brought to the ground.

Fifteen adult Barred Owls (11 -♀, 4 - ♂) were captured using these methods. Six morphological measurements were recorded (weight, wing chord length, tail length, foot pad length, moult score and the number of complete tail bars on the central tail feather). Weight was measured with either an Avinet or Accu-Weigh spring scale (± 20 g); wing chord was measured from the bend at the wrist to the tip of the longest primary of an unflattened wing in its closed position; tail length was measured from the insertion of one of the central tail feathers to the feather tip; foot pad was measured as the distance from the base of the talon of the hallux to that of the middle front toe, with the toes fully extended (Duncan 1992). The moult of the primaries and rectrices was scored as the number of complete feathers, and the relative size of new feathers; the number of complete tail bars on the central tail feathers was counted as a possible method of determining the sex (Carpenter 1992). Owls were classed as adults (> 2 years) by the lack of buffy tips on the rectrices (Forsman *et al.* 1984). Owl sex was determined based on weight (females are approximately 25% heavier; Johnsgard 1988), presence of a brood patch and vocalizations (Elderkin 1987). Aluminum leg bands (U.S. Fish and Wildlife Service) were put on the owl's right leg and the owls were fitted with back-pack style radio-transmitters (AVM Electronics, Livermore, CA). Transmitter harnesses were constructed of 2.5 cm wide Teflon tubular ribbon, with two strands of nylon coated braided cable running through the Teflon ribbon (Duncan

1992). Tubular copper clamps secured the harness where it crossed at the owl's sternum and at the radio-transmitter. Feathers trapped under the harness were laid on top of the harness, so that the harness sat immediately next to the owl's skin, facilitating more normal thermoregulation. The radio-transmitter and harness weighed 32 g, or on average 3.5% and 4.6% of female and male body mass respectively. Radio-transmitters emitted a signal at a rate of 60 beats per minute with the signal detectable up to 10 km if the observer was on the ground. Radio-transmitter battery life ranged from eight to 12 months.

2.2.2 Radio-tracking

Radio-marked Barred Owls were located through triangulation or by direct observation. Triangulation used a single 5 element Yagi antenna (AVM Electronics, Livermore, CA). This was either in the form of a vehicle roof-mount antenna (2 m above the roof of a pickup truck), or held by a person while standing on the ground (hand-held). The Yagi antenna was combined with a telemetry receiver (Lotek Engineering, Newmarket, ON) in order to determine the direction and strength of the radio-signal. The direction of the signal to the nearest degree was read from a compass rosette mounted on the inside of the truck roof, and the direction was corrected by determining the direction the truck was pointed. In the case of the hand-held Yagi, the direction of the signal was simply read from a compass. A minimum of three strong directional signals were recorded and plotted onto 1:50,000 topographical maps or 1:25,000 forest inventory maps. The signal directions were then entered to the

Locate II computer program (Pacer, Truro, NS). Locate II calculated the estimated owl location and surrounding error polygon. Estimated owl locations with error polygons greater than 10 hectares were not used in the analysis, since larger error polygons indicate less accurate estimates of the owl location.

Barred Owls were relocated on average every fifth day, with locations being separated in time by a minimum of two days. Owls were relocated both during the day and during the night. Only one location was used for the period during which any nesting female owl was on the nest. During the breeding period, owls were tracked on average for 3.4 months obtaining an average of 21 (range 12 - 36) relocations per owl, and in the non-breeding for 5.5 months, with an average of 35 (range 24 - 43) relocations per owl. A total of 270 locations were obtained during the breeding period and 455 locations during the non-breeding period.

2.3 Home Range

Home range values were calculated separately for breeding (1 April - 31 August) and non-breeding (1 September - 31 March) periods. The breeding period was approximated as the period when courtship began prior to egg laying until the time when young owls left their parent's territory. Home range values were calculated using the 95% and 50% Minimum Convex Polygon (95MCP , 50MCP) range estimator with the computer program Home Range (Ackerman *et al.* 1990). The 95% Minimum Convex Polygon home range has the outer most 5% of the animal's locations removed. These are assumed to represent excursions outside the normal home range (Ackerman

et al. 1990). The 95MCP was considered to represent the total home range. The 50% Minimum Convex Polygon home range has the outermost 50% of the animal's locations removed. The area within the remaining 50% of the locations was considered the core area of the home range (Ackerman *et al.* 1990). Numerous home range estimators exist (White and Garrott 1990); however, many employ statistical computations requiring the assumption a bivariate normal distribution, and the independence of successive relocations. These assumptions are often impossible to meet (McNay *et al.* 1994, Gautestad and Mysterud 1995). I therefore chose to use a home range estimator that was not statistical, and that made few assumptions of the data. Furthermore, the use of the Minimum Convex Polygon estimator is widespread in the literature, facilitating comparisons.

Breeding and non-breeding home range values failed to approximate a normal distribution and were therefore log transformed. A *t*-test ($\propto$ 0.05) was performed to determine if breeding and non-breeding home ranges differed in size (Zar 1996).

2.4 Habitat Selection

The updated (1993) version of forest inventories for Prince Albert National Park (Padbury *et al.* 1978) and the Saskatchewan Northern Provincial Forest (Lindenas 1985) were used to classify the available habitat into 12 types (Table 1). The composition of Barred Owl home ranges (95MCP and 50MCP), 100 1.5 km radius (706 hectare) circular buffers, and the entire study area were then calculated based on the 12 habitat types. Additionally, the habitat that each individual owl relocation fell within

Table 1. Habitat classification by habitat cover type and age. Data from Prince Albert National Park Biophysical Resource Inventory and Saskatchewan Forest Inventory.

Habitat Type	Cover Vegetation Description
Deciduous[1]	Trembling Aspen +/or Balsam Poplar +/or White Birch (<20% conifer)
Mixedwood[1]	Combination of deciduous and coniferous species: Trembling Aspen, Balsam Poplar, White Birch, White Spruce, Black Spruce, Jack Pine, Balsam Fir (≥20% conifer, ≥20% deciduous)
Coniferous[1]	White Spruce +/or Black Spruce+/or Jack Pine +/or Tamarack +/or Balsam Fir (<20% deciduous)
Treed Muskeg	Black Spruce +/or Tamarack, excessive moisture and retarded tree growth
Open	Cut Over, Burn Over, Flooded Land, Sand, Clearing, Open Muskeg, Herbs, Shrubs
Water	Lakes, Rivers, Creeks

[1]Could occur in three age classes: Young (<50 years). Mature (50-79 years), and Old (80+ years).

was determined. Radio-marked Barred Owl relocations with an associated error polygon of no more than four hectares were included in habitat selection analysis. An error polygon limit of four hectares was imposed on relocations used in habitat selection as greater accuracy of the owl location was desired. Relocations were again separated by at least two days. As for the home range, the year was divided into breeding and non-breeding periods.

2.4.1 Home Range Composition

An initial assessment of habitat selection was based on home range habitat composition, where the home range is thought of as a form of habitat selection based on where the animal chooses to live (Johnson 1980). Habitat composition of Barred Owl breeding and non-breeding home ranges was compared to the habitat composition of 100 1.5 km radius buffers randomly distributed within the study area. Owl home range habitat composition values failed to approximate a normal distribution and nonparametric statistics were therefore applied. Differences in habitat composition were tested with the Mann-Whitney *U*-test.

Aebischer *et al.* (1993) have criticized habitat selection analysis which does not include a way of cross referencing to other habitat types selected. The stated problem is, "avoidance of one habitat type will almost invariably lead to an apparent preference for other types" (Aebischer *et al.* 1993). To get around this, they proposed that all habitat comparisons (use versus available) include a ratio of two habitat types; therefore selection of a habitat type is being assessed with reference to selection for all

other habitat types. This is referred to as a Log-ratio Compositional Analysis.

In Log-ratio Compositional Analysis, a ratio of the natural log (*ln*) of the percent observed habitat use of one habitat type over a second (constant) habitat type is calculated. From this value, the ratio of the *ln* of the percent available of the two habitat types is subtracted ($ln(X_{Ui}/X_{Uj})$-$ln(X_{Ai}/X_{Aj})$). This was performed for all owls for all habitat types yielding a table of differences (see Appendix B). If all habitats were being used equally, these differences would be expected to be equal for all habitat types. These data did not approximate a normal distribution, the null hypothesis of equal differences among habitat types was tested using a Kruskal-Wallis test (Zar 1996). Further investigations into which habitats were of greater importance were made using a ranking matrix. Again a ratio of one habitat type over a second habitat type was calculated for habitat use and available habitat. The mean and standard error were calculated for the sample of owls and significant deviation from no habitat selection was assessed from the distribution of *t* (n-1 degrees of freedom) at $\propto$ 0.05 (see Appendix B). Habitat types were given ranks, with the habitat type used most being assigned the highest rank. The habitat composition of home ranges was defined as the habitat use by owls and the habitat composition of the study area considered the available habitat. All zero values were replaced with a value of 0.01%, since a zero numerator or denominator is invalid in a log-ratio transformation. Aebischer *et al.* (1993), recommend replacing all zero values with a value less than the non-zero proportion.

Differences between Barred Owl breeding and non-breeding home range habitat composition were tested using a Mann-Whitney *U*-test. As well, differences in habitat

composition of core owl home ranges (50MCP) were compared to the habitat composition of the total home range (95MCP). This was performed for both breeding and non-breeding home ranges. Differences were tested using the Mann-Whitney *U*-test as the data failed to approximate a normal distribution.

2.4.2 Owl Habitat Use and Study Area Composition

Habitat selection based on owl relocations was compared to the available habitat within the entire study area (Fig. 3). The habitat class "water" was not included in owl habitat use analysis, since "water" is not used by Barred Owls. Chi-square goodness-of-fit tests were applied to determine if owls were using habitat in proportion to its availability (Neu *et al.* 1974, Byers *et al.* 1984). In order to determine which habitat types were being selected, Bonferroni Confidence Intervals ($\propto$ 0.05) were constructed (Neu *et al.* 1974, Byers *et al.* 1984). Log-ratio Compositional Analysis was also performed, with owl habitat use representing habitat use and the study area habitat composition representing available habitat. Ranking matrices were constructed to determine habitat importance. Again, zero values were replaced by 0.01%. Barred Owl habitat use during the breeding and non-breeding periods was compared with the Mann-Whitney *U*-test (Zar 1996).

2.4.3 Owl Habitat Use and Home Range Composition

Aebischer *et al.* (1993) argued that defining available habitat using the arbitrary

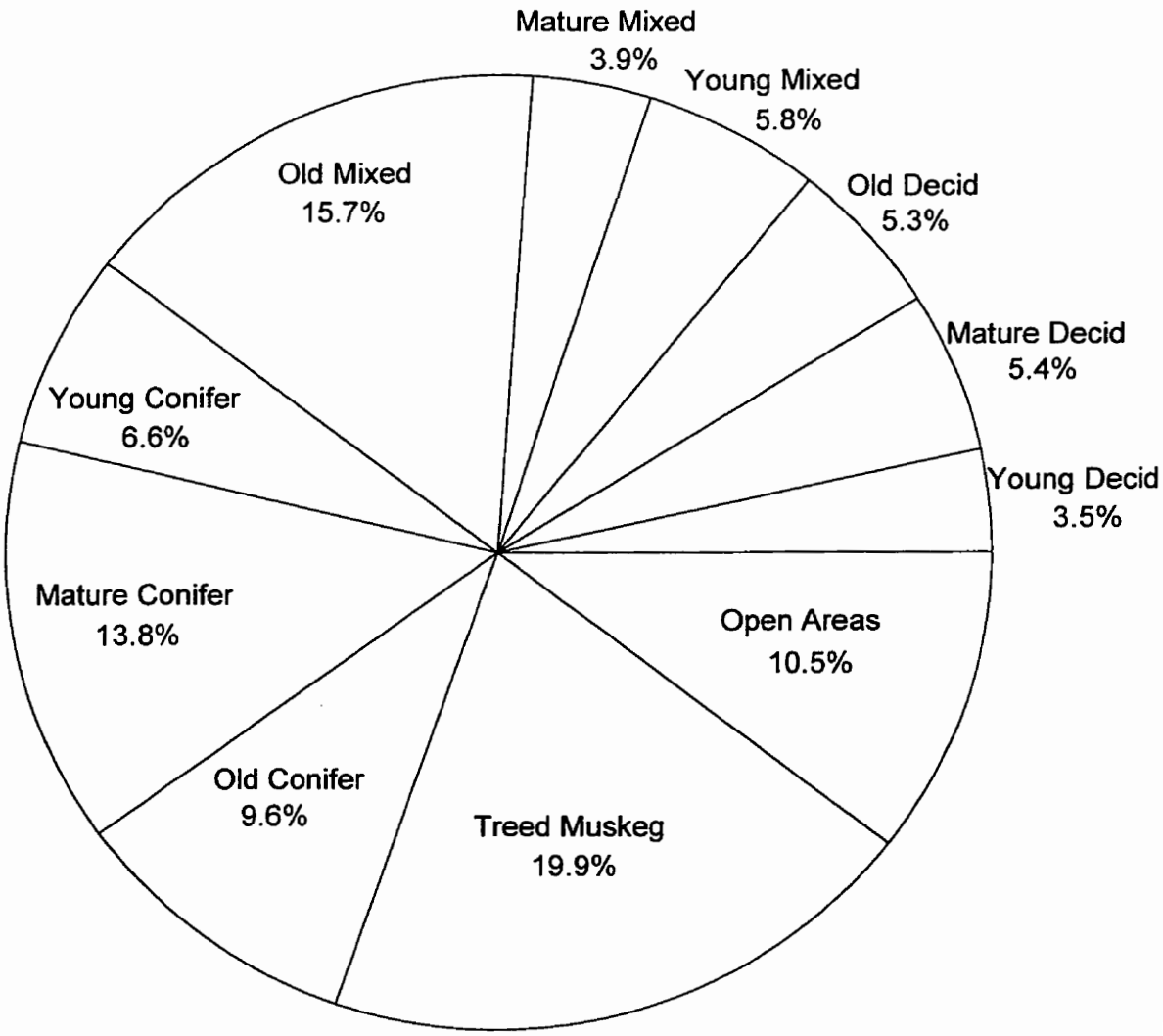


Figure 3. Habitat composition of the study area. Data from Prince Albert National Park Biophysical Resource Inventory and Saskatchewan Forest Inventory.

definition of a study area is not valid, since the entire study area may not be available to the animal due to interspecific and intraspecific competition. I therefore tested to see if owls were selecting habitat types within their home ranges. Bonferroni Confidence Intervals were constructed ($\propto$ 0.05), and Log-ratio Compositional Analysis was performed to determine the importance of habitat types. Owl habitat use again represented habitat use and home range (95MCP) habitat composition represented available habitat. In Log-ratio Analysis, habitats that were absent from a large proportion of owl home ranges (>70% of owl home ranges) were removed from the analysis as these were not present as available habitat to the majority of owls (Aebischer *et al.* 1993). For data on the breeding period five habitats were removed: young deciduous, old deciduous, young mixedwood, young conifer and treed muskeg. Analysis of non-breeding home ranges did not include three habitats: young deciduous, young mixedwood, and young conifer. Zero values were replaced by 0.01%.

3 RESULTS

3.1 Home Range

Barred Owl breeding and non-breeding home ranges differed significantly in size (t=8.803, P<0.001, df=23; Table 2). Breeding home ranges averaged 148.6 hectares (♂=173.5, n=3; ♀=140.2, n=9), and non-breeding home ranges averaged 1234.0 hectares (♂=1331.0, n=4; ♀=1190.9, n=9). Both breeding and non-breeding home range values were calculated for 10 owls. The breeding home ranges of eight owls were entirely contained with the non-breeding home ranges. Breeding home ranges of

Table 2. Barred Owl breeding and non-breeding home range values calculated using the 95% Minimum Convex Polygon estimator. Breeding and non-breeding home ranges were significantly ($P<0.05$) different in size.

	Home Range (ha)	
Owl	Breeding	Non-breeding
Beaverglen ♂	91.4	1403.5
Shady Lake ♂	363.5	2010.5
Hillcrest ♂	66.7	1181.2
Birch Bay ♂	-	728.9
Birch Bay ♀	101.9	-
Beartrap ♀	-	1000.8
Paignton ♀	106.0	573.4
Heart Lakes ♀	129.0	1573.3
Candle Lake ♀	50.0	610.9
Prospect ♀	55.7	689.1
Spruce River ♀	341.8	1086.5
Summit ♀	38.1	588.8
Whelan Bay ♀	144.8	1917.1
Waskesiu ♀	-	2678.4
Whiteswan ♀	294.3	-
Mean	148.6	1234.0
SD	111.6	630.7

the remaining two owls, which were females, did not overlap at all with their non-breeding home ranges.

3.2 Habitat Selection

3.2.1 Home Range Composition

Barred Owl breeding home ranges differed significantly from random buffers in habitat composition for seven out of 12 habitat types (Fig. 4). Barred Owl breeding home ranges were composed of less young deciduous (z=-2.024, P=0.042), less young mixedwood (z=-2.623, P=0.008), more old mixedwood (z=-4.513, P<0.001), less young coniferous (z=-3.003, P=0.003), less mature coniferous (z=-2.171, P=0.029), less old coniferous (z=-2.114, P=0.034), and less treed muskeg (z=-4.066, P<0.001) than found in random buffers. Barred Owl non-breeding home ranges and random buffers differed significantly in habitat composition for five habitat types (Fig. 5). Barred Owl non-breeding home ranges were composed of significantly more mature and old deciduous (z=-2.529, P=0.011, z=-2.341, P=0.019), more old mixedwood (z=-2.659, P=0.007), and less treed muskeg and open areas (z=-2.756, P=0.005, z=-2.241, P=0.025) than found in random buffers.

Based on Log-ratio Compositional Analysis, Barred Owl breeding and non-breeding home ranges were composed of habitat that differed significantly from that found at random (H=22.366, P=0.008, H=21.790, P=0.010). This indicated that home ranges did not arbitrarily occur across the forest, but were found in specific habitats. The ranking matrix for the breeding period (Table 3) indicates that old mixedwood >

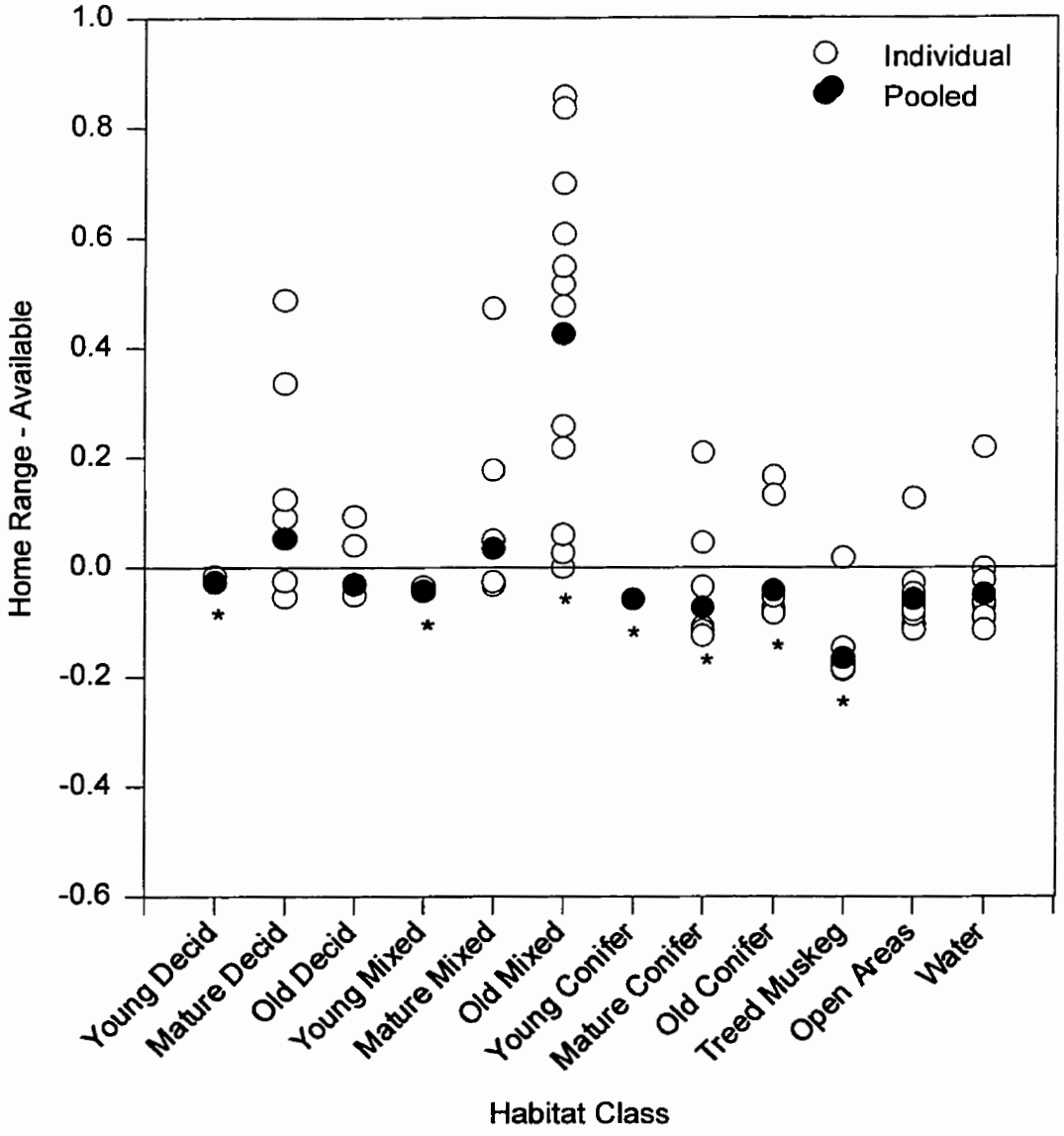


Figure 4. Barred Owl habitat selection based on breeding home range habitat composition compared to habitat available within random 1.5 km buffers. Home range represents the proportion of each habitat within home ranges and available habitat the proportion of each habitat within the buffers. Significant differences (*) determined using a Mann-Whitney *U*-test ($P<0.05$).

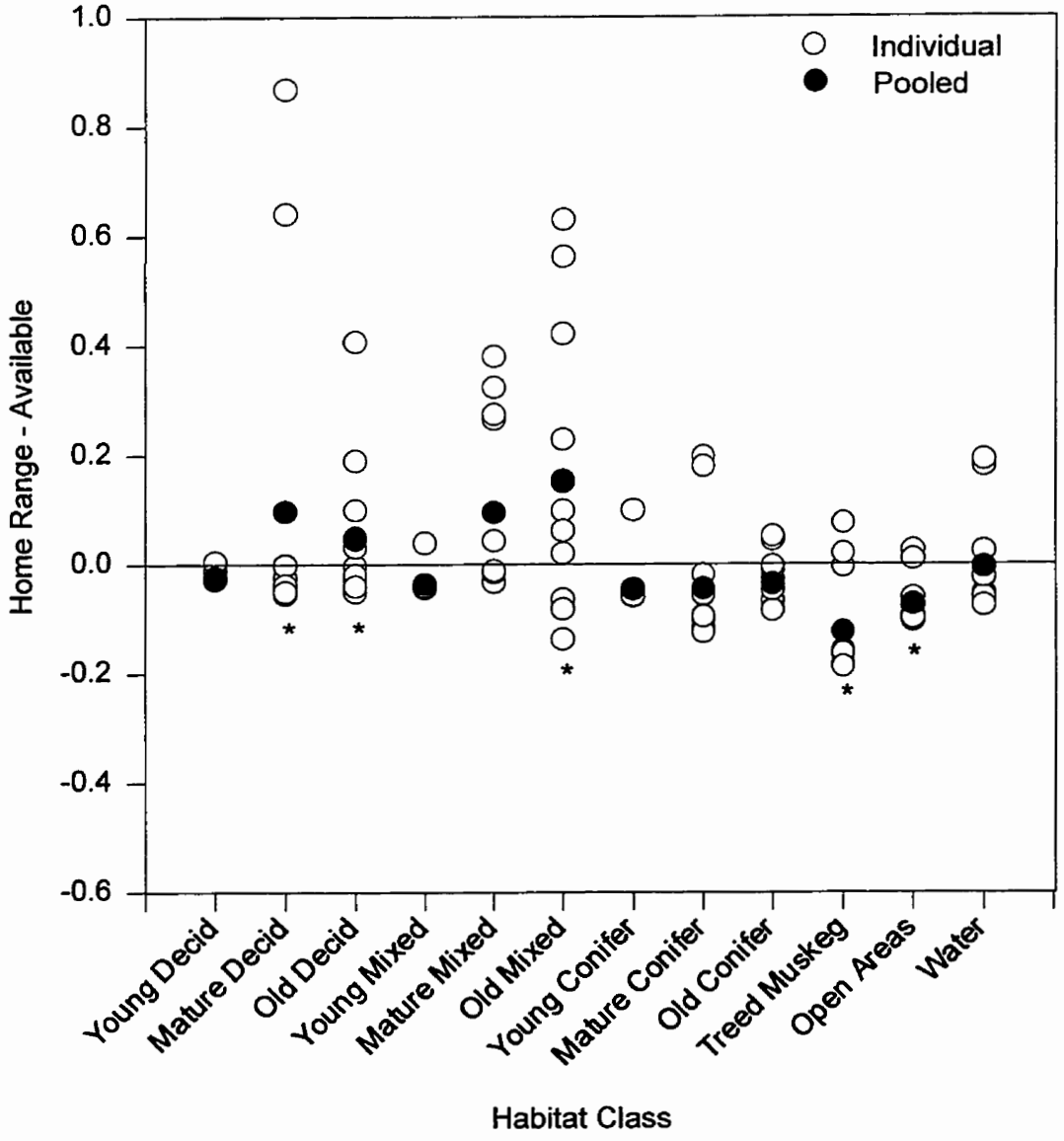


Figure 5. Barred Owl habitat selection based on non-breeding home range habitat composition compared to available habitat within random 1.5 km buffers. Home range represents the proportion of each habitat within home ranges and available habitat the proportion of each habitat within the buffers. Significant differences (*) determined using a Mann-Whitney *U*-test ($P<0.05$).

Table 3. Ranking matrix for Barred Owl breeding home range habitat composition (n=12) compared to study area habitat composition. A triple sign represents significant deviation from random at $P < 0.05$ (+ selected, - avoided).

	Habitat Type											
Habitat Type	Young Decid	Mature Decid	Old Decid	Young Mixed	Mature Mixed	Old Mixed	Young Conifer	Mature Conifer	Old Conifer	Treed Muskeg	Open Areas	Water
Young Decid		-	-	+	-	---	+	-	-	+	---	---
Mature Decid	+		+	+++	+	---	+++	+	+	+++	-	-
Old Decid	+	-		+	-	---	+	-	-	+	---	---
Young Mixed	-	---	-		-	---	+	-	-	+	---	---
Mature Mixed	+	-	+	+++		---	+++	+	+	+++	-	-
Old Mixed	+++	+++	+++	+++	+++		+++	+++	+++	+++	+	+
Young Conifer	-	---	-	-	---	---		-	-	-	---	---
Mature Conifer	+	-	+	+	-	---	+		+	+	-	-
Old Conifer	+	-	+	+	-	---	+	-		+	-	-
Treed Muskeg	-	---	-	-	-	---	+	-	-		---	---
Open Areas	+++	+	+++	+++	+	---	+++	+++	+++	+++		-
Water	+++	+	+++	+++	+	---	+++	+	+	+++	-	

open areas > water > mature deciduous > young mixedwood > mature conifer > old conifer > old deciduous > young deciduous > young mixedwood > treed muskeg (where ">" refers to greater importance according to rank). During the non-breeding period, habitat types were ranked as old mixedwood > mature mixedwood > open areas > old deciduous > mature deciduous > water > old conifer > mature conifer > treed muskeg > young deciduous > young mixedwood (Table 4). Habitat composition of breeding home ranges differed significantly from habitat composition of non-breeding home ranges for three habitat types (Fig. 6). Breeding home ranges contained significantly less old deciduous (z=-2.580, P=0.009), more old mixedwood (z=-2.121, P=0.033) and less treed muskeg (z=-2.046, P=0.040) than did non-breeding home ranges. Breeding core home ranges (50MCP) did not differ significantly in habitat composition from breeding total home ranges (95MCP) (Fig. 7). Non-breeding core home ranges contained significantly less water (z=-2.167, P=0.030) than non-breeding total home ranges (Fig. 8).

3.2.2 Owl Habitat Use and Study Area Composition

Barred Owls did not use available habitat within the study area at random, either during the breeding (Chi-Square=578.347, P<0.001, df=10) or the non-breeding (Chi-Square=760.787, P<0.001, df=10) periods. Evaluated by Bonferroni Confidence Intervals, Barred Owls during the breeding period, selected against young deciduous, old deciduous, young mixedwood, young conifer, mature conifer, old conifer, treed muskeg and open areas (Fig. 9). They selected for mature deciduous and old

Table 4. Ranking matrix for Barred Owl non-breeding home range habitat composition (n= 13) compared to study area habitat composition. A triple sign represents significant deviation from random at $P < 0.05$ (+ selected, - avoided).

	Habitat Type											
Habitat Type	Young Decid	Mature Decid	Old Decid	Young Mixed	Mature Mixed	Old Mixed	Young Conifer	Mature Conifer	Old Conifer	Treed Muskeg	Open Areas	Water
Young Decid		---	---	+++	---	---	+++	---	---	-	---	---
Mature Decid	+++		-	+++	-	-	+++	+	+	+	-	-
Old Decid	+++	+		+++	-	-	+++	+	+	+	-	+
Young Mixed	---	---	---		---	---	+++	---	---	---	---	---
Mature Mixed	+++	+	+	+++		-	+++	+++	+++	+++	+	+
Old Mixed	+++	+	+	+++	+		+++	+++	+++	+++	+++	+++
Young Conifer	---	---	---	---	---	---		---	---	---	---	---
Mature Conifer	+++	-	-	+++	---	---	+++		-	+	-	-
Old Conifer	+++	-	-	+++	---	---	+++	+		+	-	-
Treed Muskeg	+	-	-	+++	---	---	+++	-	-		---	-
Open Areas	+	+	+	+++	-	---	+++	+	+	+++		+
Water	+++	+	-	+++	-	---	+++	+	+	+	-	

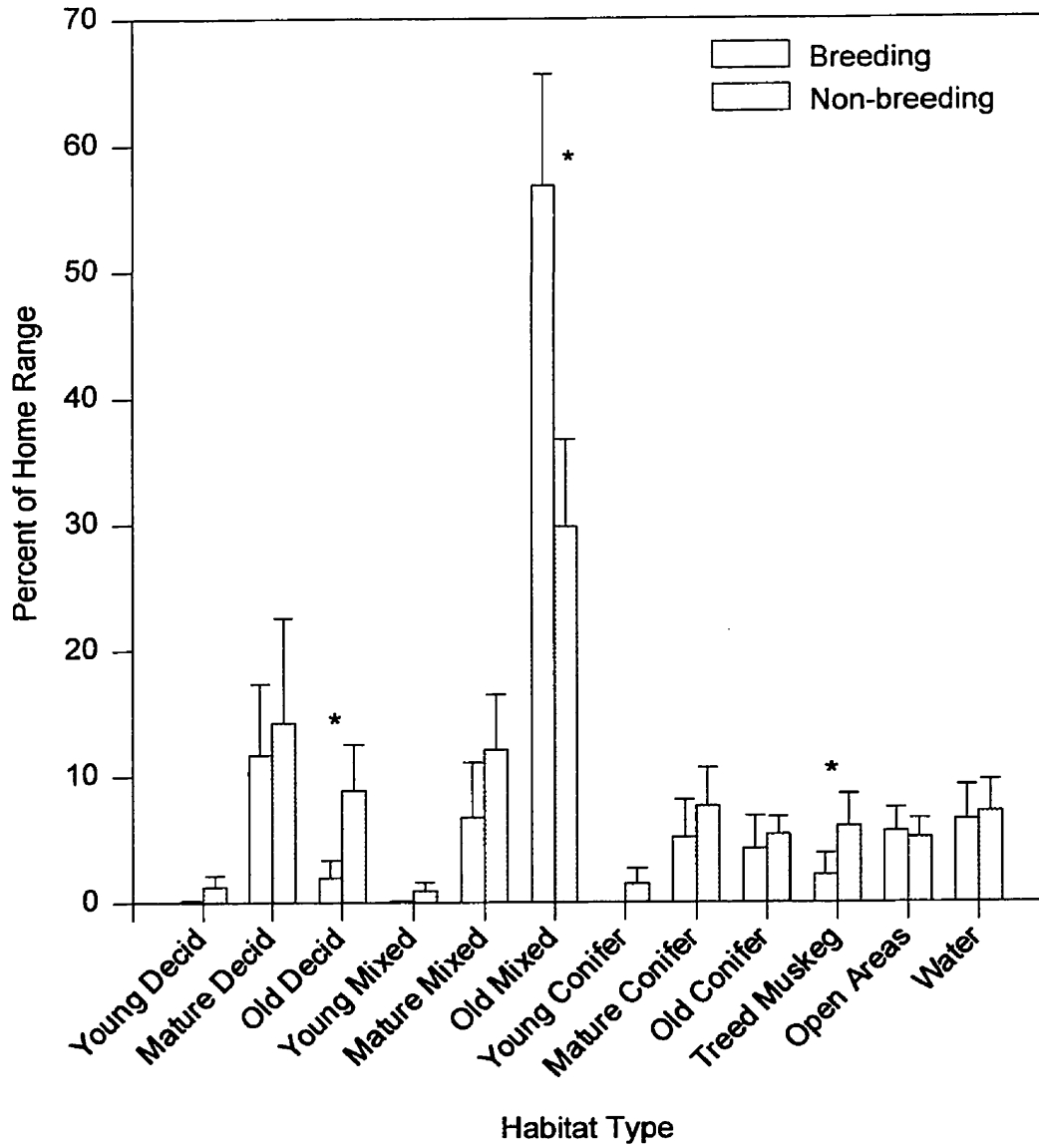


Figure 6. Habitat composition (mean +SE) of Barred Owl breeding (n=12) and non-breeding (n=13) home ranges. Significant (*) differences ($P<0.05$).

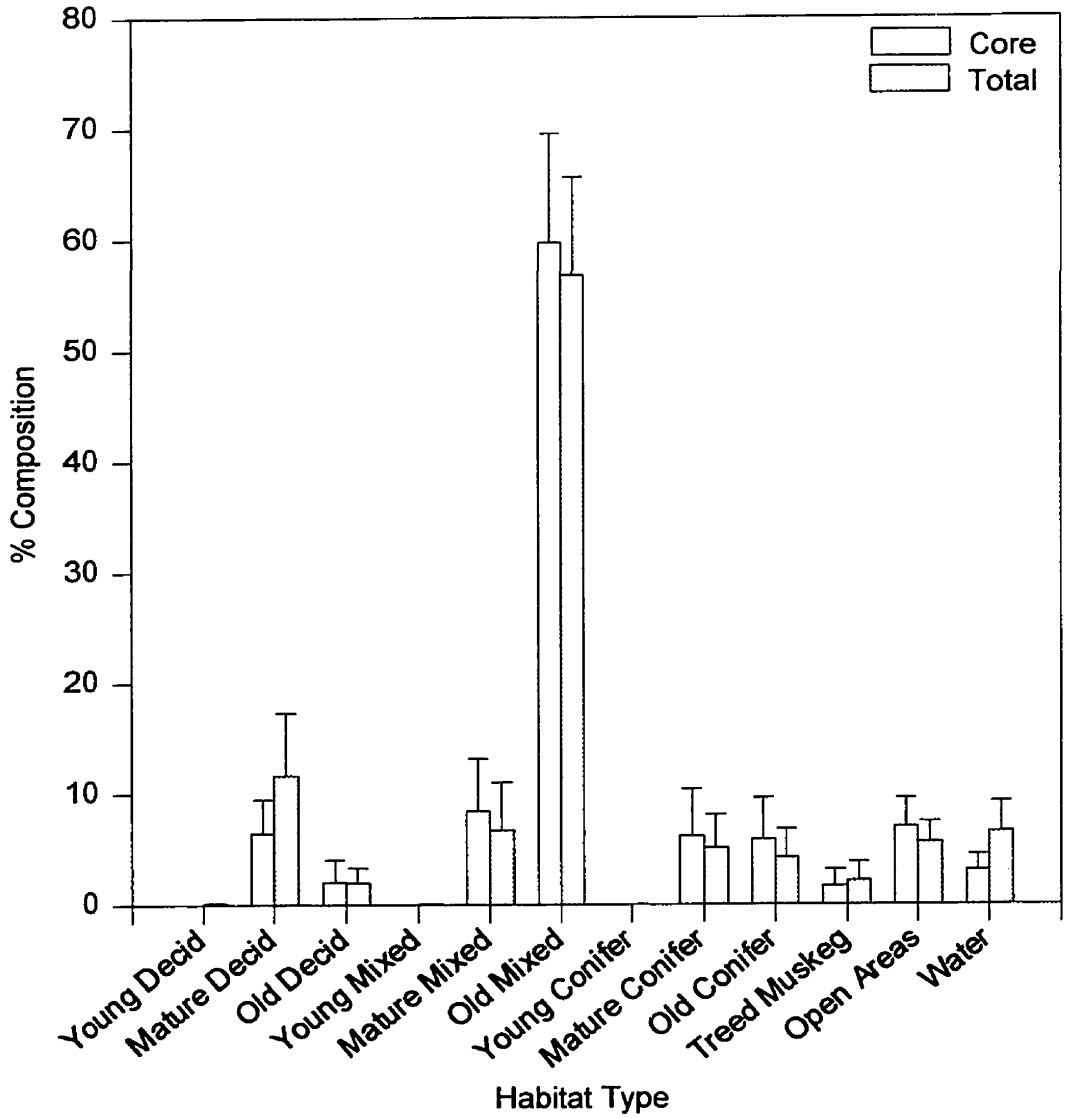


Figure 7. Habitat composition (mean +SE) of Barred Owl core (50% Minimum Convex Polygon) breeding home range and total (95% Minimum Convex Polygon) breeding home range (n=12). Significant (*) differences ($P<0.05$).

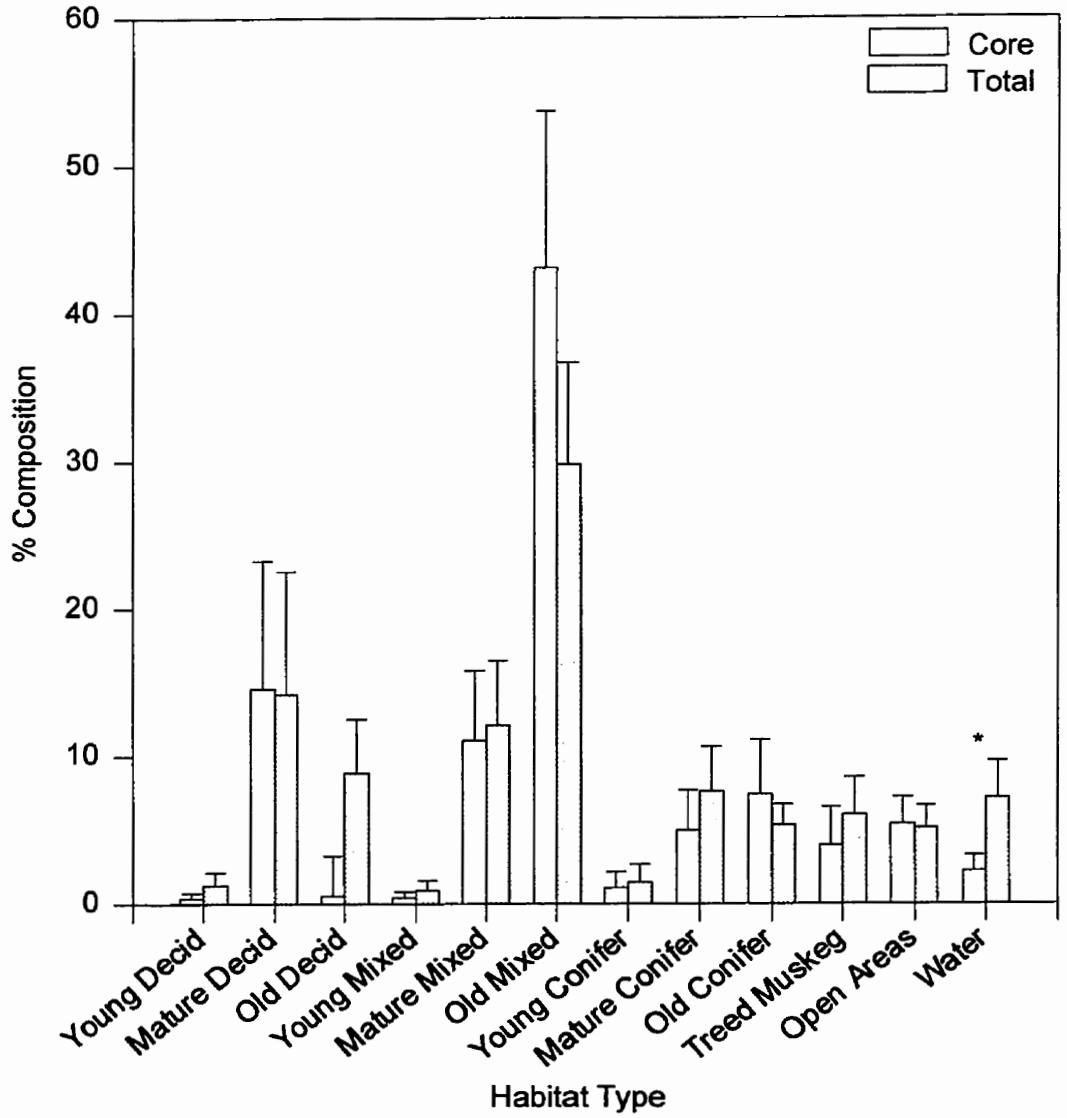


Figure 8. Habitat composition (mean +SE) of Barred Owl core (50% Minimum Convex Polygon) non-breeding home range and total (95% Minimum Convex Polygon) non-breeding home range (n=13). Significant (*) differences (P<0.05).

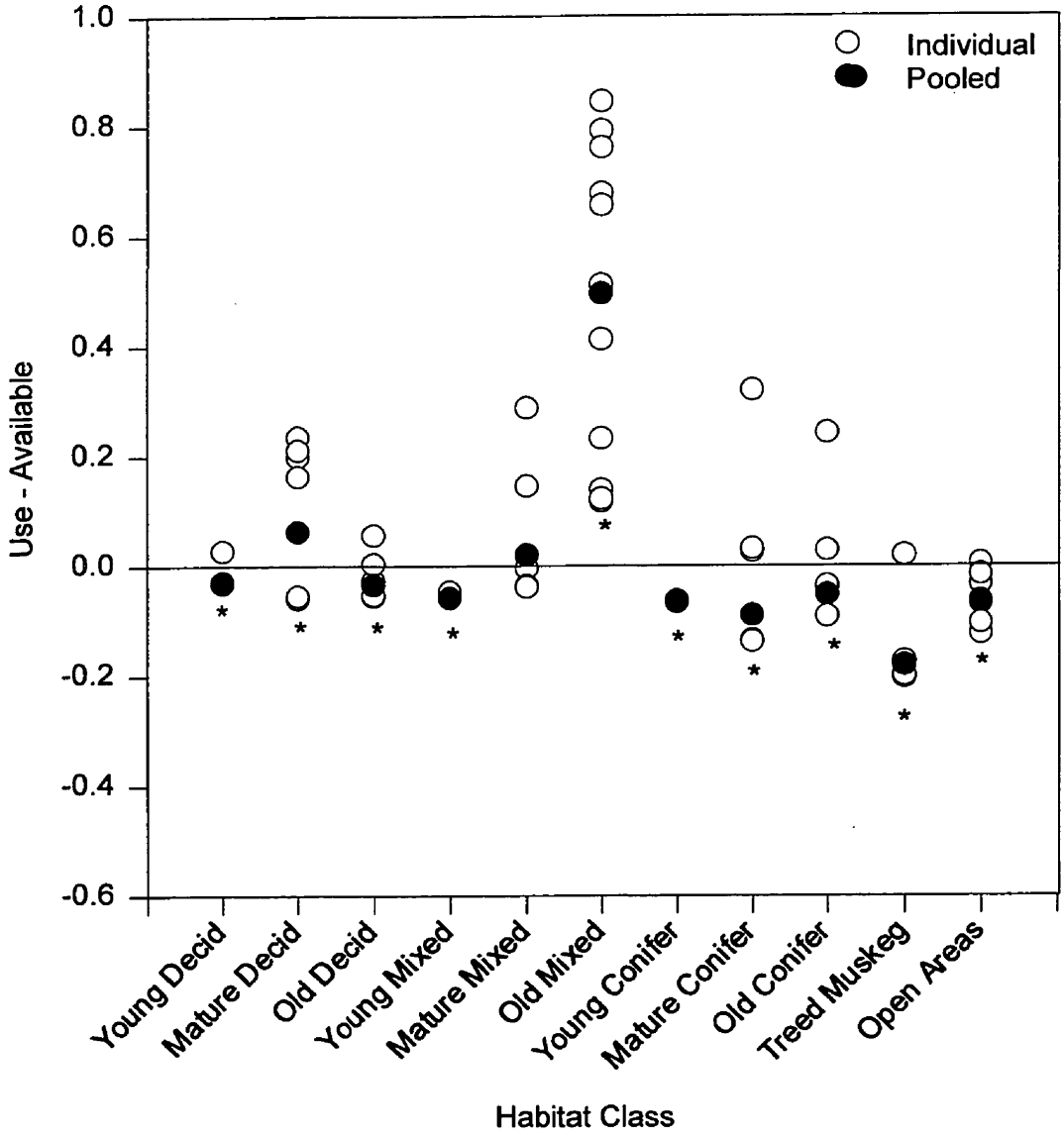


Figure 9. Barred Owl habitat selection based on breeding (n=12) owl habitat use compared to available habitat within the study area. Where use represents the proportion of owl locations in a habitat type and available represents the expected proportion of locations in a habitat type. Significant differences (*) determined through Bonferroni Confidence Intervals ($\propto$ = 0.05).

mixedwood (Fig. 9). During the non-breeding period, Barred Owls selected against young deciduous, young mixedwood, young conifer, mature conifer, old conifer, treed muskeg, and open areas. Mature deciduous, mature mixedwood, and old mixedwood were selected for by Barred Owls in the non-breeding period (Fig. 10).

Based on Log-ratio Compositional Analysis, Barred Owls did not use the available habitat within the study area at random during either the breeding (H=39.028, P<0.001) or non-breeding (H=50.064, P<0.001) periods. During the breeding period, habitat was ranked as old mixedwood > mature mixedwood > mature deciduous > old conifer > open areas > old deciduous > young deciduous > mature conifer > treed muskeg > young mixed > young conifer (Table 5). Non-breeding period owl habitat use compared to the study area available habitat resulted in a ranking of old mixedwood > mature mixedwood > old deciduous > mature deciduous > mature conifer > young deciduous > old conifer > open areas > young conifer > treed muskeg > young mixedwood (Table 6).

Habitat use by Barred Owls during the breeding period did not significantly differ from habitat use during the non-breeding period (Fig. 11).

3.2.3 Owl Habitat Use and Home Range Composition

According to Bonferroni Confidence Intervals, during the breeding period Barred Owls used all habitat in proportion to its availability within their home ranges except for young mixedwood which was selected against (Fig. 12). During the non-breeding period, Barred Owls exhibited habitat selection for seven habitat types when compared

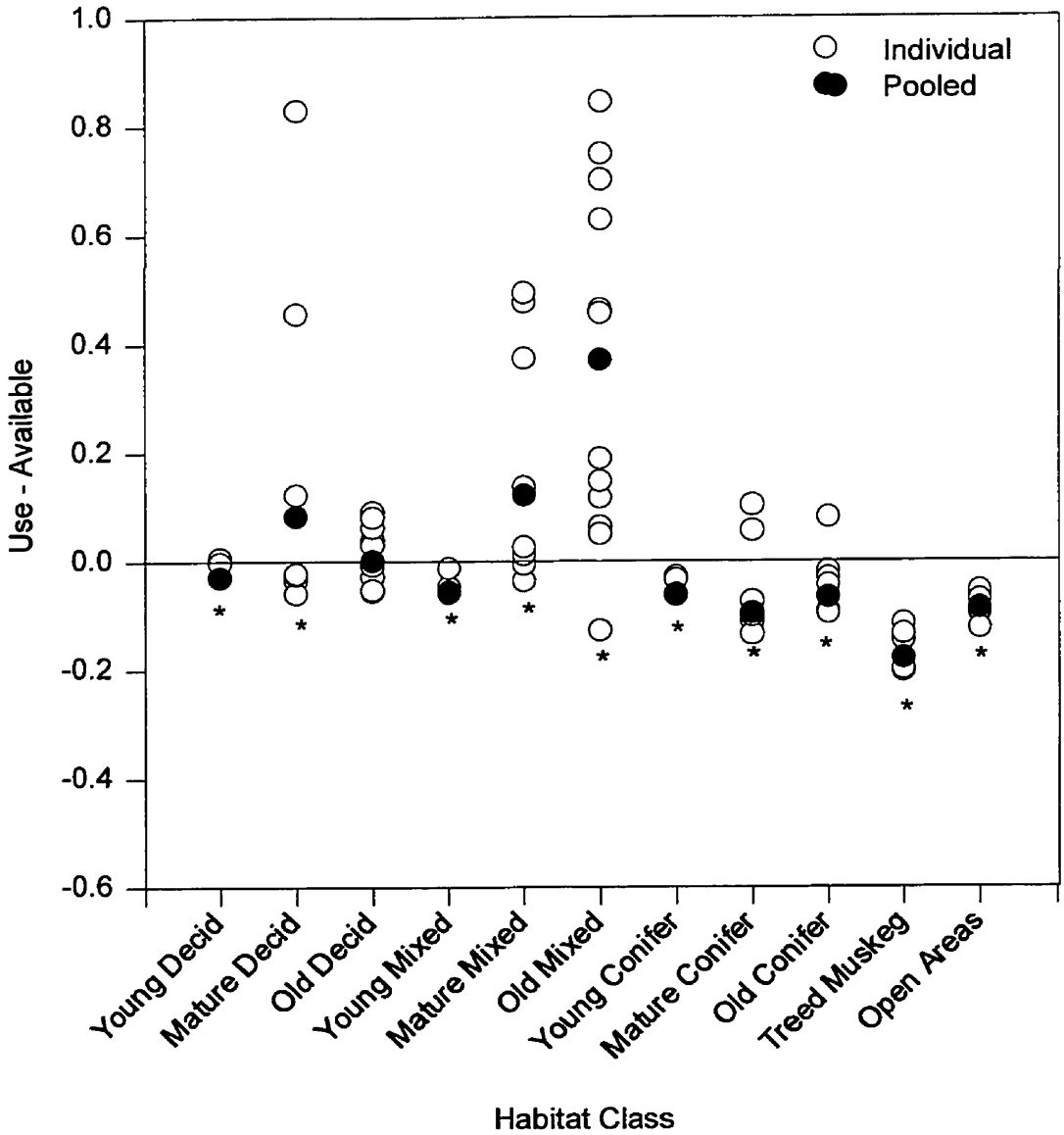


Figure 10. Barred Owl habitat selection based on non-breeding (n=13) owl habitat use compared to available habitat within the study area. Where use represents the proportion of owl locations in a habitat type and available represents the expected proportion of locations in a habitat type. Significant differences (*) determined through Bonferroni Confidence Intervals ($\propto$ = 0.05).

Table 5. Ranking matrix for Barred Owl breeding habitat use, based on radio-locations for 12 Barred Owls compare to the study area habitat composition. A triple sign represents significant deviation from random at $P < 0.05$ (+ selected avoided).

	Habitat Type											
Habitat Type	Young Decid	Mature Decid	Old Decid	Young Mixed	Mature Mixed	Old Mixed	Young Conifer	Mature Conifer	Old Conifer	Treed Muskeg	Open Areas	Rank
Young Decid		-	---	+++	-	---	+++	+	-	+	-	4
Mature Decid	+		+	+++	-	---	+++	+	+	+++	+	8
Old Decid	+	-		+++	-	---	+++	+	-	+	-	5
Young Mixed	---	---	---		---	---	+	-	---	+	---	1
Mature Mixed	+	+	+	+++		---	+++	+	+	+++	+	9
Old Mixed	+++	+++	+++	+++	+++		+++	+++	+++	+++	+++	10
Young Conifer	---	---	---	-	---	---		-	---	-	---	0
Mature Conifer	-	-	-	+	-	---	+		-	+	-	3
Old Conifer	+	-	+	+++	-	---	+++	+		+++	+	7
Treed Muskeg	-	---	-	-	---	---	+	-	---		-	2
Open Areas	+	-	+	+++	-	---	+++	+	-	+		6

Table 6. Ranking matrix for Barred Owl non-breeding habitat use, based on radio-locations for 13 barred Owls compared to the study area habitat composition. A triple sign represents significant deviation from random at $P < 0.05$ (+ selected, - avoided).

	Habitat Type											
Habitat Type	Young Decid	Mature Decid	Old Decid	Young Mixed	Mature Mixed	Old Mixed	Young Conifer	Mature Conifer	Old Conifer	Treed Muskeg	Open Areas	Rank
Young Decid		-	-	+++	---	---	+++	-	-	+	-	5
Mature Decid	+		-	+++	---	---	+++	+	+	+	+	7
Old Decid	+	+		+++	-	---	+++	+	+	+++	+	8
Young Mixed	---	---	---		---	---	-	-	-	-	-	0
Mature Mixed	+++	+	+	+++		---	+++	+++	+++	+++	+++	9
Old Mixed	+++	+++	+++	+++	+++		+++	+++	+++	+++	+++	10
Young Conifer	-	-	---	+	---	---		-	-	+	-	2
Mature Conifer	+	-	-	+	---	---	+		+	+	+	6
Old Conifer	+	-	-	+	---	---	+	-		+	+	4
Treed Muskeg	-	-	---	+	---	---	-	-	-		-	1
Open Areas	+	-	-	+	---	---	+	-	-	+		3

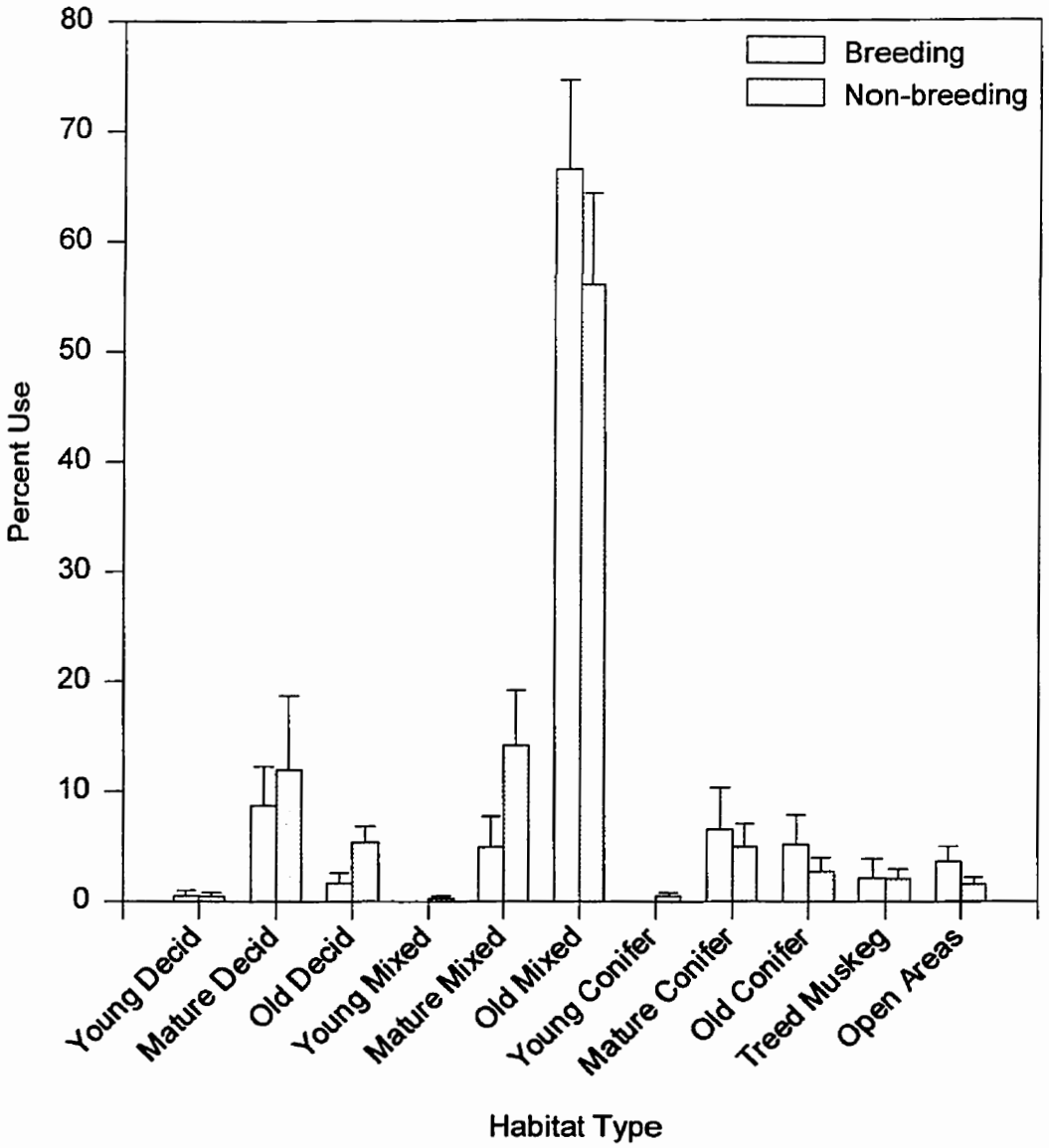


Figure 11. Habitat use by Barred Owls (mean +SE) during the breeding (n=12) and non-breeding (n=14) periods. * Indicates a significant difference ($P<0.05$).

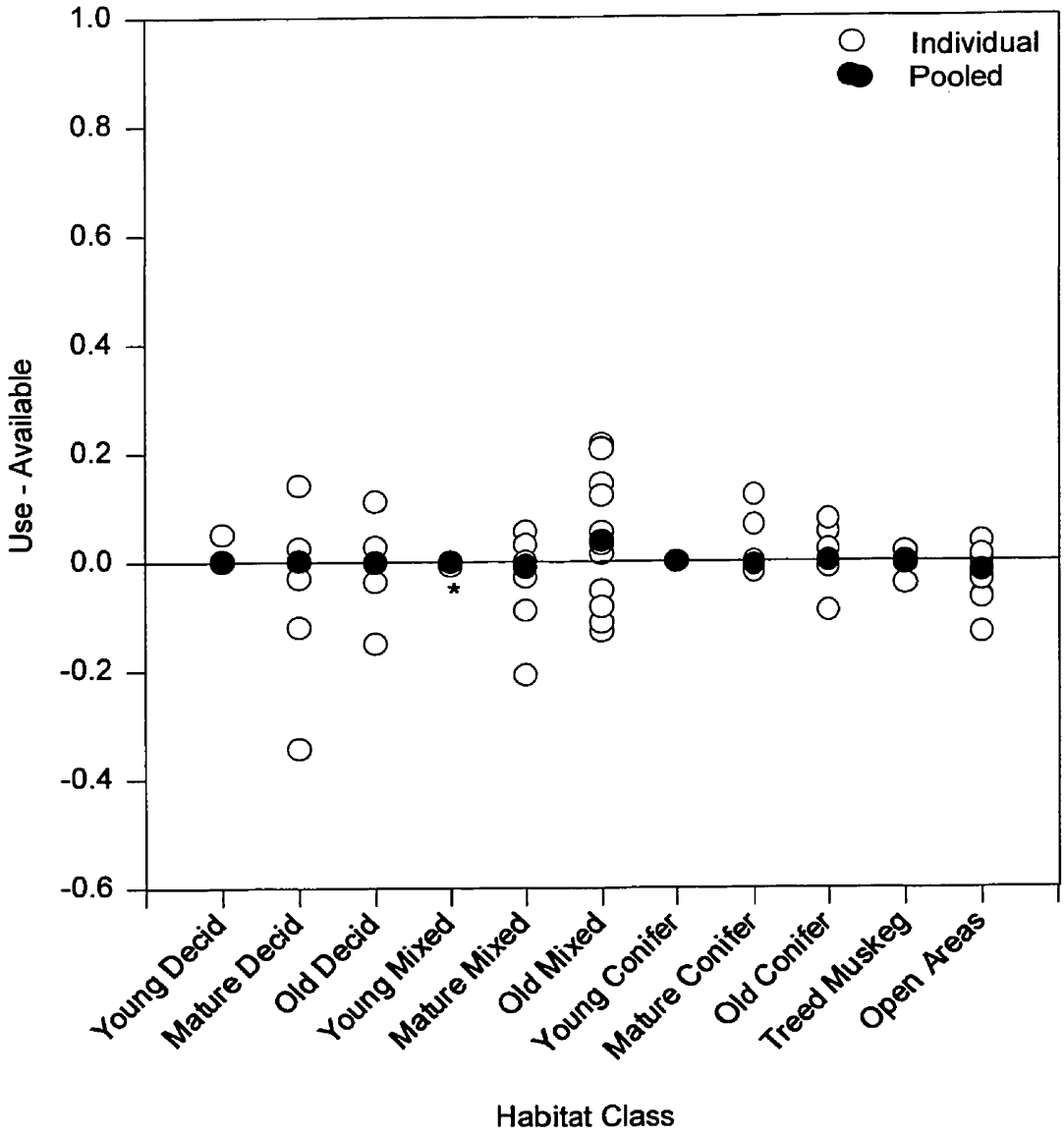


Figure 12. Barred Owl habitat selection based on breeding owl habitat use compared to available habitat within breeding home ranges (n=12). Where use represents the proportion of owl locations in a habitat type and available represents the expected proportion of locations in a habitat type. Significant differences (*) determined through Bonferroni Confidence Intervals ($\propto = 0.05$).

to habitat availability with their non-breeding home ranges (Fig. 13). Barred Owls selected against old deciduous, young conifer, mature conifer, old conifer, treed muskeg, and open areas. Barred Owls selected for old mixedwood during the non-breeding period. Log-ratio Compositional Analysis revealed that Barred Owl use of habitat in the breeding and non-breeding periods was not significantly different (H=1.119, P=0.891, H=11.662, P=0.070) from that expected by the habitat available within the breeding and non-breeding home ranges. Habitat use within the breeding period was ranked as old conifer > old mixedwood > mature deciduous > mature mixedwood > mature conifer > open areas (Table 7). Non-breeding habitat types were ranked as old mixedwood > mature mixedwood > old deciduous > mature deciduous > old conifer > mature conifer > treed muskeg > open areas (Table 8).

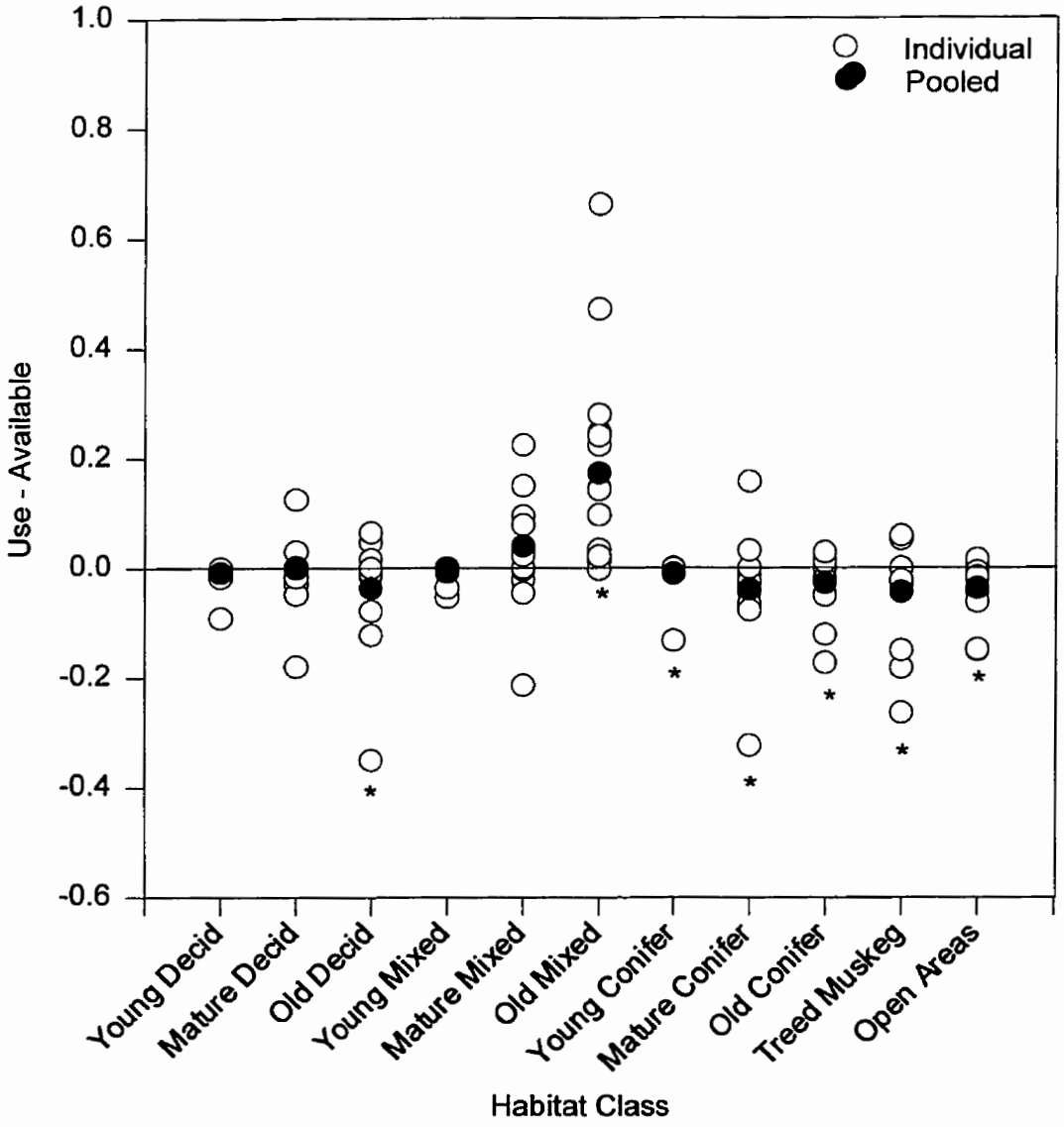


Figure 13. Barred Owl habitat selection based on non-breeding owl habitat use compared to available habitat within non-breeding home ranges (n=13). Where use represents the proportion of owl locations in a habitat type and available represents the expected proportion of locations in a habitat type. Significant differences (*) determined through Bonferroni Confidence Intervals ($\propto = 0.05$).

Table 7. Ranking matrix for Barred Owl breeding habitat use, based on radio-locations for 12 Barred Owls, compared to home range habitat composition. A triple sign represents significant deviation from random at $P < 0.05$ (+ selected, - avoided).

Habitat	Habitat Type						
Type	Mature Decid	Mature Mixed	Mature Old Mixed	Mature Conifer	Old Conifer	Open Areas	Rank
Mature Decid		-	-	+	-	+++	3
Mature Mixed	+		-	+	-	+	2
Old Mixed	+	+		+	-	+++	4
Mature Conifer	-	-	-		-	+	1
Old Conifer	+	+	+	+		+++	5
Open Areas	---	-	---	-	---		0

Table 8. Ranking matrix for Barred Owl non-breeding habitat use, based on radio-locations for 13 Barred Owls compared to home range habitat composition. A triple sign represents significant deviation from random at $P < 0.05$ (+ selected, - avoided).

Habitat	Habitat Type								
Type	Mature Decid	Mature Old Decid	Mature Mixed	Mature Old Mixed	Mature Conifer	Old Conifer	Treed Muskeg	Open Areas	Rank
Mature Decid		-	-	---	+	+	+	+	4
Old Decid	+		-	---	+	+	+	+++	5
Mature Mixed	+	+		-	+++	+++	+++	+++	6
Old Mixed	+++	+++	+		+++	+++	+++	+++	7
Mature Conifer	-	-	---	---		-	+	+	2
Old Conifer	-	-	---	---	+		+	+	3
Treed Muskeg	-	-	---	---	-	-		+	1
Open Areas	-	---	---	---	-	-	-		0

4 DISCUSSION

4.1 Home Range

Barred Owls in the boreal forest of Saskatchewan maintained relatively small home ranges in the breeding period and large home ranges during the non-breeding period as predicted. Non-breeding home ranges overlapped breeding period home ranges entirely, for most owls (80%). The remaining owls shifted their non-breeding home ranges more than 20 km and established breeding home ranges the following year within their non-breeding home ranges. Non-breeding home ranges were essentially expansions of the smaller breeding home ranges. I predicted that Barred Owl home ranges in the boreal forest would be larger than those previously reported for this species. However, during the breeding period, home range size was similar to that reported by Elody and Sloan (1985) for Barred Owls in Michigan, and less than half the size of that reported by Hamer (1988) in Washington. In my study, non-breeding home ranges were on average eight times greater in size than breeding home ranges. Hamer (1988) found an increase of just over two times from breeding to annual home ranges in Washington Barred Owls. Non-breeding home range size in the boreal forest of this study was the largest recorded for this species to date. During both the breeding and non-breeding periods male and female home ranges were similar in size (Table 2). This corroborates Hamer's (1988) findings in Washington.

Barred Owls are thought to be limited by nest site availability (Devereux and Mosher 1984). The expansion of the non-breeding home range to include the breeding home range is thought to occur to protect the relatively scarce nest site (Lundberg

1979). However, to remain on a home range throughout the year requires that all resources required throughout the year be present within the home range. Prey availability is considered to be the major factor determining home range size in birds (Schoener 1968, Lindstedt *et al.* 1986). Data in the same study area (Mazur unpublished data), agree with the classification of the Barred Owl as a generalist predator. As a generalist predator, Barred Owls should be able to use the most available prey within its home range, facilitating year-round residency. The size of Barred Owl non-breeding home ranges is likely determined by the availability of prey. Due to patch depletion or prey cycling, Barred Owl multi-year home ranges may in fact be larger than those of just one year. Carey *et al.* (1992), found the two-year home range of Spotted Owls to be significantly larger than the home range during only one year. The authors attributed this to depletion of prey within patches of the home range; therefore, the Spotted Owls would hunt alternate patches annually.

Barred Owls are known to maintain rigid home range boundaries (Nicholls and Fuller 1987, Hamer 1988), except for the extensive overlap which occurs between mates throughout the year (Hamer 1988). Intraspecific competition is the primary mechanism involved in home range boundary maintenance. In this study, neighbouring Barred Owls were observed actively defending home range boundaries I mapped using radiotelemetry. Both the male and female of a pair were involved in territorial defense which consisted of calling and chasing of intruders. Exclusive home ranges result in the securement of resources for the territory holding owls. Nicholls and Fuller (1987), found Barred Owl home ranges to be persistent over time, with the same territory maintained

for numerous years, even if its occupants had changed. This is likely a result of intraspecific competition between neighbours. Spotted Owls exhibit moderate to large home range overlap between neighbours (Forsman *et al.* 1984, Hamer 1988). This was attributed to the very large size of their home ranges, at least twice as large as non-breeding Barred Owl home ranges in this study, resulting in the Spotted Owls' inability to effectively defend the entire area.

Hamer (1988), suggested that 10.6 months of radio-tracking was required to estimate a Barred Owl's entire annual home range, with their home ranges peaking in size during the winter. However, his home range calculation began in the spring, when home ranges are the smallest. If home range calculation began in September, a much shorter period would be needed to estimate the annual home range. Home range values reported in this study have been divided into breeding and non-breeding periods. Non-breeding values are comparable to annual values as the non-breeding values include the period when home ranges are the largest, as well as the breeding home range.

4.2 Habitat Selection

I predicted that Barred Owls would not use habitat at random, but select specific habitat types. Habitat selection can be viewed as a series of choices, hierarchical in nature, with each choice relying on the previous (Johnson 1980, Morris 1987). Barred Owls are forest-dwelling birds, according to first order habitat selection (Johnson 1980). The placement of a home range or where an animal chooses to live, is considered

second order habitat selection (Johnson 1980, Morris 1987). Barred Owls in this study also displayed strong second order habitat selection. Breeding home ranges were found in areas of old mixedwood forest, open areas, water and mature deciduous forests, and avoided young forests and coniferous forests (Fig. 4, Table 3). The breeding home range must provide resources for successful reproduction. Of these a suitable nest site is of extreme importance (Lundberg 1979, Orians and Wittenberger 1991). Barred Owls primarily nest in tree cavities, which are considered to be quite scarce (Devereux and Mosher 1984). In the boreal forest of Alberta, Lee *et al.* (1995) found old aspen mixedwood stands to have the greatest density of standing dead trees broken at the top (snags). Furthermore, old aspen mixedwood was the only class which contained large diameter (>40 cm dbh) trees and snags, which are the minimum size needed to serve as a suitable nest tree for Barred Owls. In the boreal forest of Saskatchewan, these figures are likely to be similar. Barred Owls in the boreal forest of Saskatchewan nested in large diameter trees, averaging 47.4 cm dbh (n=15; Mazur *et al.* In press). The hardwood component of mixedwood forests is probably necessary for successful Barred Owl nesting, since *Populus* spp. tend to decay faster than softwoods and break off creating a snag instead of uprooting like conifers (Peterson and Peterson 1992). Mazur *et al.* (In press) found 55% of Barred Owl nests in hardwood snags (*Populus tremuloides, P. balsamifera, Betula papyrifera*). Thirty-three percent (5) of nests were in conifers, but only two were in conifer snags.

Non-breeding home range placement was also non-random. Barred Owl home ranges contained more mature and old mixedwood, mature and old deciduous, open

areas and water than expected at random. (Fig. 5, Table 4). Barred Owls typically maintain non-breeding home ranges that encompass the breeding home range and consequently the nest site. This is thought to be a strategy that secures the nest site (Lundberg 1979). However, the habitat within the non-breeding home range must supply the resources necessary for survival outside the breeding period. Prey availability presumably contributes to the size of the non-breeding home range and the habitats within (Lindstedt *et al.* 1986). Mature and old aspen mixedwood forests in Alberta contained the highest species diversity and abundance of potential prey of Barred Owls (McDonald 1995, Roy *et al.* 1995, Schieck and Nietfeld 1995). Red squirrels (*Tamiasciurus hudsonicus*), considered an important prey species for Barred Owls, are most abundant in old mixedwood forests in Saskatchewan boreal forest (Mazur unpublished data). The association with water reflects the presence and abundance, at times, of amphibians in the diet of the Barred Owl. However, this is only a factor during ice-free periods. The high proportion of old mixedwood forest in non-breeding home ranges may simply be an artifact of the placement of breeding home ranges within areas of old mixedwood forests.

Barred Owl non-breeding home ranges contained less old mixedwood forest than breeding home ranges (Fig. 6). Considering that nest sites were found almost exclusively in old mixedwood forest, breeding home ranges would be predicted to be composed largely of old mixedwood, given their relatively small size. Non-breeding home ranges represent considerably larger areas (see home range section), introducing greater geographic variation, and hence greater potential forest stand

variability.

No difference was observed between the habitat composition of the core area of breeding home ranges and the total area of breeding home ranges (Fig. 7). The core represents the area tightly surrounding the nest, and therefore highly representative of nest site habitat. Due to the smaller size of breeding home ranges, the total home range may only encompass a few individual forest stands, reducing their variability. In the same way, non-breeding core and total home range habitat composition was similar (Fig. 8). Water was more abundant in the total non-breeding home range, and old mixedwood appeared to be less abundant in the total home range, but the difference was not significant (Fig. 8). Again, I argue that the increasing size of the total home range captures greater geographic and forest variability.

Monitoring the habitat use of a number of animals in a population provides an estimate the population habitat use over time and space (Aebischer *et al.* 1993). Habitat use by radio-marked Barred Owls was compared to the available habitat in the entire study area and within owl home ranges. Prey availability is probably the most important factor in owl non-breeding habitat use (Morris 1987). Roost sites may also play an important role. Barred Owls are primarily active at night (Johnsgard 1988), but are known to hunt during the day as well (Caldwell 1972). Nocturnal owl locations were considered to be representative of foraging sites, and diurnal locations of roosting sites. Barred Owls were not found to use roost sites repeatedly; instead, they were typically found to roost in the same stand they had hunted in during the night. Therefore, Barred Owl habitat use represents both roosting and foraging habitat. Similar conclusions

have been drawn for the closely related Spotted Owl (Carey *et al.* 1989).

During the breeding period, Barred Owls used mature and old mixedwood, and mature deciduous forest more than expected, based on available habitat within the study area (Fig. 9, Table 5). The significant selection against and moderate rank of open areas suggests that these are not as important as suggested by the home range composition. However, in order to forage in this habitat, Barred Owls would have to hunt from adjacent forest edges, resulting in many of the locations indicating use of the adjacent forest and not the open area. Therefore, the use of open areas may be under-represented. Habitat use in the non-breeding period also suggested selection for mature and old mixedwood, and mature and old deciduous forests (Fig. 10, Table 6). However, there was considerably more variation in owl use of mature deciduous than in the breeding period (Figs. 9 and 10). Overall, Barred Owls used habitat in the same proportion during the breeding and non-breeding periods (Fig. 11). This presumably reflects the preference of certain habitats for essential resources such as prey and roost sites.

Habitat selection at the second order, that of home range placement, affects all subsequent habitat choices (Orians and Wittenberger 1991). Habitat within home ranges determines the availability of patches that must provide all the necessary resources. It may be argued that habitat within a wide area is potentially available to a Barred Owl, since the owl is mobile and endothermic. However, due to intraspecific competition and nest site tenacity, only the habitat within an individual's home range is truly available. During the breeding period, Barred Owls used habitat in proportion to its

availability within their home ranges (Fig. 12, Table 7). Only young mixedwood was shown to be selected against. This suggests that where a Barred Owl chooses to live is the primary form of habitat selection during the breeding period. However, given the size of Barred Owl breeding home ranges, only a few forest stands may be present, leaving the owls little choice. Conversely, in the non-breeding period, Barred Owls further selected habitat from that available within their home ranges (Fig. 13, Table 8). Barred Owls continued to use old mixedwood heavily, and to a lesser extent mature mixedwood, and mature deciduous (Fig. 13, Table 8). This continued selection of old mixedwood forest reinforces the importance of this forest type. The larger variation of available forest types within non-breeding home ranges may have allowed for the selection to be discerned by this study.

Habitat use by Barred Owls in Saskatchewan boreal forest confirms what I predicted corroborating the findings of Van Ael (1996) and Takats (1997). These findings also agree in with the habitat selection of Barred Owls found in other regions (Elody and Sloan 1985, Bosakowski *et al.* 1987, Nicholls and Fuller 1987, Hamer 1988). Morris (1987) suggested that individuals should forage in habitats that maximize their fitness. This would include hunting to feed an incubating female, nestlings and the individual itself. As a generalist predator, Barred Owls should then forage in habitats that provide the highest level of available prey. In the boreal forest, this is the old mixedwood forest (McDonald 1995, Roy *et al.* 1995, Schieck and Nietfeld 1995). The structural complexity of this habitat leads to a high biological diversity. Refuge from inclement weather or predators is also often considered a feature for which a habitat is

selected. Barrows and Barrows (1981) found that Spotted Owls select roost sites with cooler mean temperatures in the summer, suggesting avoidance of heat stress. This microhabitat selection occurred within the habitat previously selected. Similar to the Spotted Owl, Barred Owls are presumably more susceptible to heat stress than cold given their thick plumage, necessary for cold tolerance. Chesterman and Stelfox (1995) found that old aspen mixedwood forest was cooler during the day in summer than young aspen mixedwood forest, and warmer during the day in winter than young and mature aspen mixedwood forest. Microclimate may therefore be a factor in the selection of old mixedwood forest by Barred Owls. Barred Owls have few natural predators. The Great Horned Owl (*Bubo virginianus*) is one that poses the highest risk. The Great Horned Owl is a bird of fragmented forests and grasslands (Fuller 1979, Johnsgard 1988), and considered an edge specialist. Fragmentation of continuous forests may therefore prove detrimental to Barred Owls as this may increase the numbers of Great Horned Owls.

Habitat selection analysis typically involves a comparison of observed and expected values (Neu *et al.* 1974, Byers *et al.* 1984). These analyses are faced with a unit sum constraint, as the proportions of habitats used all add to total one. Therefore, selection of one habitat will naturally lead to the avoidance of others (Aebischer *et al.* 1993). Aebischer *et al.* (1993) recommended analysis of habitat used versus available habitat where a ratio of the proportions of two habitats used is made with all habitat types. The same ratio would be made for available habitat types. The result is habitat selection being evaluated in relation to selection for all other habitats, removing the unit

sum constraint. Analysis of habitat selection by Barred Owls using log-ratio compositional analysis revealed few differences from the analysis methods faced by the unit sum constraint (Mann-Whitney *U*-tests and Bonferroni Confidence Intervals). Old mixedwood forest was ranked highest by log-ratio compositional analyses in all cases except for owl use and home range composition, where old mixedwood ranked second highest behind old conifer (Table 7). Through Mann-Whitney *U*-tests and Bonferroni Confidence Intervals old mixedwood was significantly selected for in all cases except for owl use and home range composition (Fig. 12). A similar pattern emerges between the analyses, where old mixedwood and mature mixedwood are selected for or ranked highly, followed by mature and old deciduous. As well, young forest types and treed muskeg are found to be ranked low and are significantly selected against (Figs. 4, 5, 9, 10, 13, Tables 3, 4, 5, 6). Discrepancy occurs in the analysis of breeding and non-breeding home range composition. In the breeding period analysis, no significant selection against open areas or water were found with Mann-Whitney *U*-tests, but the observed minus expected values suggest an avoidance of these habitats (Fig. 4). Similarly, in the non-breeding period, significant selection against open areas was found with the Mann-Whitney *U*-test (Fig. 5). Contradicting this, the log-ratio analysis ranked open areas and water second and third highest during the breeding period, and open areas third highest during the non-breeding period (Tables 3, 4). I believe that the log-ratio compositional analysis ranks are misleading, because the contribution to the home range area by open areas and water was small (breeding: open areas 6%, water 7%; non-breeding: open areas 5%). When compared to values generated at random

(open areas: 12%, water 8%), it seems that these habitats were not favoured as reflected by the high ranks in the log-ratio compositional analysis. For the data in this study, the log ratio compositional analysis revealed few differences in habitat selection than revealed through other analysis methods. The main conclusions of this study were the same regardless of the analysis method.

Habitat selection involves a series of choices, and therefore can be thought of as a number of levels of selection. Barred Owls exhibit strong first order habitat selection, being found exclusively in forests. In the second order, Barred Owls selected specific habitats in which they placed their home ranges or used for hunting and roosting. Characteristics of these selected habitat types are what drives the second order habitat selection. These include nests sites, which are considered an important limiting factor of Barred Owls and prey availability among others.

In the boreal forest of Canada, forestry as an industry contributes significantly to local and national economies (Stelfox 1995a, Cumming *et al.* In press). These economic gains are often achieved with the loss of natural ecological processes of the forest. Past and current harvest schedules are based on merchantable forests, employing short rotations, that result in monoculture type forest stands with low structural heterogeneity. This has resulted in the "unmixing" of the mixedwood forest (Stelfox *et al.* 1995, Cumming *et al.* In press). The old mixedwood forest a highly species-diverse forest type in the boreal forest; the rain forest of the north (Stelfox 1995b). Attempting to understand the ecological requirements of each species and managing for each species is unrealistic. Instead, harvest practices that result in forest

structure close to those occurring under natural conditions are preferred (Kabzems *et al.* 1995, Stelfox *et al.* 1995). Harvesting plans should attempt to mimic natural disturbance processes, such as fire, in order to maintain forest stand and structural diversity. The Barred Owl in the boreal forest is strongly selective of old forests, particularly old mixedwood forest. As a top predator in this habitat, it is likely very sensitive to changes in the structural environment. The presence or absence of a Barred Owl population from managed forest would indicate a healthy old mixedwood forest or lack thereof. Based on this study, management of forests specifically for Barred Owls is not recommended, but instead, the continued maintenance of the boreal forest mosaic which includes areas of old mixedwood forest, including the stand structure, should be the primary goal.

5 SUMMARY

In the boreal forest of Saskatchewan, Canada, Barred Owls maintained relatively small home ranges in the breeding period, and large home ranges in the non-breeding period. Non-breeding home ranges were on average eight times larger than breeding home ranges. Non-breeding home ranges were expansions of breeding home ranges, with breeding home ranges contained within non-breeding home ranges. The non-breeding home ranges were the largest recorded to date for this species. This is attributed to lower prey densities in the boreal forest compared to more southern regions of the Barred Owl's range.

Barred Owls were not found to use habitat at random. Breeding home ranges

were placed in areas of old mixedwood forest, open areas, water and mature deciduous forest. The primary factor influencing breeding home range placement is believed to be nest site availability. In the boreal forest, old mixedwood forest contains the highest densities of large trees and snags used for nesting by Barred Owls. Non-breeding home ranges were found to contain higher proportions of mature and old mixedwood forest, mature and old deciduous forest, open areas, and water than expected at random. Non-breeding home ranges contained less old mixedwood forest than breeding home ranges.

Compared to the habitat available within the study area, Barred Owls selected old mixedwood and mature deciduous forest for roosting and foraging during the breeding period. Similarly, in the non-breeding period Barred Owls selected mature and old mixedwood forest, and mature and old deciduous forest for roosting and foraging. Barred Owls demonstrated an avoidance of young forest and treed muskeg during both breeding and non-breeding periods. When compared to habitat available within the owl's home range, Barred Owls did not demonstrate further habitat selection during the breeding period. This suggests that the placement of the home range is the primary level of habitat selection. During the non-breeding period, Barred Owls further selected old mixedwood forest within their home ranges and avoided coniferous forest, old deciduous forest, treed muskeg and open areas.

In the boreal forest of Saskatchewan, Canada, Barred Owls maintained large home ranges, and selected specific habitat types. Their large area requirements and specific habitat needs make them susceptible to habitat alternations, and therefore a

good potential candidate as a management indicator of old mixedwood forest in this region. This study provides baseline habitat and area selection data for the Barred Owl essential for its use as a forest management tool.

6 LITERATURE CITED

Ackerman, B.B., F.A. Leban, M.D. Samuel, and E.O. Garton. 1990. User's Manual for Program HOME RANGE. 2nd ed. Technical Report 15, Forestry, Wildlife and Range Experiment Station, University of Idaho, Moscow, Idaho. 80 pages.

Aebischer, N.J., P.A. Robertson, and R.E. Kenward. 1993. Compositional analysis of habitat use from animal radio-tracking data. Ecology 74(5):1313-1325.

Alcock, J. 1989. Animal Behavior: An Evolutionary Approach. Fourth Edition, Sinauer Associates, Inc. Sunderland, MS. 596 pages.

Barrows, C.W. 1981. Roost selection by spotted owls: an adaptation to heat stress. Condor 83:302-309.

Bent, A.C. 1961. Northern Barred Owl. *In* Life Histories of North American birds of prey. Part II. Dover Publishing Inc., New York.

Bosakowski, T. 1994. Landsat reveals negative effect of forest fragmentation on Barred Owl distribution. Records of New Jersey Birds 20(3):66-70.

Bosakowski, T., and D.G. Smith. 1992. Comparative diets of sympatric nesting raptors in the eastern deciduous forest biome. Can. J. Zool. 70:984-992.

Bosakowski, T., R. Speiser, and J. Benzinger. 1987. Distribution, density, and habitat relationships of the barred owl in northern New Jersey. *In:* Biology and Conservation of Northern Forest Owls: Symposium Proceedings (R.W. Nero, R.J. Clark, R.J. Knapton, and R.H. Hamre, *Eds*). USDA Forest Serv. Gen. Tech. Rep. RM-142. pp. 135-143.

Boxall, P.C., and P.H.R. Stepney. 1982. The distribution and status of the barred owl in Alberta. Can. Field Nat. 96(1):46-50.

Burt, W.H. 1943. Territoriality and home range concepts as applied to mammals. J. Mamm. 24:346-352.

Byers, C.R., R.K. Steinhorst, and P.R. Krausman. 1984. Clarification of a technique for analysis of utilization-availability data. J. Wildl. Manage. 48(3):1050-1053.

Caldwell, L.D. 1972. Diurnal hunting by a Barred Owl. Jack-Pine Warbler 50(3):93-94.

Carey, A.B., S.P. Horton, and B.L. Biswell. 1992. Northern spotted owls: influence of prey base and landscape character. Ecol. Mono. 62(2):223-250.

Carey, A.B., S.P. Horton, and J.A. Reid. 1989. Optimal sampling for radiotelemetry studies of spotted owl habitat and home range. Res. Pap. PNW-RP-416, Portland, OR. 17 pages.

Carey, A.B., and K.C. Peeler. 1995. Spotted Owls: Resource and Space Use in Mosaic Landscapes. J. Raptor Res. 29(4):223-239.

Carey, A.B., J.A. Reid, and S.P. Horton. 1990. Spotted owl home range and habitat use in southern Oregon Coast Ranges. J. Wildl. Manage. 54:11-17.

Carpenter, T.W. 1992. Utility of wing length, tail length and tail barring in determining the sex of Barred Owls collected in Michigan and Minnesota. Condor 94:794-795.

Chesterman, D., and J.B. Stelfox. 1995. Relationships between microclimate and stand age and structure in aspen mixedwood forests in Alberta. *In:* Relationships between stand age, stand structure, and biodiversity in aspen mixedwood forests in Alberta (J.B. Stelfox, *Ed*). Jointly published by Alberta Environmental Centre (AECV95-R1), Vegreville, AB, and Canadian Forest Service (Project No. 0001A) Edmonton, AB. pp. 13-27.

Cody, M.L. 1985. Habitat Selection in Birds. Academic Press, Orlando, FL.

Cumming, S.G., P.J. Burton, S. Prahacs, and M.R. Garland. In Press. Potential conflicts between timber supply and habitat protection in the boreal mixedwood of Alberta, Canada: A simulation study. For. Ecol. Manage. :000-000.

Devereux, J.G., and J.A. Mosher. 1984. Breeding ecology of Barred Owls in the central Appalachians. J. Raptor Res. 18:49-58.

Duncan, J.R. 1987. Movement strategies, mortality, and behavior of radio-marked Great Gray Owls in southeastern Manitoba and northern Minnesota. *In:* Biology and Conservation of Northern Forest Owls: Symposium Proceedings (R.W. Nero, R.J. Clark, R.J. Knapton, and R.H. Hamre, *Eds*). USDA Forest Serv. Gen. Tech. Rep. RM-142 pp. 101-107.

Duncan, J.R. 1992. Influence of prey abundance and snow cover on Great Gray Owl breeding dispersal. Unpublished Ph.D. Thesis, University of Manitoba, Winnipeg, MB. 127 pages.

Duncan, J.R., and P.H. Hayward. 1994. Review of technical knowledge: Great Gray Owls. *In:* Flammulated, Boreal, and Great Gray Owls in the United States: A technical conservation assessment (G.D. Hayward, and J. Verner, *Eds*). USDA Forest Serv. Gen. Tech. Rep. RM-253 Fort Collins, CO. pp. 159-175.

Dunstan, T.C., and S.D. Sample. 1972. Biology of Barred Owls in Minnesota. Loon 44:111-115.

Elderkin, M.F. 1987. The breeding and feeding ecology of a barred owl *Strix varia* Barton population in Kings County, Nova Scotia. Unpublished M.Sc. Thesis, Acadia University, Wolfville, N.S., Canada. 203 pages.

Elody, B.I., and N.F. Sloan. 1984. A mist net technique useful for capturing Barred Owls. N.A. Bird Bander 9:13-14.

Elody, B.I., and N.F. Sloan. 1985. Movements and habitat use of Barred Owls in the Huron Mountains of Marquette County, Michigan, as determined by radiotelemetry. Jack-Pine Warbler 63:3-8.

Environment Canada Parks. 1986. Prince Albert National Park Resource Description and Analysis. Environment Canada Parks, Prairie and Northern Region, Winnipeg. 2 vols.

Ford, R.G., and D.W. Krumme. 1979. The Analysis of Space Use Patterns. J. Theor. Biol. 76:125-155.

Forsman, E.D., E.C. Meslow, and H.M. Wight. 1984. Distribution and biology of the Spotted Owl in Oregon. Wildl. Monogr. 87:1-64.

Fretwell, S.D., and H.L. Lucas. 1970. On territorial behaviour and other factors influencing habitat distribution in birds. Acta Biotheoretica 19:16-36.

Fuller, M.R. 1979. Spatiotemporal ecology of four sympatric raptor species. Unpublished Ph.D. Thesis, University of Minnesota, Minneapolis. 220 pages.

Gautestad, A.O., and I. Mysterud. 1995. The home range ghost. Oikos 74:195-204.

Grant, J. 1966. The Barred Owl in British Columbia. Murrelet 47(2):39-45.

Hamer, T.E. 1988. Home range size of the Northern Barred Owl and Northern Spotted Owl in western Washington. Unpublished M.Sc. Thesis, Western Washington University. 86 pages.

Hamer, T.E., E.D. Forsman, A.D. Fuchs, and M.L. Walters. 1994. Hybridization between Barred and Spotted Owls. Auk 111(2):487-492.

Hayward, G.D., P.H. Hayward, and E.O. Garton. 1993. Ecology of Boreal Owls in the northern Rocky Mountains, U.S.A. Wildl. Monogr. 124:1-59.

Hayward, G.D., and J. Verner. 1994. Flammulated, Boreal, and Great Gray Owls in the United States: A technical conservation assessment. U.S. Department of Agriculture, Forest Service, Rocky Mountain and Range Experiment Station, Gen. Tech. Rep. RM-253., Fort Collins, CO. 214 pages.

Hildén, O. 1965. Habitat Selection in Birds. Ann. Zool. Fenn. 2:53-75.

Hildén, O., and T. Solonen. 1987. Status of the Great Gray Owl in Finland. *In:* Biology and Conservation of Northern Forest Owls: Symposium Proceedings (R.W. Nero, R.J. Clark, R.J. Knapton, and R.H. Hamre, *Eds*). USDA Forest Serv. Gen. Tech. Rep. RM-142. pp. 115-120.

Houston, S. 1959. First records of the Barred Owl in Saskatchewan. Blue Jay 17(3):94.

Johnsgard, P.A. 1988. North American Owls. Smithsonian Institution Press, Washington. 295 pages.

Johnson, D.H. 1980. The comparison of usage and availability measurements for evaluating resource preference. Ecology 61(1):65-71.

Kabzems, R., D. Coopersmith, and R. Negrave. 1995. Mixedwoods By Design. Forest Science Research. British Columbia Ministry of Forests.

Korpimäki, E. 1981. On the ecology and biology of Tengmalm's Owl (*Aegolius funereus*) in southern Ostrobothnia and Suomenselka, western Finland. Acta Univ. Ouluensis Ser. A. Sci. Rerum Nat. 118 Biol. 13. 84 pages.

Korpimäki, E. 1986. Niche relationships and life-history tactics of three sympatric Strix owl species of Finland. Orn. Scand. 17:126-132.

Korpimäki, E. 1987. Sexual size dimorphism and life-history traits of Tengmalm's Owl: A review. *In:* Biology and Conservation of Northern Forest Owls: Symposium Proceedings (R.W. Nero, R.J. Clark, R.J. Knapton, and R.H. Hamre, *Eds*). USDA Forest Serv. Gen. Tech. Rep. RM-142. pp. 157-161.

Lack, D. 1933. Habitat Selection in Birds. J. Anim. Ecol. 2:239-262.

Laidig, K.J., and D.S. Dobkin. 1995. Spatial Overlap and Habitat Associations of Barred Owls and Great Horned Owls in Southern New Jersey. J. Raptor Res. 29(3):151-157.

Lee, P.C., S. Crites, M. Nietfeld, H. Van Nguyen, and J.B. Stelfox. 1995. Changes in snag and down woody material characteristics in a chronosequence of aspen mixedwood forests in Alberta. *In:* Relationships between stand age, stand structure, and biodiversity in aspen mixedwood forests in Alberta (J.B. Stelfox, *Ed*). Jointly published by Alberta Environmental Centre (AECV95-R1), Vegreville, AB, and Canadian Forest Service (Project No. 0001A) Edmonton, AB. pp. 49-61.

Lindenas, D.G. 1985. Forest inventory interpretation and mapping manual. Forestry Branch, Saskatchewan Parks and Renewable Resources.

Lindstedt, S.L., B.J. Miller, and S.W. Buskirk. 1986. Home range, time and body size in mammals. Ecology 67:413-418.

Lundberg, A. 1976. Breeding success and prey availability in a Ural Owl, *Strix uralensis* Pall. population in central Sweden. Zoon 4:65-72.

Lundberg, A. 1979. Residency, migration and a compromise: adaptations to nest-site scarcity and food specialization in three Fennoscandian owl species. Oecologia (Berlin) 41:273-281.

Lundberg, A. 1981. Population ecology of the Ural Owl *Strix uralensis* in central Sweden. Orn. Scand. 12:111-119.

Marks, J.S., D.P. Hendricks, and V.S. Marks. 1984. Winter food habits of Barred Owls in western Montana. Murrelet 65:28-29.

Marti, C.D. 1974. Feeding Ecology of four sympatric owls. Condor 76:45-61.

Mazur, K.M., P.C. James, and S.D. Frith. In Press. Barred Owl nest site characteristics in the boreal forest of Saskatchewan, Canada. *In*: Biology and conservation of owls of the northern hemisphere: Second international symposium; 1997 February 5-9; Winnipeg, Manitoba. Gen. Tech. Rep. NC- . St. Paul MN: U.S. Department of Agriculture, Forest Service, North Central Forest Experiment Station: 000-000.

McCallum, D.A. 1994. Methods and Terminology used with studies of habitat associations. *In:* Flammulated, boreal, and great gray owls in the United States: A technical conservation assessment (G.D. Hayward, and J. Verner, *Eds*). USDA Forest Serv. Gen. Tech. Rep. RM-253. pp. 5-8.

McDonald, L. 1995. Relationships between northern flying squirrels and stand age and structure in aspen mixedwood forests in Alberta. *In:* Relationships between stand age, stand structure, and biodiversity in aspen mixedwood forests in Alberta (J.B. Stelfox, *Ed*). Jointly published by Alberta Environmental Centre (AECV95-R1), Vegreville, AB, and Canadian Forest Service, Edmonton, AB. pp. 227-240.

McGarigal, K., and J.D. Fraser. 1984. The effect of forest stand age on owl distribution in south western Virginia. J. Wildl. Manage. 48:1393-1398.

McNab, B.K. 1963. Bioenergetics and the determination of home range size. Am. Nat. 97:133-140.

McNay, R.S., J.A. Morgan, and F.L. Bunnell. 1994. Characterizing Independence of Observations in Movements of Columbian Black-Tailed Deer. J. Wildl. Manage. 58(3):422-429.

Mikkola, H. 1983. Owls of Europe. Buteo Books, Vermillion, SD. 397 pages.

Morris, D.W. 1987. Ecological scale and habitat use. Ecology 68(2):362-369.

Nero, R.W., R.J. Clark, R.J. Knapton, and R.H. Hamre. 1987. Biology and Conservation of Northern Forest Owls: Symposium Proceedings. USDA Forest Serv. Gen. Tech. Rep. RM-142, Fort Collins, CO. 309 pages.

Neu, C.W., C.R. Byers, and J.M. Peek. 1974. A technique for analysis of utilization-availability data. J. Wildl. Manage. 38(3):541-545.

Newton, I. 1979. Population Ecology of Raptors. Buteo Books, Vermillion, South Dakota. 399 pages.

Nicholls, T.H., and M.R. Fuller. 1987. Territorial aspects of Barred Owl home range and behavior in Minnesota. *In:* Biology and Conservation of Northern Forest Owls: Symposium Proceedings (R.W. Nero, R.J. Clark, R.J. Knapton, and R.H. Hamre, *Eds*). USDA Forest Serv. Gen. Tech. Rep. RM-142. pp. 121-128.

Nicholls, T.H., and D.W. Warner. 1972. Barred Owl habitat use as determined by radiotelemetry. J. Wildl. Manage. 36:213-224.

Noble, G.K. 1939. The role of dominance in the social life of birds. Auk 56:263-273.

Orians, G.H., and J.F. Wittenberger. 1991. Spatial and temporal scales in habitat selection. Am. Nat. 137:829-849.

Padbury, G.A., W.K. Head, and W.E. Souster 1978. Biophysical resource inventory of the Prince Albert National Park, Saskatchewan. Saskatchewan Institute of Pedology Publication S185, Saskatoon, SK.

Peterson, E.B., and N.M. Peterson. 1992. Ecology, management, and use of aspen and balsam poplar in the prairie provinces, Canada. For. Can., Northwest Reg., North. For. Cent., Edmonton, AB. (Spec. Rep. 1.). 252 pages.

Pettingill, O.S., Jr. 1985. Ornithology in Laboratory and Field. Fifth ed. Academic Press, Inc., Orlando, Florida. 403 pages.

Pitelka, F.A. 1959. Numbers, breeding schedule, and territoriality in Pectoral Sandpipers of northern Alaska. Condor 61(4):233-264.

Pulliam, H.R., and B.J. Danielson. 1991. Sources, sinks, and habitat selection: A landscape perspective on population dynamics. Am. Nat. 137:50-66.

Redpath, S.M. 1995. Habitat fragmentation and the individual: Tawny Owls *Strix aluco* in woodland patches. J. Anim. Ecol. 64:652-661.

Rogers, T.H. 1966. The fall migration. Northern Rocky Mountain-Intermountain region. Aud. Field Notes 20:74.

Roy, L.D., J.B. Stelfox, and J.W. Nolan. 1995. Relationship between mammal biodiversity and stand age and structure in aspen mixedwood forests in Alberta. *In:* Relationships between stand age, stand structure, and biodiversity in aspen mixedwood forests in Alberta (J.B. Stelfox, *Ed*). Jointly published by Alberta Environmental Centre (AECV95-R1), Vegreville, AB, and Canadian Forest Service (Project No. 0001A) Edmonton, AB. pp. 159-189.

Schieck, J., and M. Nietfeld. 1995. Bird species richness and abundance in relation to stand age and structure in aspen mixedwood forests in Alberta. *In:* Relationships between stand age, stand structure, and biodiversity in aspen mixedwood forests in Alberta (J.B. Stelfox, *Ed*). Jointly published by Alberta Environmental Centre (AECV95-R1), Vegreville, AB, and Canadian Forest Service (Project No. 0001A) Edmonton, AB. pp. 115-157.

Schoener, T.W. 1968. Sizes of feeding territories among birds. Ecology 49(1):123-141.

Seeley, T.D. 1977. Measurement of nest cavity volume by the honey bee (*Apis mellifera*). Behavioral Ecology and Sociobiology 2:201-227.

Servos, M.C. 1987. Summer habitat use by Great Gray Owls in southeastern Manitoba. *In:* Biology and Conservation of Northern Forest Owls: Symposium Proceedings (R.W. Nero, R.J. Clark, R.J. Knapton, and R.H. Hamre, *Eds*). USDA Forest Serv. Gen. Tech. Rep. RM-142. pp. 108-114.

Seton, E.T. 1909. Lives of Game Animals. Charles T. Branford Company, Boston.

Sharp, D.U. 1989. Range extension of the Barred Owl in western Washington and first breeding record on the Olympic Peninsula. J. Raptor Res. 23(4):179-180.

Southern, H.N. 1954. Tawny Owls and their prey. Ibis 96:384-410.

Southern, H.N., and V.P.W. Lowe. 1968. The pattern of distribution of prey and predation in Tawny Owl territories. J. Anim. Ecol. 37:75-97.

Stelfox, J.B. 1995a. Introduction. *In:* Relationships between stand age, stand structure, and biodiversity in aspen mixedwood forests in Alberta (J.B. Stelfox, *Ed*). Jointly Published by the Alberta Environmental Centre (AECV95-R1), Vegreville, AB, and Canadian Forest Service (Project No. 0001A) Edmonton, AB. pp. 1-12.

Stelfox, J.B. (editor) 1995b. Relationship between stand age, stand structure, and biodiversity in aspen mixedwood forests in Alberta. Jointly Published by the Alberta Environmental Centre (AECV95-R1), Vegreville, AB, and Canadian Forest Service (Project No. 0001A) Edmonton, AB. 308 pages.

Stelfox, J.B., L.D. Roy, P.C. Lee, J. Schieck, S. Crites, L.H. Crampton, and L. McDonald. 1995. Recommendations. *In:* Relationships between stand age, stand structure, and biodiversity in aspen mixedwood forests in Alberta (J.B. Stelfox, *Ed*). Jointly published by Alberta Environmental Centre (AECV95-R1), Vegreville, AB, and Canadian Forest Service (Project No. 0001A) Edmonton, AB. pp. 271-280.

Takats, D.L. 1997. Barred Owl habitat use and distribution in the Foothills Model Forest. Final Report, Foothills Model Forest, Hinton, AB. 44 pages.

Taylor, J.A.L., and E.D. Forsman. 1976. Recent range extensions of the Barred Owl in western North America, including the first records for Oregon. Condor 78:560-561.

Van Ael, S.M. 1996. Modelling Barred Owl habitat in northwestern Ontario. Unpublished M.Sc.F. Thesis, Lakehead University, Thunder Bay. 90 pages.

Viitala, J., E. Korpimäki, P. Palokangas, and M. Koivula. 1995. Attraction of Kestrels to vole scent marks visible in ultraviolet light. Nature 373(2):425-427.

White, G.C., and R.A. Garrott. 1990. Analysis of Wildlife Radio-tracking Data. Academic Press, San Diego, CA. 383 pages.

Whitham, T.G. 1986. Costs and benefits of territoriality: behavioral and reproductive release by competing aphids. Ecology 67:139-147.

Zar, J.H. 1996. Biostatistical Analysis. 3rd ed. Prentice-Hall Inc., Upper Saddle River, NJ. 662 pages.

APPENDICES

Table A1. Breeding home range size (95MCP), number of radio-relocationsand number of months radio-tracked for 12 Barred Owls.

Owl	Sex	Home Range (ha)	# Relocations	# Months Tracked
Beaverglen	M	91.4	12	2
Shady Lake	M	363.5	35	5
Hillcrest	M	66.7	19	3
Candle Lake	F	50	16	3
Heart Lakes	F	129	18	3
Birch Bay	F	101.9	14	2
Paignton Beach	F	106	19	3
Prospect	F	55.7	30	5
Spruce River	F	341.8	32	5
Summit	F	38.1	36	5
Whelan Bay	F	144.8	18	4
Whiteswan	F	294.3	21	4

Table A2. Non-breeding home range size (95MCP), number of radio-relocations and number of months radio-tracked for 13 Barred Owls.

Owl	Sex	Home Range (ha)	# Relocations	# Months Tracked
Beaverglen	M	1403.5	27	4
Shady Lake	M	2010.5	29	5
Hillcrest	M	1181.2	43	7
Birch Bay	M	728.9	41	4
Candle Lake	F	610.9	36	7
Heart lakes	F	1573.3	24	4
Paignton Beach	F	573.4	39	6
Prospect	F	689.1	38	5
Beartrap	F	1000.8	42	7
Spruce River	F	1086.5	39	7
Summit	F	588.8	36	6
Waskesiu River	F	2678.4	28	3
Whelan Bay	F	1917.1	33	7

Appendix B Habitat Selection Data

Table B1. Habitat composition of breeding home ranges (95% Minimum Convex Polygon) for 12 radio-marked Barre Owls.

Owl	Young Deciduous	Mature Deciduous	Old Deciduous	Young Mixed	Mature Mixed	Old Mixed	Young Conifer	Mature Conifer	Old Conifer	Treed Muskeg	Open Areas	Water
1	0	0	0	0	0.210318	0.400702	0	0.333153	0	0	0.055827	0
2	0	0	0	0	0	0.841468	0	0	0	0	0.048763	0.109768
3	0	0	0	0	0	1	0	0	0	0	0	0
4	0	0	0.143786	0	0	0.749786	0	0	0	0	0.062841	0.043587
5	0	0	0	0	0	0.658078	0	0	0	0	0.009628	0.332294
6	0	0	0	0	0	0.978527	0	0	0	0	0	0.021473
7	0	0.144868	0.090829	0	0.504422	0.143013	0	0.016129	0.010327	0.011521	0.027308	0.051583
8	0	0.541532	0	0	0.002106	0.169548	0	0.088629	0	0	0.086154	0.112032
9	0	0.390139	0	0	0	0.360482	0	0.009059	0.00029	0	0.240031	0
10	0	0	0	0	0	0.618487	0	0	0.250028	0.040433	0.066867	0.024185
11	0	0.178734	0	0	0.081806	0.202874	0	0.169461	0.030984	0.204698	0.040255	0.091189
12	0.011206	0.029903	0	0.007419	0.006779	0.690901	0	0	0.215896	0.002603	0.035294	0

Table B2. Habitat composition of non-breeding home ranges (95% Minimum Convex Polygon) for 13 radio-marked Barred Owls.

Owl	Young Deciduous	Mature Deciduous	Old Deciduous	Young Mixed	Mature Mixed	Old Mixed	Young Conifer	Mature Conifer	Old Conifer	Treed Muskeg	Open Areas	Water
1	0	0.029915	0.047654	0	0.021894	0.24175	0	0.321558	0.047344	0.262512	0.020933	0.004313
2	0	0	0.022437	0	0.002674	0.565046	0	0.009525	0.129337	0	0.015329	0.255651
3	0	0.054058	0.150374	0	0.413341	0.205024	0	0.067409	0.058204	0.029932	0.011608	0.010051
4	0	0	0.011007	0	0	0.706277	0	0	0	0	0.013327	0.266643
5	0	0	0.081971	0	0	0.773784	0	0	0	0.004996	0.039298	0.099951
6	0	0.014757	0.100017	0	0.356803	0.296765	0	0.068703	0.074207	0.021226	0.016411	0.050962
7	0	0.029163	0.457697	0	0.298622	0.062316	0	0.029969	0.018282	0.028764	0.053612	0.021576
8	0	0.052892	0.240506	0	0.307323	0.163643	0	0.021896	0.001317	0.002192	0.14043	0.069733
9	0	0.922856	0	0	0.018846	0.00623	0	0	0	0.024439	0.012142	0.015487
10	0	0.695573	0	0	0.076179	0.079631	0	0.028874	0.0819	0	0.037844	0
11	0.016798	0.016782	0.031743	0.003157	0.017871	0.372007	0.000799	0.303658	0.037615	0.182468	0.016463	0.000139
12	0.032484	0.004385	0.01012	0.082821	0.021545	0.061495	0.157974	0.105528	0.136157	0.207086	0.124218	0.052682
13	0.113104	0.027847	0	0.033128	0.038344	0.340175	0.030765	0.033177	0.111659	0.020287	0.165677	0.085838

Table B3. Proportional Barred Owl breeding period habitat use, based on 12 radio-marked Barred Owls.

Owl	Young Deciduous	Mature Deciduous	Old Deciduous	Young Mixed	Mature Mixed	Old Mixed	Young Conifer	Mature Conifer	Old Conifer	Treed Muskeg	Open Areas
1	0	0	0	0	0.181818	0.272727	0	0.454546	0	0	0.090909
2	0	0	0.111111	0	0	0.833333	0	0	0	0	0.055556
3	0	0	0	0	0	0.947368	0	0	0.052632	0	0
4	0	0	0	0	0	1	0	0	0	0	0
5	0	0	0	0	0	1	0	0	0	0	0
6	0	0	0.027778	0	0.055556	0.916667	0	0	0	0	0
7	0	0.294	0.058824	0	0.323529	0.294118	0	0	0	0.029412	0
8	0	0.258	0	0	0.032258	0.387097	0	0.16129	0	0	0.129032
9	0	0.27	0	0	0	0.567568	0	0	0.054054	0	0.108108
10	0	0	0	0	0	0.666667	0	0	0.333333	0	0
11	0	0.222	0	0	0	0.277778	0	0.166667	0.055556	0.222222	0.055556
12	0.0625	0	0	0	0	0.8125	0	0	0.125	0	0

Table B4. Proportional Barred Owl non-breeding period habitat use, based on 14 radio-marked Barred Owls.

Owl	Young Deciduous	Mature Deciduous	Old Deciduous	Young Mixed	Mature Mixed	Old Mixed	Young Conifer	Mature Conifer	Old Conifer	Treed Muskeg	Open Areas
1	0	0	0.095238	0	0	0.904762	0	0	0	0	0
2	0	0	0.095238	0	0	0.904762	0	0	0	0	0
3	0	0.02439	0.146342	0	0.512195	0.219512	0	0.02439	0.073171	0	0
4	0	0	0	0	0	1	0	0	0	0	0
5	0	0	0	0	0	0.785714	0	0.142857	0	0.071429	0
6	0	0	0.085714	0	0	0.857143	0	0	0	0.057143	0
7	0	0	0.027027	0	0.162162	0.783784	0	0	0.027027	0	0
8	0	0	0.117647	0	0.529412	0.205882	0	0	0	0.088235	0.058824
9	0	0.181818	0.136364	0	0.409091	0.272727	0	0	0	0	0
10	0	0.888889	0	0	0.055556	0.027778	0	0	0	0	0.027778
11	0	0.515152	0	0	0.030303	0.30303	0	0.060606	0.060606	0	0.030303
12	0	0	0.047619	0	0.047619	0.619048	0	0.238095	0.047619	0	0
13	0.034483	0.034483	0	0.034483	0.172414	0.344828	0.034483	0.034483	0.172414	0.068966	0.068966
14	0.032258	0.032258	0	0	0.064516	0.612903	0.032258	0.193548	0	0	0.032258

Table B5. Log-ratio differences of breeding home range habitat composition compared to study area available habita for 12 Barred Owls.

Owl	Young Decid/Water	Mat Decid/Water	Old Decid/ Water	Young Mixed/Water	Mature Mixed/Water	Old Mixed/Water	Young Conifer/Water	Mature Conifer/Water	Old Conifer/Water	Treed Muskeg/Wate
1	1.0049413	0.329519	0.399408	0.554309	8.479759	7.658922	0.256793	7.614551	-0.11237	-0.90496
2	-5.99601	-6.67143	-6.60155	-6.44664	-6.1724	1.3999	-6.74416	-7.49759	-7.11333	-7.90591
3	1.004941	0.329519	0.399408	0.554309	0.828554	8.573461	0.256793	-0.49664	-0.11237	-0.90496
4	-5.07241	-5.74783	1.592967	-5.52304	-5.2488	2.208144	-5.82056	-6.57399	-6.18972	-6.98231
5	-7.10366	-7.77909	-7.7092	-7.5543	-7.28005	0.046425	-7.85181	-8.60524	-8.22098	-9.01356
6	-4.36443	-5.03986	-4.96997	-4.81507	-4.54082	3.182379	-5.11258	-5.86601	-5.48175	-6.27433
7	-5.24083	1.362155	0.965196	-5.69147	3.108778	0.382862	-5.98898	-1.65921	-1.72081	-2.40395
8	-6.01642	1.905142	-6.62196	-6.46706	-3.14566	-0.22253	-6.76457	-0.73096	-7.13374	-7.92632
9	1.004941	8.598607	0.399408	0.554309	0.828554	7.553147	0.256793	4.009646	0.95254	-0.90496
10	-4.48337	-5.15879	-5.0889	-4.934	-4.65976	2.60467	-5.23152	-5.98495	2.223472	-0.39104
11	-5.81058	1.002481	-6.41611	-6.26121	0.719972	0.162767	-6.55873	0.123047	-1.19184	-0.09636
12	5.723934	6.030076	0.399408	4.860928	5.044907	8.203701	0.256793	-0.49664	7.56501	2.354285

Table B6. Log-ratio differences of non-breeding home range habitat composition compared to study area available habitat for 13 Barred Owls.

Owl	Young Decid/Water	Mat Decid/Water	Old Decid/ Water	Young Mixed/Water	Mature Mixed/Water	Old Mixed/Water	Young Conifer/Water	Mature Conifer/Water	Old Conifer/Water	Treed Muskeg/Wate
1	-2.759199	2.2663109	2.8018249	-3.209832	2.453198	3.3894706	-3.507347	3.8149841	2.2835165	3.203783
2	-6.841459	-7.516881	-2.033704	-7.292091	-3.731525	0.1562124	-7.589607	-3.78652	-0.793768	-8.751358
3	-3.605346	2.0118722	3.1048322	-4.055979	4.5451234	2.3785423	-4.353494	1.4064315	1.6438747	0.1862795
4	-6.883556	-7.558978	-2.788022	-7.334189	-7.059944	0.3372148	-7.631704	-8.385134	-8.00087	-8.793456
5	-5.902323	-6.577745	0.2010909	-6.352955	-6.07871	1.4097339	-6.650471	-7.403901	-7.019636	-3.900923
6	-5.22872	-0.909829	1.0736667	-5.679353	2.77466	1.1249856	-5.976868	-0.197918	0.2634058	-1.780828
7	-4.369208	0.6308634	3.4540505	-4.81984	3.4561672	0.4237797	-5.117356	-0.168051	-0.278041	-0.617388
8	-5.54231	0.0531101	1.6374849	-5.992943	2.3117874	0.2161382	-6.290458	-1.655007	-4.082044	-4.364762
9	-4.037611	4.417026	-4.643144	-4.488243	1.0248737	-1.547413	-4.785759	-5.539189	-5.154924	-0.448759
10	1.0049413	9.1768403	0.3994079	0.5543088	7.4642174	6.0431079	0.2567931	5.1688787	6.5957069	-0.904959
11	5.8007083	5.1243762	5.8316051	3.6784047	5.6862285	7.2565593	2.0073024	7.1937902	5.4895562	6.2761432
12	0.5214035	-2.156528	-1.25037	1.0067075	-0.065573	-0.482202	1.3549395	0.198057	0.8371555	0.4638922
13	1.280792	-0.796213	-6.355633	-0.397758	0.0226987	0.7401246	-0.769283	-1.44725	0.1506234	-2.347454

Table B7. Log-ratio differences of breeding owl habitat use compared to study area available habitat for 12 Barred Owls.

Owl	Young Decid/Open	Mat Decid/Open	Old Decid/Open	Young Mixed/Open	Mature Mixed/Open	Old Mixed/Open	Young Conifer/Open	Mature Conifer/Open	Old Conifer/Open	Treed Muskeg/Oper
1	-5.715037	-6.159848	-6.134418	-6.23042	1.6927341	0.6953142	-6.36176	1.3343299	-6.733293	-7.456551
2	-5.222561	-5.667371	1.3711738	-5.737944	-5.320382	2.3047521	-5.869283	-6.595077	-6.240817	-6.964075
3	1.097408	0.6525972	0.6780267	0.5820247	0.9995869	8.752975	0.4506851	-0.275108	6.3450535	-0.644106
4	1.097408	0.6525972	0.6780267	0.5820247	0.9995869	8.8070423	0.4506851	-0.275108	0.0791521	-0.644106
5	1.097408	0.6525972	0.6780267	0.5820247	0.9995869	8.8070423	0.4506851	-0.275108	0.0791521	-0.644106
6	1.097408	0.652597	6.304848	0.582025	7.319556	8.720031	0.4506851	-0.275108	0.0791521	-0.644106
7	1.097408	8.639162	7.055154	0.582025	9.081462	7.583267	0.4506851	-0.275108	0.0791521	5.0398739
8	-6.098029	1.345744	-6.51741	-6.61341	-0.38671	0.695314	-6.744752	-0.051964	-7.116285	-7.839543
9	-5.888309	1.568888	-6.30769	-6.40369	-5.98613	1.25493	-6.535032	-7.260825	-0.613995	-7.629823
10	1.097408	0.652597	0.678027	0.582025	0.999587	8.401577	0.4506851	-0.275108	8.1908801	-0.644106
11	-5.222561	2.038892	-5.64194	-5.73794	-5.32038	1.20614	-5.869283	0.8235043	0.0791521	0.7421884
12	7.5351596	0.652597	0.678027	0.582025	0.999587	8.599403	0.4506851	-0.275108	7.2100509	-0.644106

Table B8. Log-ratio differences of non-breeding owl habitat use compared to study area available habitat for 13 Barr Owls.

Owl	Young Decid/Open	Mat Decid/Open	Old Decid/Open	Young Mixed/Open	Mature Mixed/Open	Old Mixed/Open	Young Conifer/Open	Mature Conifer/Open	Old Conifer/Open	Treed Muskeg/Ope
1	1.097408	0.6525972	5.2831968	0.5820247	0.9995869	8.7069588	0.4506851	-0.275108	0.0791521	-0.644106
2	1.097408	0.6525972	7.5369918	0.5820247	0.9995869	8.7069588	0.4506851	-0.275108	0.0791521	-0.644106
3	1.097408	6.1493655	7.9665544	0.5820247	9.5408776	7.2906948	0.4506851	5.2216603	6.6745327	-0.644106
4	1.097408	0.6525972	0.6780267	0.5820247	0.9995869	8.8070423	0.4506851	-0.275108	0.0791521	-0.644106
5	1.097408	0.6525972	0.6780267	0.5820247	0.9995869	8.5658798	0.4506851	6.9893212	0.0791521	5.9271831
6	1.097408	0.652597	7.431628	0.582025	0.999587	8.652892	0.4506851	-0.275108	0.0791521	5.7040361
7	1.097408	0.652597	6.277448	0.582025	8.390768	8.563421	0.4506851	-0.275108	5.6785735	-0.644106
8	-5.279727	-5.72454	1.371165	-5.79511	3.196804	0.849455	-5.92645	-6.652243	-6.297983	-0.238652
9	1.097408	8.158189	7.89594	0.582025	9.31611	7.507758	0.4506851	-0.275108	0.0791521	-0.644106
10	-4.529421	4.118325	-4.9488	-5.04481	1.692734	-0.4033	-5.176144	-5.901937	-5.547677	-6.270935
11	-4.616424	3.485813	-5.03581	-5.13181	0.999587	1.899287	-5.263147	0.4180392	0.7722992	-6.357938
12	1.097408	0.652597	6.843844	0.582025	7.165404	8.32747	0.4506851	7.5001468	6.244969	-0.644106
13	0.4042608	-0.04055	-5.85817	-0.11112	1.915872	1.206134	-0.242462	-0.968255	0.995437	-0.644106

Table B9. Log-ratio differences of breeding owl habitat use compared to home range habitat composition for 12 Barred Owls.

Owl	Mature Decid/Open	Mature Mixed/Open	Old Mixed/Open	Mature Conifer/Open	Old Conifer/Open
1	-6.324843	1.326363	1.9709604	1.7863442	-6.324843
2	-6.305855	-6.305855	2.8481505	-6.305855	-6.305855
3	0	0	9.2103404	0	0
4	-6.48776	-6.48776	2.4791791	-6.48776	-6.48776
5	-4.971132	-4.971132	4.2246845	-4.971132	-4.971132
6	0	0	9.2103404	0	0
7	1.8382629	-3.711647	0.6769956	0.02832	-6.877543
8	0.485735	-7.783353	0.4066739	-3.27712	-6.718642
9	-6.529769	-6.529769	2.2245746	-6.529769	1.318868
10	1.4906678	0.7091271	1.6173534	1.437389	-0.261757
11	-0.165754	-1.649883	2.9742836	-5.866298	1.8110838
12	1.6686572	2.9162424	1.6557625	-0.521019	-0.972379

Table B10. Log-ratio differences of non-breeding owl habitat use compared to home range habitat composition for 13 Barred Owls.

Owl	Mature Decid/Open	Old Decid/Open	Mature Mixed/Open	Old Mixed/Open	Mature Conifer/Open	Old Conifer/Open	Treed Muskeg/Open
1	-0.357021	6.036337	-0.044875	6.6636947	-2.731835	-0.816101	-2.528957
2	5.3275849	6.477978	1.745734	5.5031035	0.4758671	-2.132664	5.3275849
3	3.9584048	4.7271042	4.9687259	4.8225747	3.7376925	4.983136	-0.947225
4	5.2062021	0.1912428	5.2062021	5.2400743	5.2062021	5.2062021	5.2062021
5	6.0790633	6.0184071	6.0790633	6.0760694	6.0790633	6.0790633	8.4106421
6	0.1061833	3.790528	4.311934	6.071715	-1.43187	4.090511	-0.257253
7	-5.768264	-1.4513	0.479808	1.102291	-5.7955	-5.30128	1.0280738
8	8.4820429	6.679873	7.533325	7.758077	1.858403	4.669932	4.1596716
9	-0.865075	-0.81197	0.253541	0.667294	-0.81197	-0.81197	-6.326321
10	-0.078048	0.222226	-0.6996	1.558654	0.963678	-0.07888	0.2222257
11	-0.019179	5.509298	6.083806	5.612999	4.860498	5.33956	-2.405432
12	2.650712	-4.02863	2.668163	2.312514	-0.53008	0.824513	-0.511095
13	1.783309	1.726023	2.156577	2.225021	3.399951	-5.38176	-3.676249

Table B11. Matrix of mean/standard error for $\ln(X_{U2}/X_{U1}) - \ln(X_{A2}/X_{A1})$, for breeding home range habitat composition of
Barred Owls compared to study area habitat. X_U represents the percent of the home range composed by a habitat and
X_A represents the percent of the study area composed by a habitat.

	Young Deciduous	Mature Deciduous	Old Deciduous	Young Mixed	Mature Mixed	Old Mixed	Young Coniferous	Mature Coniferous	Old Coniferous	Treed Muskeg	Open Areas	Water
Young Deciduous		-1.75386	-0.16515	0.619835	-1.82446	-6.1187	1.361235	-0.6252	-0.62622	0.435921	-2.79092	-2.73387
Mature Deciduous	2.091285		1.685234	2.599443	0.097686	-3.58671	3.171885	1.050619	1.155075	2.38322	-1.0351	-1.00888
Old Deciduous	0.176849	-1.46711		0.671143	-1.51938	-5.47509	1.398623	-0.45816	-0.43063	0.553803	-2.54457	-2.26559
Young Mixed	-0.60481	-2.25269	-0.612		-2.14289	-6.4879	0.767147	-1.05004	-1.01729	0.013085	-3.17311	-2.79696
Mature Mixed	1.995836	-0.07639	1.698154	2.514369		-3.7485	3.154994	1.076719	1.062352	2.368197	-1.07587	-1.04784
Old Mixed	6.582413	2.337771	6.100293	7.301705	3.699811		7.943078	3.50725	5.21161	6.821134	2.014258	2.077391
Young Coniferous	-1.25744	-2.83207	-1.20498	-0.71926	-2.50663	-6.92885		-1.66909	-1.45363	-0.5163	-3.64253	-2.96625
MatureConiferous	0.719542	-1.07617	0.510262	1.181514	-1.19705	-4.60242	1.893814		0.023755	1.070833	-2.0119	-1.66406
Old Coniferous	0.823724	-1.04836	0.496531	1.360417	-1.06937	-4.92029	1.934604	-0.02426		1.321517	-2.02821	-1.88053
Treed Muskeg	-0.52129	-2.29475	-0.60046	-0.01603	-2.19271	-5.86865	0.663725	-1.13976	-1.17336		-3.0285	-2.69868
Open Areas	3.832574	0.919819	3.403216	4.461852	1.473627	-2.86779	5.186818	2.252302	2.509734	3.983184		-0.13104
Water	2.804721	0.571515	2.82997	3.322957	0.830828	-3.09685	4.267968	1.614154	1.81856	3.246822	-0.28914	

Table B12. Matrix of mean/standard error for $\ln(X_{U2}/X_{U1}) - \ln(X_{A2}/X_{A1})$, for non-breeding home range habitat compositi of 13 Barred Owls compared to study area habitat. X_U represents the percent of the home range composed by a habit and X_A represents the percent of the study area composed by a habitat.

	Young Deciduous	Mature Deciduous	Old Deciduous	Young Mixed	Mature Mixed	Old Mixed	Young Coniferous	Mature Coniferous	Old Coniferous	Treed Muskeg	Open Areas	Water
Young Deciduous		-2.51544	-2.37142	3.54031	-3.76242	-5.77631	3.480376	-2.36866	-2.68544	-1.4658	-4.83235	-2.74948
Mature Deciduous	2.5154438		-0.18711	3.148492	-2.04478	-1.6299	3.447068	0.754022	0.47735	1.676152	-0.36035	-0.10557
Old Deciduous	2.3714159	0.187108		2.990206	-0.84673	-2.08995	3.263443	0.961763	0.656915	1.809886	-0.05479	0.11996
Young Mixed	-3.540309	-3.14849	-2.99021		-4.52467	-6.80343	3.106276	-3.14611	-3.55333	-2.32034	-6.57699	-3.63482
Mature Mixed	3.7624155	2.044779	0.846725	4.524666		-0.69687	4.861243	2.975494	2.246479	3.14527	1.12039	0.846278
Old Mixed	5.7763064	1.629898	2.089946	6.803427	0.696866		7.061075	2.968684	2.758132	3.609543	3.334243	2.432446
Young Coniferous	-3.480376	-3.44707	-3.26344	-3.10628	-4.86124	-7.06108		-3.45463	-3.9528	-2.70153	-7.295	-4.18876
MatureConiferous	2.3686558	-0.75402	-0.96176	3.146107	-2.97549	-2.96868	3.454628		-0.54444	1.075259	-1.28642	-0.66841
Old Coniferous	2.6854404	-0.47735	-0.65692	3.553328	-2.24648	-2.75813	3.952801	0.54444		1.112521	-1.00161	-0.5266
Treed Muskeg	1.4658002	-1.67615	-1.80989	2.320337	-3.14527	-3.60954	2.701529	-1.07526	-1.11252		-2.36745	-1.49698
Open Areas	4.8323542	0.360348	0.054786	6.576988	-1.12039	-3.33424	7.295003	1.286425	1.001605	2.367454		0.232167
Water	2.749475	0.1056	-0.12	3.6348	-0.846	-2.432	4.1888	0.6684	0.5266	1.497	-0.232	

Table B13. Matrix of mean/standard error for $\ln(X_{U2}/X_{U1}) - \ln(X_{A2}/X_{A1})$, for breeding habitat use by 12 Barred Owls compared to study area habitat. X_U represents the percent of owl locations in a habitat and X_A represents the percent o the study area composed by a habitat.

	Young Deciduous	Mature Deciduous	Old Deciduous	Young Mixed	Mature Mixed	Old Mixed	Young Coniferous	Mature Coniferous	Old Coniferous	Treed Muskeg	Open Areas
Young Deciduous		-1.10113	-0.22616	2.473914	-1.19551	-10.5155	2.689897	0.349715	-0.88443	1.55762	-0.72704
Mature Deciduous	1.101134		0.793382	2.617759	-0.02777	-4.44565	2.739769	1.454681	0.261247	3.456552	0.47805
Old Deciduous	0.2261643	-0.79338		2.196089	-1.11942	-7.77054	2.360164	0.431672	-0.44828	1.90375	-0.43364
Young Mixed	-2.473914	-2.61776	-2.19609		-2.9725	-55.4715	ERR	-1.15824	-2.48465	0.157226	-2.40876
Mature Mixed	1.1955102	0.027773	1.119419	2.972504		-4.96937	3.109368	1.615039	0.233644	2.656007	0.414059
Old Mixed	10.515506	4.445649	7.770536	55.47145	4.96937		56.37534	6.35995	5.672594	9.78611	5.450405
Young Coniferous	-2.689897	-2.73977	-2.36016	ERR	-3.10937	-56.3753		-1.29277	-2.61796	-0.0218	-2.54497
MatureConiferous	-0.349715	-1.45468	-0.43167	1.158238	-1.61504	-6.35995	1.292769		-0.88935	1.214031	-1.55661
Old Coniferous	0.8844342	-0.26125	0.448279	2.484654	-0.23364	-5.67259	2.617959	0.889348		2.198167	0.087176
Treed Muskeg	-1.55762	-3.45655	-1.90375	-0.15723	-2.65601	-9.78611	0.021799	-1.21403	-2.19817		-2.12905
Open Areas	0.7270436	-0.47805	0.43364	2.408764	-0.41406	-5.45041	2.544967	1.556612	-0.08718	2.129053	

Table B14 Matrix of mean/standard error for $\ln(X_{U2}/X_{U1}) - \ln(X_{A2}/X_{A1})$, for non-breeding habitat use by 13 Barred Owls compared to study area habitat. X_U represents the percent of owl locations in a habitat and X_A represents the percent o the study area composed by a habitat.

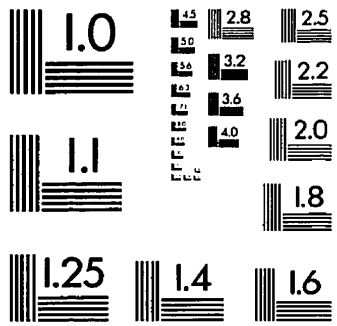
	Young Deciduous	Mature Deciduous	Old Deciduous	Young Mixed	Mature Mixed	Old Mixed	Young Coniferous	Mature Coniferous	Old Coniferous	Treed Muskeg	Open Areas
Young Deciduous		-1.85384	-2.08971	2.313509	-3.89839	-10.1017	20.93532	-0.82383	-0.50411	0.7888	-0.34017
Mature Deciduous	1.8450748		-0.54574	2.782127	-2.18963	-3.7028	2.523191	0.924818	1.159438	1.737599	1.825501
Old Deciduous	2.0791232	0.545672		3.218819	-0.88944	-3.85713	2.592747	1.259535	1.714099	2.65116	1.633218
Young Mixed	-2.315135	-2.76334	-3.20278		-4.84759	-14.413	-0.71608	-1.82087	-1.85598	-0.32934	-1.61491
Mature Mixed	3.9124549	2.015281	0.835385	5.05474		-2.19739	4.588159	3.166312	3.465214	3.970643	3.753994
Old Mixed	8.1974433	3.686987	4.018864	10.22423	2.186323		9.070322	4.411031	6.056902	5.857366	5.938654
Young Coniferous	-1.425389	-2.13993	-2.31261	0.497564	-3.70648	-9.89417		-1.84699	-1.0365	0.073429	-1.02305
MatureConiferous	0.9471453	-1.04844	-1.37152	1.939623	-3.14004	-5.95781	1.839871		0.325669	1.093895	0.501677
Old Coniferous	0.4808869	-1.074	-1.59026	1.79126	-3.11382	-6.37486	1.160927	-0.32294		1.058451	0.208794
Treed Muskeg	-0.909668	-1.8859	-3.02632	0.379922	-3.89041	-8.77631	-0.07353	-1.13053	-1.05901		-1.11576
Open Areas	0.3418374	-1.81507	-1.62853	1.64263	-3.86376	-5.86781	1.341947	-0.50169	-0.22256	1.115763	

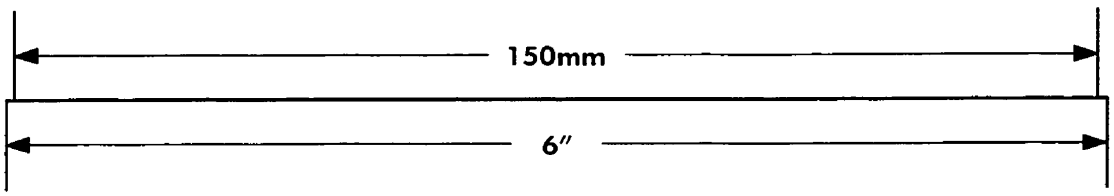
Table B15. Matrix of mean/standard error for $\ln(X_{U2}/X_{U1}) - \ln(X_{A2}/X_{A1})$, for breeding habitat use by 12 Barred Owls compared to home range habitat composition. X_U represents the percent of owl locations in a habitat and X_A represents the percent of the home range composed by a habitat.

	Mature Deciduous	Mature Mixed	Old Mixed	Mature Coniferous	Old Coniferous	Open Areas
Mature Deciduous		-0.33746	-1.40855	0.306664	-1.23898	2.243788
Mature Mixed	0.337461		-0.43233	0.516526	-0.70426	2.003931
Old Mixed	1.40855	0.432325		1.542739	-0.5366	2.952124
Mature Coniferous	-0.30666	-0.51653	-1.54274		-1.49262	1.828756
Old Coniferous	1.238979	0.704264	0.536595	1.492618		3.482806
Open Areas	-2.24379	-2.00393	-2.95212	-1.82876	-3.48281	

Table B16. Matrix of mean/standard error for $\ln(X_{U2}/X_{U1}) - \ln(X_{A2}/X_{A1})$, for non-breeding habitat use by 13 Barred Owls compared to home range habitat composition. X_U represents the percent of owl locations in a habitat and X_A represents the percent of the home range composed by a habitat.

	Mature Deciduous	Old Deciduous	Mature Mixed	Old Mixed	Mature Coniferous	Old Coniferous	Treed Muskeg	Open Areas
Mature Deciduous		-0.6524	-1.46057	-2.83706	1.103954	0.769228	1.5486	2.030605
Old Deciduous	0.652397		-0.48817	-2.85299	1.421091	1.2608	1.7547	2.830439
Mature Mixed	1.460573	0.488171		-2.07654	2.807994	2.779025	2.5464	4.318207
Old Mixed	2.837055	2.852994	2.076536		3.3986	3.598737	3.8178	6.776502
Mature Coniferous	-1.10395	-1.42109	-2.80799	-3.3986		-0.12156	0.4958	1.273767
Old Coniferous	-0.76923	-1.2608	-2.77903	-3.59874	0.121556		0.5702	1.184129
Treed Muskeg	-1.54863	-1.75474	-2.5464	-3.81781	-0.49582	-0.57018		0.535296
Open Areas	-2.03061	-2.83044	-4.31821	-6.7765	-1.27377	-1.18413	-0.535	





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