

Habitat associations of five forest owl species in the Manitoba Escarpment with special consideration to forest fragmentation and slope

by

Heather L. Hinam

A Thesis Submitted to the Faculty of Graduate Studies
in Partial Fulfillment of the Requirements for the degree of

Master's of Science (Zoology)

Department of Zoology
University of Manitoba

Winnipeg, Manitoba
© Heather Hinam, 2001



**National Library
of Canada**

**Acquisitions and
Bibliographic Services**

395 Wellington Street
Ottawa ON K1A 0N4
Canada

**Bibliothèque nationale
du Canada**

**Acquisitions et
services bibliographiques**

395, rue Wellington
Ottawa ON K1A 0N4
Canada

Your file Votre référence

Our file Notre référence

The author has granted a non-exclusive licence allowing the National Library of Canada to reproduce, loan, distribute or sell copies of this thesis in microform, paper or electronic formats.

The author retains ownership of the copyright in this thesis. Neither the thesis nor substantial extracts from it may be printed or otherwise reproduced without the author's permission.

L'auteur a accordé une licence non exclusive permettant à la Bibliothèque nationale du Canada de reproduire, prêter, distribuer ou vendre des copies de cette thèse sous la forme de microfiche/film, de reproduction sur papier ou sur format électronique.

L'auteur conserve la propriété du droit d'auteur qui protège cette thèse. Ni la thèse ni des extraits substantiels de celle-ci ne doivent être imprimés ou autrement reproduits sans son autorisation.

0-612-62752-7

Canada

**THE UNIVERSITY OF MANITOBA
FACULTY OF GRADUATE STUDIES

COPYRIGHT PERMISSION**

**HABITAT ASSOCIATIONS OF FIVE FOREST OWL SPECIES IN THE MANITOBA
ESCARPMENT WITH SPECIAL CONSIDERATION TO FOREST FRAGMENTATION AND
SLOPE**

BY

HEATHER L. HINAM

**A Thesis/Practicum submitted to the Faculty of Graduate Studies of The University of
Manitoba in partial fulfillment of the requirement of the degree
of
MASTER OF SCIENCE**

HEATHER L. HINAM © 2001

Permission has been granted to the Library of the University of Manitoba to lend or sell copies of this thesis/practicum, to the National Library of Canada to microfilm this thesis and to lend or sell copies of the film, and to University Microfilms Inc. to publish an abstract of this thesis/practicum.

This reproduction or copy of this thesis has been made available by authority of the copyright owner solely for the purpose of private study and research, and may only be reproduced and copied as permitted by copyright laws or with express written authorization from the copyright owner.

ABSTRACT

This study describes an inferred use versus availability analysis for five forest owl species with respect to forest stand characteristics, fragmentation and slope. Locations for Great Horned Owls (*Bubo virginianus*), Great Gray Owls (*Strix nebulosa*), Barred Owls (*S. varia*), Boreal Owls (*Aegolius funereus*) and Northern Saw-whet Owls (*A. acadicus*) were obtained through nocturnal surveys conducted from mid- March to early June 1999 and 2000. Species' locations were computerized as the centre of home range plots and overlaid on digital forest resource inventory maps. Stand type, age, degree of fragmentation, amount of water edge, elevation and slope characteristics within plots were compared with similar data from stratified random sites to determine whether plots occupied by owls differed significantly.

The five forest owl species in this study were not distributed randomly with respect to habitat type, degree of fragmentation and elevation and slope characteristics. Barred, Great Gray and Northern Saw-whet owl plots contained significantly smaller proportions of unnatural opening/burn areas and the associated young, open forest than random, but did not differ in terms of forest edge to area ratios. Great Horned Owl plots contained significantly larger edge to area ratios than random, whereas, Boreal Owl plots had significantly smaller edge to area ratios. Boreal Owl plots contained significantly greater proportions of treed muskeg and significantly smaller proportions of natural openings and deciduous forest. Barred Owl plots contained significantly greater proportions of dense forest (crown closure class 4), whereas Northern Saw-whet Owls plots contained significantly greater proportions of crown closure class 3 than what was randomly available. Boreal Owl and Barred Owl plots contained significantly larger amounts of forest edge bordering water bodies.

Boreal Owls were found at higher elevations than random, which may be a result of this species seeking out cooler microclimates. However the difference in elevation in the Manitoba Escarpment might not be sufficient to provide a significant temperature variation at the higher elevations.

Great Gray Owls and Great Horned Owl plots were found significantly more often than random in areas with low to non-existent slopes. Northern Saw-whet Owl plots were found significantly more often on northerly-facing slopes.

ACKNOWLEDGEMENTS

The help and goodwill of so many people made this project possible. First and foremost, I would like to thank my advisor and friend, Dr. James R. Duncan, for daring to take me on as his first graduate student and for allowing me free reign to make this project my own.

I would like to thank the Riding Mountain National Park staff for bending over backwards to make research in the park possible and enjoyable. Thanks to Paul Tarelton for pointing me in the right direction. Special thanks to Ken Kingdon, Geraldine David, Wybo and Sharon Vanderschuit, Angela Bidinosti and Sean Frey for going beyond the call of duty and making me feel like one of the family. Thanks to wardens Debbie Kilfoyle, Roger Baird and Blair Fyton for offering to stand around in the dark with me.

I would have been homeless in the Duck Mountains without the amazing generosity of Nancy McLennan who invited a complete stranger into her home and then offered her services as a field assistant. I never would have met Nancy if it had not been for Dan Soprovich, who, by introducing me to numerous enthusiastic volunteers, ensured my stay in the Ducks was enjoyable and productive. A special thank you to my honorary grandparents, Hugh and Phyllis Hornbeck, for helping me with the completion of this thesis, and for welcoming me into their home and lives. Field work in the Duck and Porcupine mountains would have been impossible without the help of the Swan River Branch of Manitoba Conservation and the special help of Ian Kitch and Eleanor Burgess. Rob Berger also made it easier to rent a field vehicle and he also supplied some owl data.

A special thank you to all the original regional volunteers from the Manitoba Nocturnal Owl Survey and all the new volunteers from throughout the Escarpment who

showed me just what can be accomplished with a little determination, some dumb luck and a lot of goodwill. You are too many to mention here, so I am including a list.

This project was made possible through funding from an NSERC Postgraduate Scholarship, Manitoba Conservation – Wildlife Branch, the Cooper Ornithological Society, the Manitoba Big Game Trophy Association, the Northern Forest Owl Symposium Fund and the Mixedwood Forest Research and Advisory Committee. In kind support was provided by Manitoba Conservation – Swan River Branch, Manitoba Conservation – Wildlife Branch, Riding Mountain National Park, Louisiana Pacific, Inc. and the Mixedwood Forest Research and Advisory Committee. Professors James R. Duncan, Spencer G. Sealy, Rick Riewe and Norm Kenkel acted as advisory committee for this M.Sc. thesis. Special thank you to Dr. Sealy for taking me on as a surrogate graduate student. Dr. Vince Crichton and Dr. Robert W. Nero reviewed earlier drafts of this thesis. Thanks to Dr. Nero for keeping me smiling.

Finally, I would like to thank my family and friends wholeheartedly for their support and understanding over the last 3 years. Thank you for being there when I just needed someone to talk to and for putting up with my moods.

It has been a long road and not everyone could finish the journey with me. I dedicate this work to the memory of two individuals who greatly affected my life.

To the late Karen Palidwor, my former boss and friend, for giving me a chance to prove myself and for helping me realize just how strong I can be.

To my late and very much missed grandmother Betty Hinam, for her unconditional love and support and for being the best listener in the whole world. I'm glad I could make you proud of me.

The following survey volunteers and other supporters made this project possible.

Thanks guys!

Roger Baird	Chris Higgs	Dan Soprovich
Verne Bauman	Pete Hildebrand	Bob Stewart
Rob Berger	Kelly Hinam	Paul Tarelton
Larry Bidlake	Mary Hinam	Dan Teillet
Angela Bidinosti	Richard Hinam	Perry Thomson
Lisa Bidinosti	Allison Hindle	Matt Tinker
Jolene Blackbird	Hugh Hornbeck	Sharon Vanderschuit
François Blouin	Phyllis Hornbeck	Wybo Vanderschuit
Gin Bullock	Brian Hunter	Bill Walley
Eleanor Burgess	Tom Kalechyn	Dale Wieback
Peter Bush	Debbie Kilfoyle	Marissa Whyte
Kathy Callen	Ken Kingdon	
Bill Clark	Ian Kitch	
Lindy Clubb	Tim Kroeker	
Vince Crighton	Pat Letain	
Shelley Currie	Lance Letain	
Carolyn Curtis	Clint Martin	
Celes Davar	Kurt Mazur	
Geraldine David	Nancy McLennan	
David Doerksen	Peter Myers	
Helen Fallding	Bernie Nemetchuk	
Chris Fenski	Carolyn Nemetchuk	
Sean Frey	Robert Nero	
Shanna Frith	Cheryl Penny	
Blair Fyten	Rick Proven	
Debbie Fyten	Glen Riddell	
Donna Grassia	John Ross	
Clif Gussie	Jacques Saquet	
Paul Hamilton	Ray Seib	

TABLE OF CONTENTS

ABSTRACT	i
ACKNOWLEDGEMENTS	iii
LIST OF FIGURES	viii
LIST OF TABLES	x
GENERAL INTRODUCTION	1
STUDY AREA	3
FIELD METHODS	5
CHAPTER 1: HABITAT ASSOCIATIONS OF FIVE FOREST OWL SPECIES IN THE MANITOBA ESCARPMENT	10
INTRODUCTION	10
METHODS	12
Habitat Characteristics	13
Statistical Analyses	14
RESULTS	15
Cover Type	16
Cutting Class	20
Crown Closure	24
DISCUSSION	28
CONCLUSIONS AND RECOMMENDATIONS	36
CHAPTER 2: THE RELATIONSHIP BETWEEN FOREST FRAGMENTATION AND SLOPE AND THE DISTRIBUTION OF FIVE FOREST OWL SPECIES IN THE MANITOBA ESCARPMENT	38
INTRODUCTION	38

METHODS	39
Forest fragmentation and water edge	39
Elevation and Slope Characteristics	40
Statistical Analyses	40
RESULTS	41
Edge-to-area Ratios	41
Water Edge	45
Elevation	45
Slope Aspect and Gradient	48
DISCUSSION	51
Forest Fragmentation	51
Water Edge	55
Elevation and Slope Characteristics	57
CONCLUSIONS AND RECOMMENDATIONS	59
SUMMARY	61
LITERATURE CITED	64
APPENDIX 1: Spatial Distribution of Survey Routes Within the Study Area	78
APPENDIX 2: Cutting class category definitions	83
APPENDIX 3: Crown closure classes definitions	84
APPENDIX 4: Number of individuals of each owl species detected in 1999 and 2000 through broadcast surveys	85
APPENDIX 5: Chi-square statistic for tests for differences in habitat variables between survey years.	86
APPENDIX 6: Z-score charts	87

LIST OF FIGURES

Fig. 1. Map of study site in the Manitoba Escarpment, Manitoba, Canada, consisting of PPF (Porcupine Provincial Forest), DMPP (Duck Mountain Provincial Park) and RMNP (Riding Mountain National Park).	4
Fig. 2. Proportional composition of cover types within 314-ha Boreal Owl (n=30), Barred Owl (n=76), Great Gray Owl (n=37) and random (n=58) plots.	17
Fig 3. Proportional composition of 160-ha Northern Saw-whet Owl (n=122), and random (n=58) plots.	18
Fig. 4. Proportional composition of cover types within 500-ha Great Horned Owl (n=85) and random (n=58) plots.	19
Fig. 5. Proportional composition of cutting classes in 314 ha Boreal Owl (n= 30), Great Gray Owl (n=37), Barred Owl (n= 76) and associated random (n= 58) plots.	21
Fig. 6. Proportional composition of cutting classes in 160-ha Northern Saw-whet Owl (n= 120), and associated random (n= 58) plots.	22
Fig. 7. Proportional composition of cutting classes in 500 ha Great Horned Owl (n= 85) and associated random (n= 58) plots.	23
Fig. 8. Proportional composition of crown closure classes in 314 ha Boreal Owl (n= 30), Great Gray Owl (n= 37) Barred Owl (n= 76) and associated random (n= 58) plots.	25
Fig. 9. Proportional composition of crown closure classes in 160 ha Northern Saw-whet Owl (n= 120) and associated random (n= 58) plots.	26
Fig. 10. Proportional composition of crown closure classes in 500 ha Great Horned Owl (n= 83) and associated random (n= 58) plots.	27
Fig. 11. Edge/area ratios for Boreal Owl (n=30), Great Gray Owl (n=36), Barred Owl (n=77) and random (n=58) 314 ha plots.	42
Fig. 12. Edge/area ratios for Northern Saw-whet Owl (n=119) and random (n=58) 160 ha plots.	43
Fig. 13. Edge/area ratios for Great Horned (n=85), and random (n=58) 500 ha plots.	44
Fig. 14. Total amount of forest edge bordering water bodies within Boreal	

Fig. 14. Total amount of forest edge bordering water bodies within Boreal Owl (n=30), Barred Owl (n=77), Great Gray Owl (n=36) and random (n=58) 314 ha plots.	46
Fig. 15. Mean elevation +/- SE of owl and random locations (n).....	47
Fig. 16. Proportion of Great Horned Owl (n=85), Great Gray Owl (n=36), Barred Owl (n=77), Northern Saw-whet Owl (n=122), Boreal Owl (n=30) and random (n=58) plots within slope gradient categories.	49

LIST OF TABLES

Table 1. Results of a Watson's U^2 test, with $\alpha=0.05$ between owl and random mean slope aspect angles.	50
---	----

GENERAL INTRODUCTION

Studies of a species' use of its habitat, specifically its distribution within its habitat, are central to the understanding of animal ecology (Morse 1980, Cody 1985). Habitat use in raptors is influenced by a number of factors, including prey selection, nesting behaviour and competition between species (Morse 1980, Janes 1985). Many studies of raptor habitat attempt to infer selection by studying the habitat occupied by a species' primary prey. However prey selection is not the only mitigating factor in habitat selection (Janes 1985). In selecting habitat, raptors must respond to cues that can be assessed easily (Morse 1980) and selection can occur at a number of scales (Manly *et al.* 1993). Being highly mobile, with large home ranges, raptors may select habitat at the landscape level as well as at the home range and nest site level (Noss and Csuti 1997, Davidson 1998, Mazur *et al.* 1998) thus large-scale forest management decisions may affect raptors' habitat relationships.

Despite living sympatrically throughout much of their ranges, the forest owl species present in the Manitoba Escarpment may respond differently to variations in their environment at the landscape level, such as differences in stand characteristics, habitat fragmentation and topographic features (Niemi and Hannonki 1997). Forest fragmentation, through forestry, agriculture and development, is becoming an increasingly prominent factor influencing the distribution of raptors (Johnson 1993, Mazur *et al.* 1997, Niemi and Hanowski 1997, Stepniski 1997, Takats 1997, Kirk and Hyslop 1998). Forest fragments vary in shape, size, degree of isolation and the remaining vegetation, thus may have both positive and negative effects on the distribution of individual owl species (Johnsgard 1988, Johnson 1993, Mazur *et al.* 1997). Decreases in

suitable habitat due to timber harvest and agricultural practices may be the main factor contributing to observed declines in some raptor populations (Kirk and Hyslop 1998). Niemi and Hanowski (1997) suggested that because forest raptors, are at the top of the food chain and have relatively large home ranges, they are highly sensitive to forest fragmentation and changes in forest composition.

In areas of rolling topography, the effects of this variation from both natural and human causes may be further compounded by variation in the degree and direction of slope. The Manitoba Escarpment, which stretches the length of west-central Manitoba, rises to an average of 350 m above the surrounding lowlands. Changes in the forested landscape in the Manitoba Escarpment are set to occur at an increasing rate. Tolko Industries (formerly Repap) has proposed a 13-year management plan for a 12-million ha forest management license agreement (FMLA) encompassing Grass River Provincial Park, Porcupine Provincial Forest, Duck Mountain Provincial Park and bordering on Riding Mountain National Park (Mount *et al.* 1996). This includes harvesting an average 3 million m³ of trees per year and the creation of 859 km of all-weather roads. Louisiana Pacific Ltd and Spruce Products also log parts of this area.

How owls in western Manitoba distribute themselves spatially in relation to landscape variation is not known. The Great Gray Owl and the Barred Owl are considered uncommon in Manitoba (Nero 1980, Duncan 1996a) and the Boreal and Northern Saw-whet owls are considered of long-term conservation concern (Duncan 1996a). The goal of this thesis is to assess the relationship between forest stand characteristics, fragmentation and slope and the spatial distribution of owls in the Manitoba Escarpment.

The specific objectives are to describe quantitatively: 1) Forest stand characteristics and forest fragmentation, as defined by edge to area ratios, at sites occupied by owls as compared with random sites in the study area. 2) The occurrence of owls with regard to elevation, slope aspect and direction compared to random locations.

STUDY AREA

Field work was conducted from 15 March to 6 June 1999 and 13 March to 1 June 2000. The study area encompassed Riding Mountain National Park (RMNP, 2,976 km²), Duck Mountain Provincial Park and Forest (DMPP, 3,770 km²) and Porcupine Provincial Forest (PPF, 2,090 km²) (Fig. 1). This area, known as the Manitoba Escarpment, represents the western shore of Glacial Lake Agassiz and is composed of a number of remnant beach ridges rising 300 to 500 m above the surrounding lowlands (McCready *et al.* 1980, Parks Canada 1997). Although the area is often considered as one region, considerable variation in vegetation exists between the southern portion in Riding Mountain and the Duck and Porcupine Mountains to the north.

Ritchie (1976) suggests that the area was first vegetated after the Wisconsin glaciers receded by a spruce-dominated boreal forest. About 10,500 BP, a shift occurred from the spruce-dominated forests as grasslands, interspersed with parkland vegetation pushed north, resulting in the different vegetation characteristics in the area of Riding Mountain (Ritchie 1976).

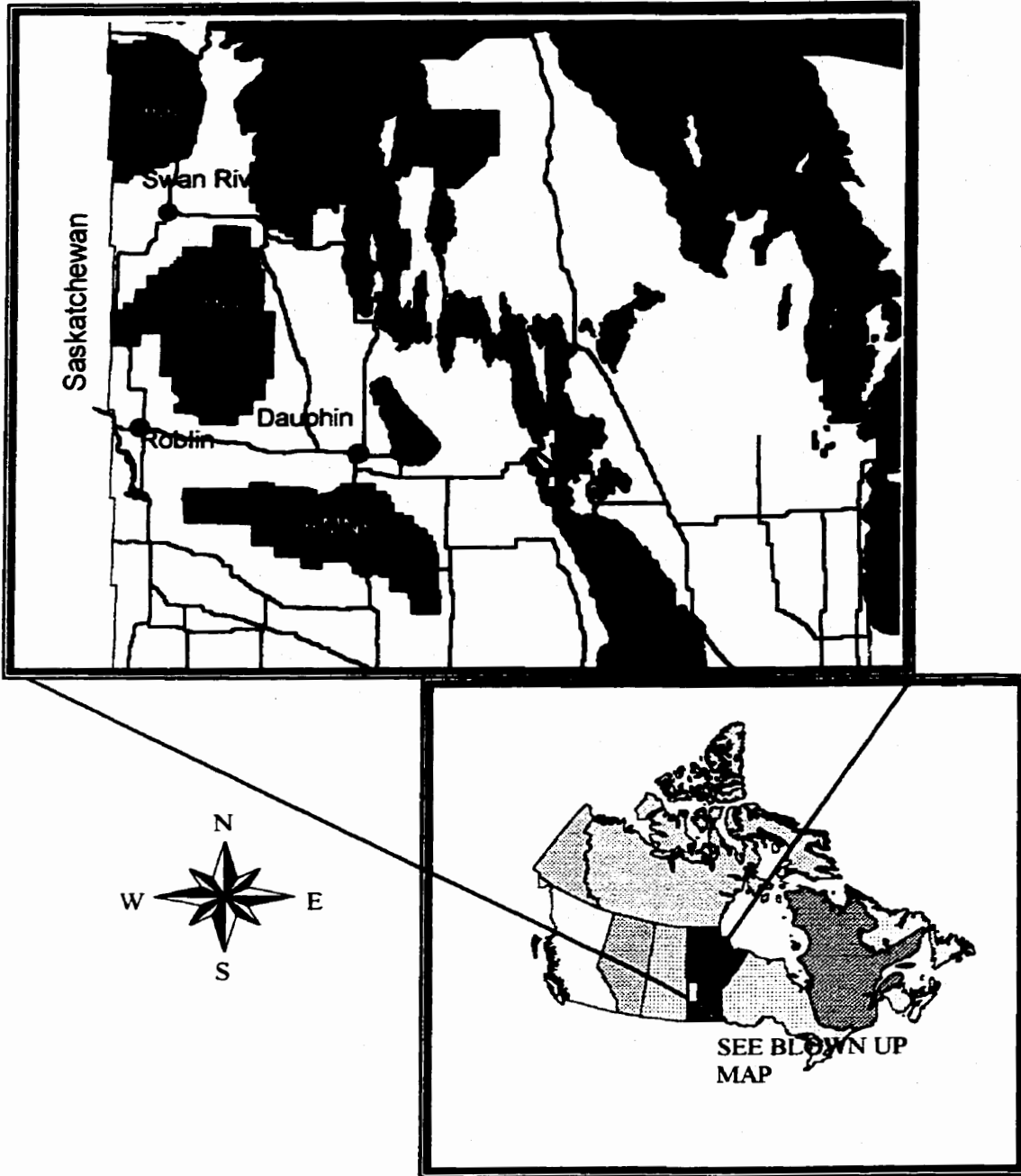


Fig. 1. Map of study site in the Manitoba Escarpment, Manitoba, Canada, consisting of PPF (Porcupine Provincial Forest), DMPP (Duck Mountain Provincial Park) and RMNP (Riding Mountain National Park). Surveys were conducted almost entirely in the parks (Appendix 1). Approximate scale: 1:4,382,000.

The current vegetation of Riding Mountain is characterized by boreal mixedwoods, dominated by Trembling Aspen (*Populus tremuloides*), Balsam Poplar (*P. balsamifera*), and White Spruce (*Picea glauca*), interspersed with lakes throughout, remnant grasslands in the west and Black Spruce (*Picea mariana*) and Tamarack (*Larix laricina*) bogs mainly in the eastern portion of the park (Baily 1968, Parks Canada 1997). The Duck and Porcupine Mountains are almost completely forested, with almost no remnant grasslands (McCready *et al.* 1980). The entire region is characterized by steeply-cut river valleys along the eastern face of the escarpment (McCready *et al.* 1980, Parks Canada 1997).

Although heavily exploited for timber and fuel wood and subjected to massive burnings through the turn of the 20th century, limited timber extraction has occurred in RMNP since its designation as a protected area in 1930 (Parks Canada 1997). Timber harvest and agricultural activities, which began in the 1880's and continue today, have greatly affected the forest vegetation of the provincial parks and forests and the surrounding land (Goldrup 1992, Parks Canada 1997).

FIELD METHODS

Owls pose a number of problems when attempting to study them in the field. Their nocturnal habits, large home ranges and secretive natures make it difficult to locate large numbers of a species to study (Fuller and Mosher 1981, Johnson *et al.* 1981, Takats and Holroyd 1997). Fuller and Mosher (1981) suggest that careful enumeration is not necessary for studies of owl occurrences. Nocturnal surveys have been found to be successful in studies of habitat preferences and population trends of owls as they allow

the coverage of large areas with relative efficiency (Fuller and Mosher 1981, Palmer 1987) making it possible to obtain enough owl locations over a large enough area to conduct landscape-level habitat assessments (Bibby *et al* 2000).

The use of playbacks of owl calls during nocturnal surveys can significantly increase the number of owls detected (Johnson *et al.* 1981, Mosher *et al.* 1990). The technique works on the assumption that 1) calling represents an individual owl's advertisement of its occupied home range and 2) that a response to playbacks of conspecific calls represents a reaction to a supposed intrusion on that home range (Laidig and Dobkin 1995). Owl locations in the present study were determined by nocturnal surveys, using playbacks of seven owl species believed to be in the area (Duncan and Duncan 1997). Surveys were conducted along 23 routes, on roads, snowmobile, all-terrain vehicle (ATV) and hiking trails, and consisted of 10-40 stations (Appendix 1). To further increase the area surveyed, volunteers with the Manitoba Nocturnal Owl Survey surveyed six previously designated routes (Duncan and Duncan 1997).

Locations were also recorded for owls that were detected during the breeding season calling at times other than during a survey and through the Duck Mountain Forest Bird Survey program conducted for Louisiana Pacific Ltd. (R. P. Berger pers. comm. 1999). Locations of known occupied nests were also recorded. All these locations were considered incidental encounters.

Seventeen routes in 1999 and 16 routes in 2000 were surveyed twice, 2 to 3 weeks apart, using broadcasts from different species each time in order to stimulate responses from the species most vocal at different times of year. Four routes in 1999 and five routes in 2000 were surveyed once. Four routes that were surveyed in 1999 were not surveyed in

2000. One route was surveyed only in 2000 as it was inaccessible in 1999. An additional route was run in 2000 in the southeastern corner of Riding Mountain National Park to compensate for a nearby route that has been flooded.

Listening stops were spaced at 0.8 km intervals. The location of each stop was recorded as Universal Transverse Mercator (UTM) coordinates, using a Global Positioning System (GPS), or plotted by hand in relation to landmarks, such as roads and water bodies on 1:50,000 topographic maps.

Surveys began at one half hour after sunset, as determined from the GPS unit, and continued until the route was finished or until one-half hour before sunrise, on nights with negligible precipitation and temperatures greater than -20°C (Mosher *et al.* 1990, Johnson 1993, Clark and Anderson 1995, Takats 1997). Each stop began with 3 minutes of listening to detect calling owls (Duncan and Duncan 1997, Takats 1997). This was then followed by 20-second broadcasts of the calls of four of the seven original target species obtained from the practice tape used by the Manitoba Nocturnal Owl Survey, separated by 1-minute listening periods, followed by a final 3-minute listening period.

Different calls were used at each of two survey periods to reflect each species' seasonal peaks in calling (Johnsgard 1988). Broadcasts from 15 March to 23 April 1999 were played in the order of: Boreal Owl, Great Gray Owl, Barred Owl and Great Horned Owl, species found to be most vocal during this period (Johnsgard 1988, Bull and Duncan 1993). The broadcast order from 24 April to 6 June was: Northern Saw-whet Owl, Eastern Screech-owl (*Otus asio*), Long-eared Owl (*Asio otus*) and Great Horned Owl to target the most vocal species of this period (Johnsgard 1988). Although it is unclear whether playbacks of larger owls inhibit responses in smaller owls (Fuller and

Mosher 1981, McGarigal and Fraser 1985, Clark and Anderson 1995), playbacks were broadcast in order from the smallest species to the largest.

At survey stops where owls were recorded calling, the time of response, species responding and the apparent distance and direction (estimated to the nearest degree) of the response were recorded. Measurements from one or more survey stops were used to estimate and plot owl locations on 1:50,000 topographic maps. Locating owls by triangulation, with practice, can be a relatively accurate and efficient method for estimating points and has been used in several owl studies (Johnson 1993, Clark and Anderson 1995). Owls that could not be located with confidence were not included in the habitat analyses. The large sample size in this study results in a lower chance of bias due to sampling error. In other words, the larger the sample the better the chance that the errors will cancel each other out.

Locations for each individual species were computerized as a separate point layer and then overlaid on digital Forest Resource Inventory (FRI) maps (Natural Resources Manitoba 1996) using the geographic information system (GIS) ArcView GIS Ver.3.1. Owl located during this study were assumed to be breeding and this assumption was supported by the discovery of occupied Great Horned Owl (5), Barred Owl (1), Northern Saw-whet Owl (1) and Great Gray Owl (1) nests during field seasons and records of pairs of all species performing courtship vocalizations and or alarm calls at many survey stops.

Fifty-eight stratified random coordinates were generated within a 2-km buffer of all 29 routes surveyed for comparison with owl locations regarding habitat composition, fragmentation and slope characteristics (Mazur *et al.* 1997, Stepnisky 1997). Two non-overlapping random locations were selected for each route to avoid spatial lumping

associated with purely random locations and to represent more accurately the area sampled by the survey. Although in ideal conditions, Boreal Owls can be heard by an observer from as far as 3.5 km (Clark and Anderson 1995). It was noted in the field that individuals of all species could be heard calling from 2 to 3 stations away from their original calling locations (1.6 – 2.4 km) depending on the variation in environmental conditions and habitat, thus the 2-km buffer represented an estimate of absolute limit within which an owl could be heard from the survey route (Mosher *et al.* 1990), and thus the actual area surveyed.

CHAPTER 1: HABITAT ASSOCIATIONS OF FIVE FOREST OWL SPECIES IN THE MANITOBA ESCARPMENT

INTRODUCTION

Identifying and understanding a species' habitat associations and resource use are necessary for its conservation (Manly *et al.* 1993, McCallum 1994, Schieck and Nietfield 1995, Niemi and Hanowski 1997). Niemi and Hanowski (1997) suggest that by improving the knowledge of a species' response to its habitat and changes therein, we may minimize many conflicts between management protocols and preservation objectives.

A number of factors may influence a species' selection of habitat including its longevity, mobility and the characteristics of the landscape (Morse 1980). Many studies describe a species' habitat requirements through some measure of habitat selection, which is often inferred by an examination of the species' occupation of a certain habitat type (Manly *et al.* 1993, McCallum 1994). This method assumes that individuals of a population choose to occupy areas where their fitness is maximized, however, this is not always the case (Manly *et al.* 1993, McCallum 1994). Describing a species' occupation of a habitat alone does not describe selection (Morse 1980). In order to describe habitat selection with any sense of validity, the species' occupation of certain habitat types must be compared with the availability of those habitat types within the study area (Manly *et al.* 1993, McCallum 1994). For the purpose of this study, the use of the term "habitat selection" refers to selection implied by this use versus availability method.

Several studies have examined the habitat relationships of northern forest owls in North America and Eurasia. Some species are relatively specialized. Cavity nesters, such as the Barred, Boreal and Northern Saw-whet owls are associated, elsewhere, with older

forests, where large trees and natural cavities are more abundant (Cannings 1993, Hayward and Hayward 1993, Duncan and Kearns 1997, Hayward 1997, Lane *et al.* 1997, Mazur *et al.* 1998). More specifically, Boreal Owls have been associated, in other areas, with old conifer forests (Hayward and Hayward 1993, Marcot 1995, Lane *et al.* 1997).

Other species tend to be less habitat-specific across their range or are associated with different habitat types in different portions of their range. The Great Horned Owl has been found in a number of different habitat types, ranging from agricultural areas to old growth forest (McInville and Keith 1974, McGarigal and Fraser 1984, Johnson 1993, Houston 1996). Great Gray Owls in eastern Manitoba were associated with mature forests of tamarack, spruce, and aspen, near open muskeg or clearings (Servos 1986, Bouchart 1991), whereas in Alberta, individuals nested predominantly in older mixedwood forest (Stepnisky 1997).

Relatively little is known of the habitat associations of forest owls in Manitoba. Great Gray Owls have been studied intensively only in the southeastern corner of the province (Collins 1980, Servos 1986, Bouchart 1991, Duncan 1992). A habitat suitability index (HSI) model has been developed for the Great Gray Owl and Barred Owl within the province, based mainly on the review of literature from other study locations (Duncan 1994, Duncan 1996b). Both HSI models have been validated to a small degree in the southeastern portion of the province (Duncan 1996b, Duncan 1996c, Duncan and Kearns 1997). The objective of this chapter of the study is to describe the breeding habitat associations of five common species of forest owls in the Manitoba Escarpment (Duncan and Duncan 1997), by way of a use versus availability analysis.

METHODS

Circular plots centred on each owl location were used to approximate owl home ranges (Mazur *et al.* 1997). Three plot sizes were selected (160, 314 and 500 ha), based on species' published home range estimates from studies conducted in habitats that most closely resembled the study area (Cannings 1987, Duncan 1992, Johnson 1993, Mazur *et al.* 1998). It was unknown if owls in this study were located in years of high or low small mammal densities. As prey-densities can affect home range sizes (Hayward *et al.* 1993, Mazur *et al.* 1997) plot sizes chosen to represent home ranges in the present study were based on average home range estimates, and are likely conservative estimates. Northern Saw-whet Owl plots were set at 160 ha, based on studies of a small number of radio-tagged individuals, which estimated home range size between 115 ha for wintering birds (Forbes and Warner 1974) and 159 ha for breeding individuals (Cannings 1987).

Boreal Owl, Great Gray and Barred owl plots were 314 ha (Bull and Duncan 1993, Hayward and Hayward 1993, Mazur *et al.* 1997). Although the Great Gray Owl's home range has been documented as large as 67 km² in Oregon (Bull and Duncan 1993), Duncan (1994) found that Great Gray Owl plots of a 1-km radius (314 ha) best differentiated habitat differences between areas used by owls and random plots in southeastern Manitoba. Mazur *et al.* (1997) compared habitat characteristics within Barred Owl home range plots with 1.5-km and 3.0-km radii and concluded that the smaller plots represented a more conservative representation of habitat area. Boreal Owl home ranges vary greatly in shape and size (229 ha to 2386 ha) depending on prey availability, geographical characteristics, such as topography of the region and breeding success (Hayward *et al.* 1993, Hayward and Hayward 1993).

Home ranges for the Great Horned Owl have been recorded between 148 ha (Houston *et al.* 1998) and 883 ha (Rohner 1997). A plot size of 500 ha was assigned as an intermediate value. Johnson (1993) found the latter plot size appropriate in determining habitat preferences of Great Horned Owls in the Rocky Mountains.

Habitat Characteristics

Birds use a variety of proximal cues in selecting a habitat to occupy (Morse 1980, Cody 1985). Other studies of owls have found associations with habitats of varying forest type (Hayward and Hayward 1993), forest age (Lehmkuhl and Raphael 1993) and density of foliage (Whitfield and Gaffney 1997). Thus, the amount (ha) of each cover type, cutting class and crown closure class was measured using digital FRI maps and ArcView GIS 3.1 (Bouchart 1991, Johnson 1993, Takats 1997). Cover type was divided into nine categories: conifer forest, softwood dominated mixedwood (s-h mixedwood), hardwood dominated mixedwood (h-s mixedwood), deciduous forest, treed muskeg, natural openings, unnatural openings/burn, water and roads/other.

Cutting class is defined by the Manitoba Conservation Forestry Branch as a measure of the state of growth, size and maturity of the forest stand in relation to its harvest rotation age. Terminology describing the age of a forest is often relative and not consistent between studies. Manitoba Conservation describes forest age in terms of cutting class with the upper classes (4 and 5) representing mature and overmature, or old forest. Hayward (1991) defines mature forest as forest that has existed long enough since its last disturbance that mortality and regeneration are prominent and regeneration stems from the parent trees. Old forest is defined as late successional forests, whose physical structure and age are influenced by processes within the stand. Trees within old forests

vary widely in size and age, resulting in a patchy structure (Hayward 1991). These definitions are similar to those supplied by Stelfox (1995), however, this second study includes age parameters for aspen-dominated mixedwood forests, delineating mature forest as forests 50 years old or older and old forest as stands greater than 120 years old. The cutting class variable is divided into six classes ranging from 0 to five (Appendix 2, Natural Resources Manitoba 1996). Mature (cutting class 4) and overmature (cutting class 5) generally match the physical characteristics of mature and old forest as described by both Hayward (1991) and Stelfox (1995), hence the terms “overmature” and “old” will be used interchangeably. Crown closure is a measure of the density of the forest canopy and is recorded as one of four percentage classes. (Appendix 3, Natural Resources Manitoba 1996).

Statistical Analyses

Habitat variables were calculated within each of 160-, 314- and 500-ha plots centred on the random coordinates for comparison with the plots of each respective species. Although the proportional composition of each habitat variable within owl plots could have been compared to the composition of the entire study area (Manly *et al.* 1993), circular plots were used for the determination of random habitat characteristics to facilitate the comparison between owl and random locations with respects to the edge-to-area variable discussed in chapter two. The use of stratified random plots thus allowed for a uniform comparison between owl and random for all habitat variables and has been used in a number of studies (Johnson 1993, Moen and Gutierrez 1997, Mazur *et al.* 1997, Gutierrez *et al.* 1998). To determine whether the proportional composition of owl plots differed significantly from random plots, a chi-square goodness-of-fit test at $\alpha=0.05$ was

applied to the variables of cover type, cutting class and crown closure separately (Neu *et al.* 1974, Byers *et al.* 1984, Servos 1986, Bouchart 1991, Johnson 1993, Mazur *et al.* 1998). This method compares the proportion of habitat types used by a species (observed) with that randomly available (expected) in the study area (Neu *et al.* 1974, Byers *et al.* 1984). As this test indicates only whether a difference exists and not the direction of the difference, Bonferroni confidence intervals were constructed for each variable to determine habitat preferences that can be inferred through such calculations (Neu *et al.* 1974, Byers *et al.* 1984, McCallum 1994).

Aebischer *et al.* (1993) suggested that in this type of analysis of habitat use, the avoidance of one habitat type by a species could lead to the apparent preference of another habitat type by what is known as the unit-sum constraint. However, in an analysis of Barred Owl habitat associations similar to this study, Mazur *et al.* (1998) found little difference between the results of the Chi-squared analysis and that of the log-ratio analysis proposed by Aebischer *et al.* (1993) to avoid unit-sum constraint problems. Mazur *et al.* (1998) concluded that the log-ratio analysis provided no further information about Barred Owl habitat associations than the aforementioned conventional methods. Thus, for the purpose of this study, only the Chi-squared test and Bonferroni confidence intervals were used.

RESULTS

In 1999, 242 owls of eight species were recorded at 912 survey stops using the methodology described in the earlier section, for a detection rate of 0.265 owls/stop. An additional 22 individuals were recorded through incidental discoveries of nesting owls

and calling owls for a total of 264 owls (Appendix 4). In 2000, 228 owls of seven species were recorded at 795 survey stops (Appendix 4) for a detection rate of 0.287 owls/stop. Eighteen additional individuals were recorded through incidental encounters, bringing the 2000 total to 246 owls. As the proportional composition of all three habitat variables within owl plots did not differ significantly between years ($\alpha > 0.01$) except for cutting class distribution in Great Horned Owl plots, the data was grouped for analysis (Appendix 5).

Cover Type

The proportional composition of the nine cover types within the plots of all five owl species differed significantly from that of the corresponding random plots ($X^2_{BOOW} = 57.3$, $p < 0.000$, $X^2_{BAOW} = 40.1$, $p < 0.0000$, $X^2_{GGOW} = 18.7$, $p = 0.0009$, $X^2_{NSWO} = 16.7$, $p = 0.0033$, $X^2_{GHOW} = 40.1$, $p < 0.0000$, Figs. 2-4). In all plots, owl and random, hardwood-dominated mixedwood forest made up the greatest proportion of the plots at values ranging between 34.1 and 45.3 percent (Figs 2-4). Both Boreal Owl and Great Gray Owl plots contained relatively large amounts of softwood-dominated mixedwood, but these values were not significantly different from random (Fig. 2). Barred Owl and Boreal Owl plots also contained relatively large but not statistically significant amounts of water (Fig. 2).

Both Barred Owl and Great Gray Owl plots contained significantly less unnatural openings/burn than what was randomly available, based on Bonferroni confidence intervals (Fig. 2). Boreal Owl plots did not contain significantly less unnatural openings/burn than random, but did contain significantly less natural openings and deciduous forest and significantly more treed-muskeg (Fig. 2).

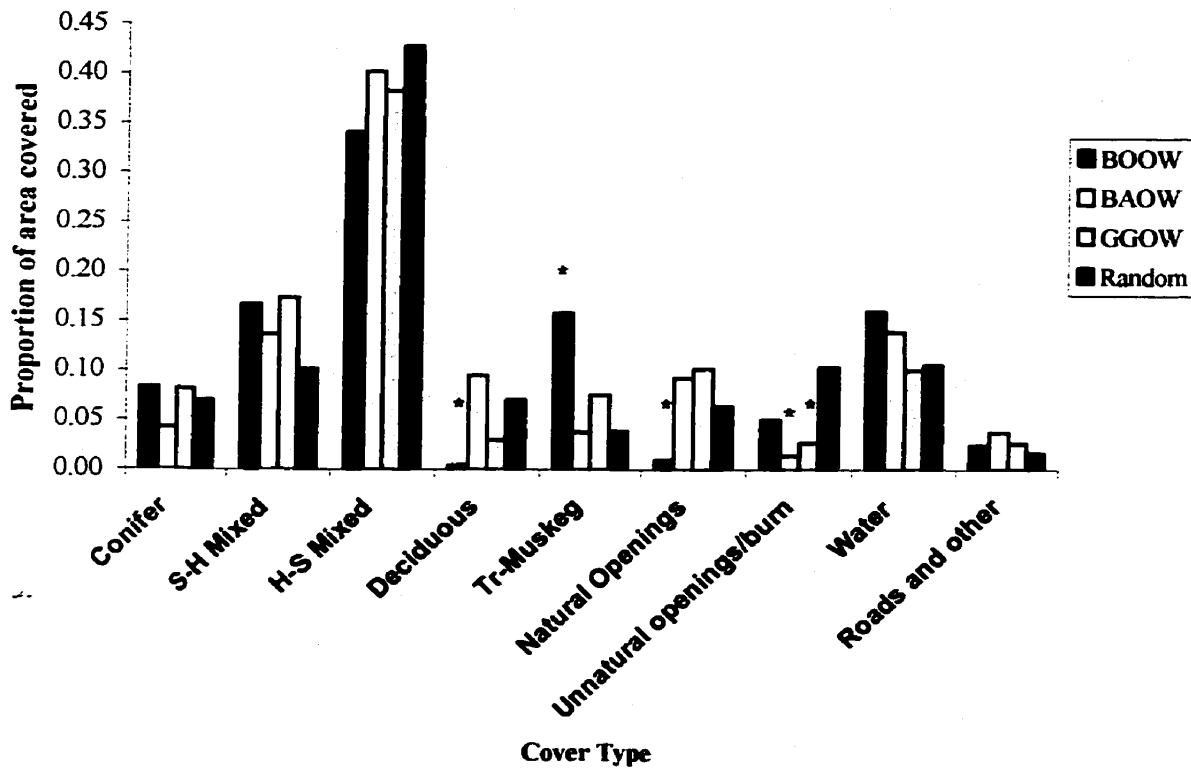


Fig. 2. Proportional composition of cover types within 314-ha Boreal Owl (n=30), Barred Owl (n=76), Great Gray Owl (n=37) and random (n=58) plots. * indicates a significant difference from random ($\alpha < 0.05$), based on Bonferroni confidence intervals.

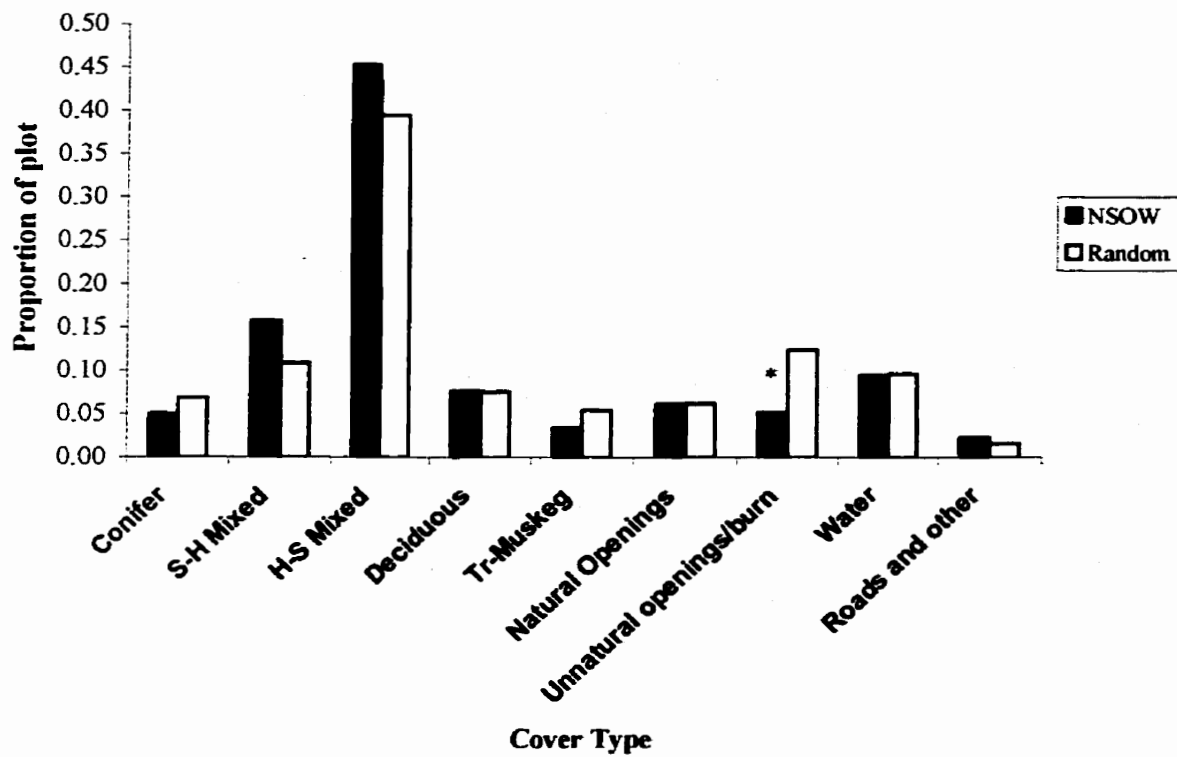


Fig. 3. Proportional composition of 160-ha Northern Saw-whet Owl (n=122), and random (n=58) plots. * indicates a significant difference from random ($\alpha < 0.05$) based on Bonferroni confidence intervals.

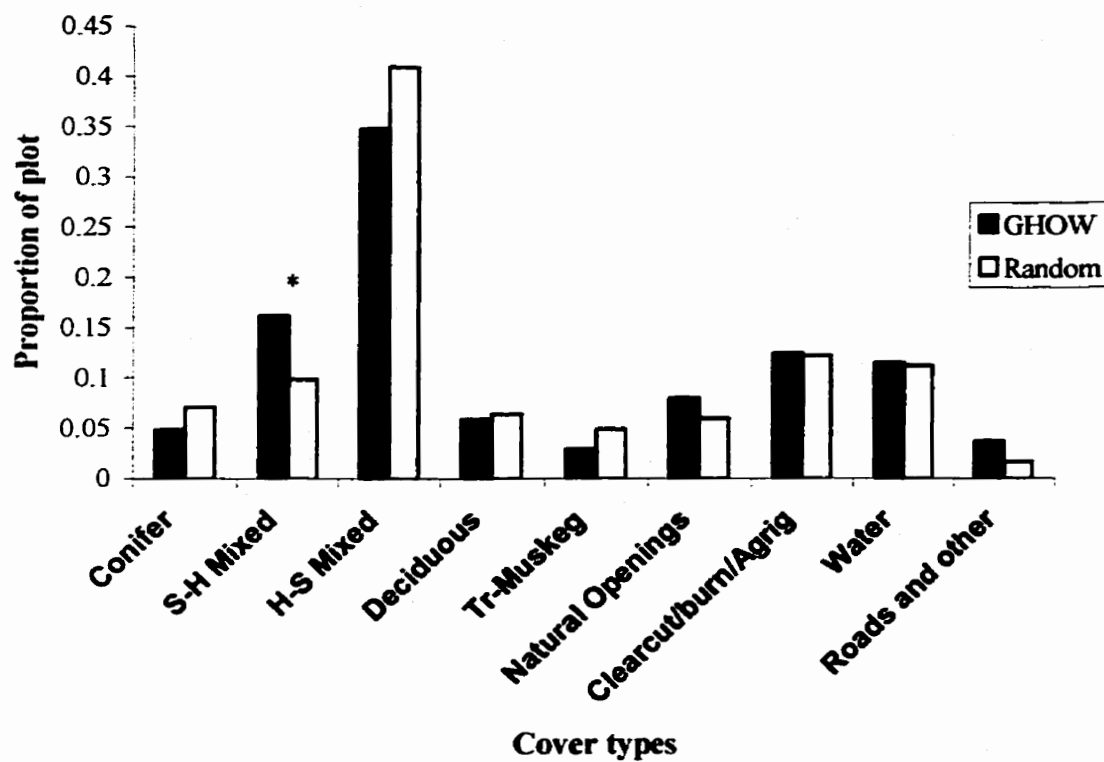


Fig. 4. Proportional composition of cover types within 500-ha Great Horned Owl (n=85) and random (n=58) plots. * indicates a significant difference from random ($\alpha < 0.05$) based on Bonferroni confidence intervals.

Northern Saw-whet Owl plots contained significantly smaller proportions of unnatural openings/burn than what was randomly available (Fig. 3). All other habitat types did not vary significantly from random (Fig. 3).

Great Horned Owl plots, like those of Boreal Owls, did not differ significantly from random with respect to the amount of unnatural openings/burn (Fig. 4). However, Great Horned Owl plots contained significantly greater proportions of softwood-dominated mixedwood than what was randomly available (Fig. 4).

Cutting Class

Plots of all species except those of Boreal Owls differed significantly from random in relation to the proportional composition of cutting classes ($X^2_{BOOW} = 10.3$, $p = 0.068$, $X^2_{BAOW} = 14.3$, $p = 0.0140$, $X^2_{GGOW} = 11.0$, $p = 0.026$, $X^2_{NSWO} = 27.7$, $p = 0.0000$, $X^2_{GHOW} = 13.7$, $p = 0.0018$, Figs. 5-7). Cutting class 1 (stands under 3 meters) made up the smallest proportion of all plots, whereas cutting classes 4 and 5 (mature and overmature stands) collectively made up the greatest proportion of all plots (Figs. 5-7).

Great Gray Owl and Barred Owl plots contained significantly smaller proportions of cutting class 0 (non-restocked forested lands) than what is available randomly in the study area (Fig. 5). The large proportion of cutting class 5 approached significance in Boreal Owl plots (Bonferroni confidence interval: $0.239 < 0.241 < 0.568$, Fig. 5).

Both Northern Saw-whet Owl and Great Horned Owl plots contained significantly greater proportions of cutting class 5 (overmature stands) (Figs. 6 and 7). Northern Saw-whet Owl plots also contained significantly smaller proportions of cutting class 0 (non-restocked forested lands) than what was randomly available (Fig. 6).

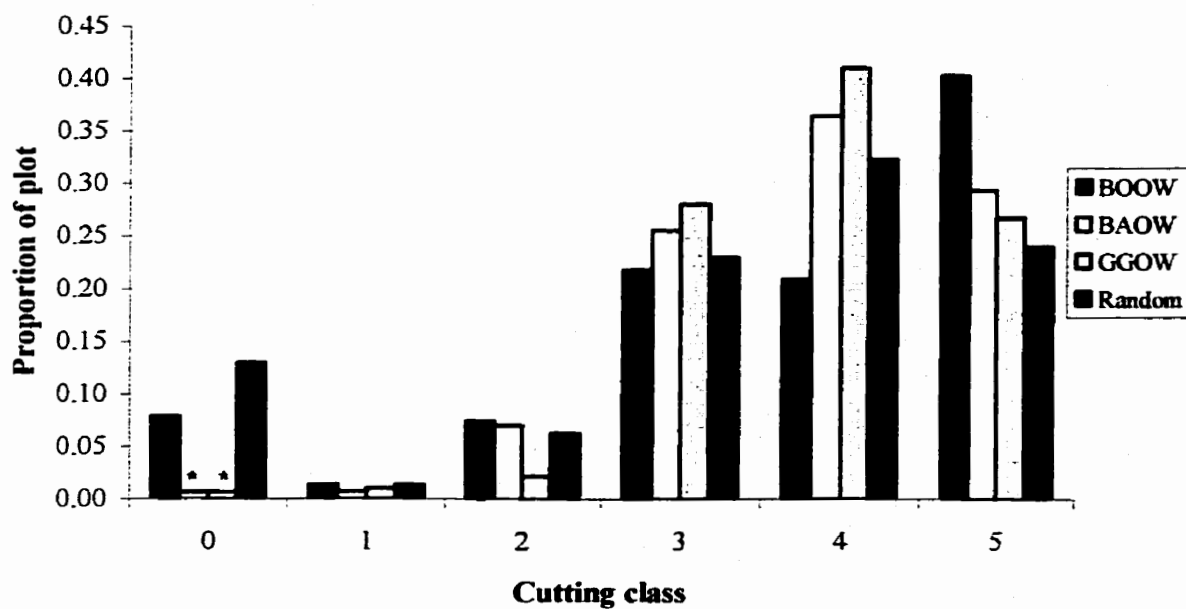


Fig. 5. Proportional composition of cutting classes in 314-ha Boreal Owl (n= 30), Great Gray Owl (n=37), Barred Owl (n= 76) and associated random (n= 58) plots.

* indicates a significant difference ($\alpha < 0.05$) from random composition based on Bonferroni confidence intervals.

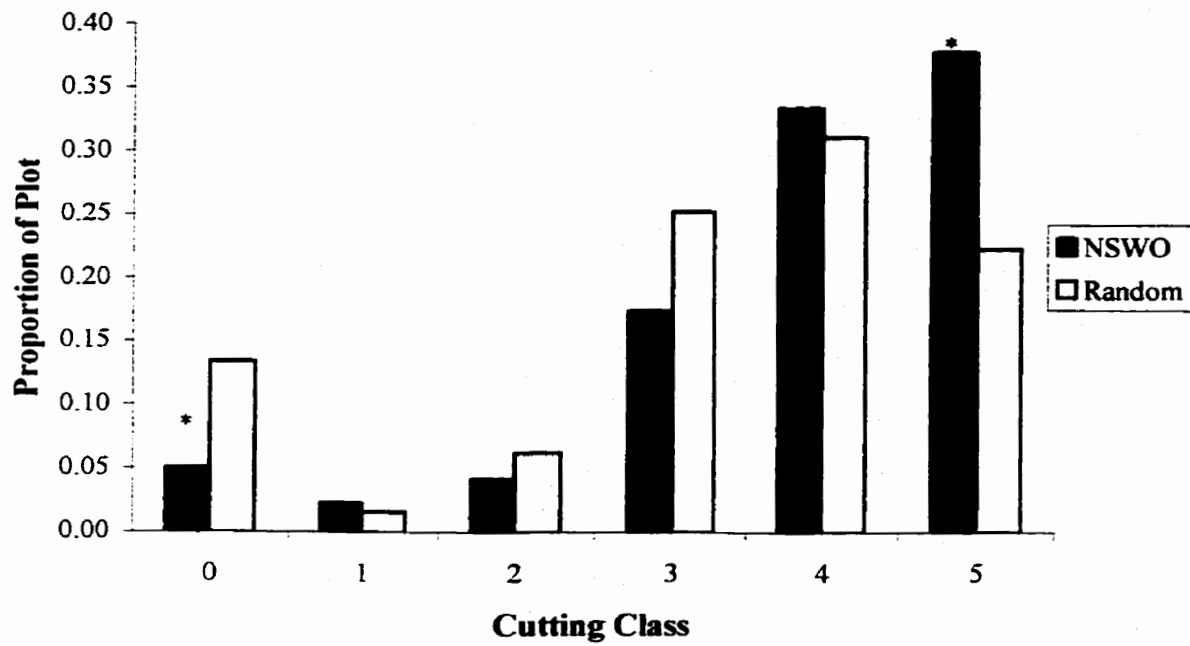


Fig. 6. Proportional composition of cutting classes in 314-ha Boreal Owl (n= 30), Great Gray Owl (n=37), Barred Owl (n= 76) and associated random (n= 58) plots.

* indicates a significant difference ($\alpha < 0.05$) from random composition based on Bonferroni confidence intervals.

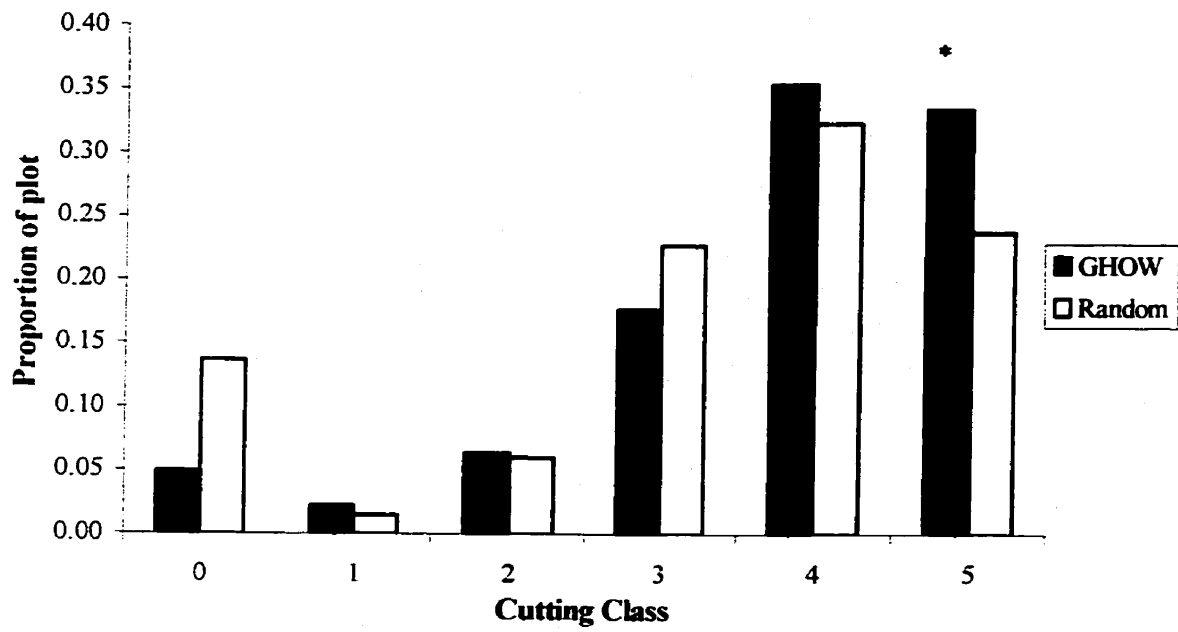


Fig. 7. Proportional composition of cutting classes in 500-ha Great Horned Owl (n= 85) and associated random (n= 58) plots. * indicates a significant difference ($\alpha < 0.05$) from random composition based on Bonferroni confidence intervals.

Crown Closure

Barred Owl, Great Gray Owl and Northern Saw-whet Owl plots differed significantly from random with respect to the proportional composition of crown closure classes ($X^2_{BAOW} = 23.3$, $p < 0.0000$, $X^2_{GGOW} = 7.8$, $p = 0.050$, $X^2_{NSWO} = 11.9$, $p = 0.0007$, Figs. 8 and 9). Boreal Owl plots did not contain significantly different proportions of crown closure classes than what was randomly available in the study area ($X^2_{BOOW} = 3.88$, $p = 0.275$, Fig. 8). Although the frequency distributions of crown closure classes in Great Horned Owl plots differed significantly from random ($X^2_{GHOW} = 16.2$, $p = 0.0010$, Fig. 10), based on Bonferroni confidence intervals, no class differed significantly from random (Fig. 10). Crown closure class 4 (71-100% canopy closure made up the greatest proportion of all plots (Figs. 8-10).

Great Gray Owl plots contained significantly less of crown closure class 0 (0-20% canopy cover, Fig. 8). Barred Owl plots contained significantly smaller proportions of crown closure class 0 and significantly greater proportions of crown closure class 4 (Fig. 8). Northern Saw-whet Owl plots also contained significantly smaller amounts of crown closure class 0 than what was randomly available (Fig. 9). These plots also contained significantly greater proportions of crown closure class 3 (51-70% canopy closure, Fig. 9).

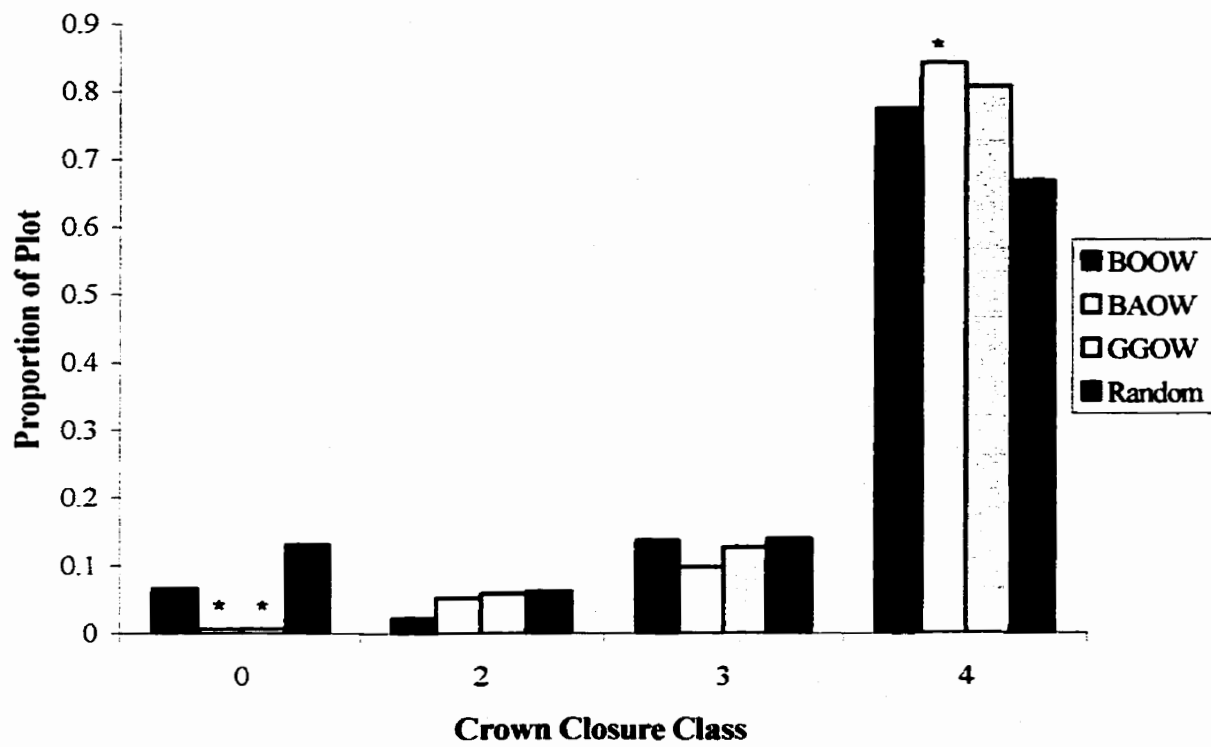


Fig. 8. Proportional composition of crown closure classes in 314-ha Boreal Owl (n= 30), Great Gray Owl (n= 37), Barred Owl (n= 76) and associated random (n= 58) plots.

* indicates a significant difference ($\alpha < 0.05$) from random composition based on Bonferroni confidence intervals.

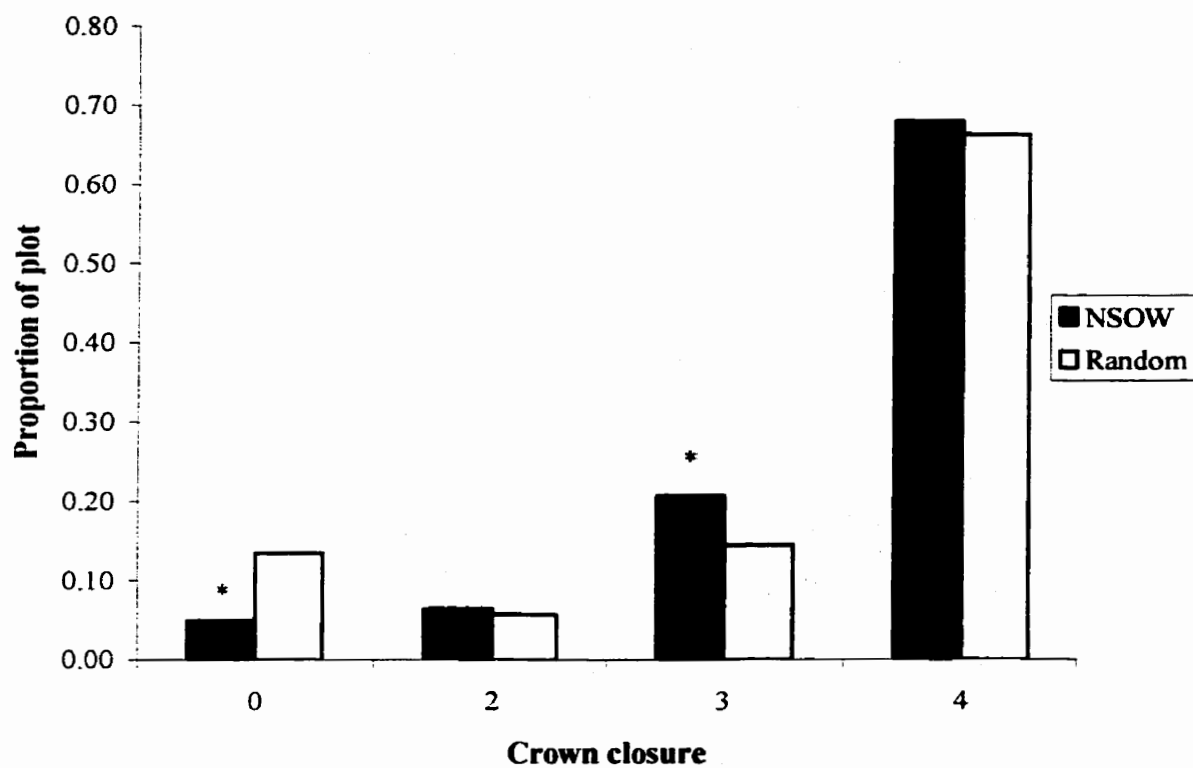


Fig. 9. Proportional composition of crown closure classes in 160-ha Northern Saw-whet Owl ($n=120$) and associated random ($n=58$) plots. * indicates a significant difference ($\alpha < 0.05$) from random composition based on Bonferroni confidence intervals.

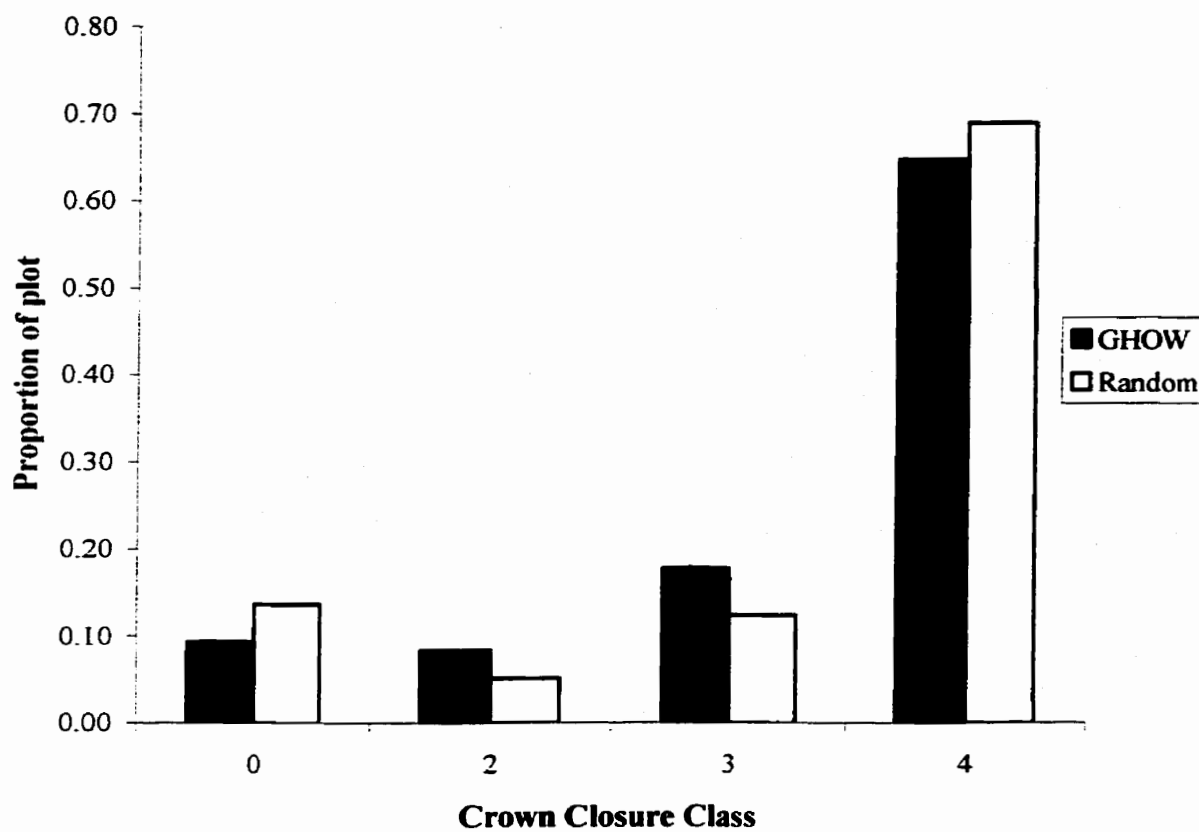


Fig. 10. Proportional composition of crown closure classes in 500-ha Great Horned Owl (n= 83) and associated random (n= 58) plots. * indicates a significant difference ($\alpha < 0.05$) from random composition based on Bonferroni confidence intervals.

DISCUSSION

The proportional composition of the plots of all five owl species differed significantly from random. Hardwood-dominated mixedwood made up the greatest proportion of all owl and random plots, reflecting this stand type's dominance within the study area (McCready *et al.* 1980). Mature and overmature mixedwood forest stands (cutting classes 4 and 5) made up the largest proportion of all plots. Barred Owls, Great Gray Owls and Northern Saw-whet Owls apparently avoided unnatural openings/burn, and thus cutting and crown closure classes 0, as inferred from the Bonferroni confidence intervals. However, all three species' plots contained amounts of natural openings in proportion to their availability in the study area. Conversely, both Great Horned Owls and Boreal Owls did not avoid unnatural openings/burn areas.

Great Gray Owls

The Great Gray Owl's apparent avoidance of young forest, resulting from clear-cuts and burns, differs from what has been found in the southeastern part of Manitoba (Nero 1980, Servos 1986, Bouchart 1991). In southeastern Manitoba, summer home ranges contained large proportions of cleared areas, which Servos (1986) suggested were used by individuals for hunting due to large densities of prey, mainly *Microtus* spp. Whitfield and Gaffney (1997) also found that clear-cuts contained high densities of prey, but that Great Gray Owls in Wyoming suffered greater mortality from predation in areas with high clear-cut density. Thus, although favourable for hunting, unnatural openings do not provide the necessary security cover for adults or juveniles, which may be vulnerable

to edge and open-area predators such as Great Horned Owls and Red-tailed Hawks (*Buteo jamaicensis*) (Duncan 1997, Whitfield and Gaffney 1997).

Owls for the present study were located during the breeding season, in early spring, hence, Great Gray Owls may forfeit open hunting areas for the greater security of closed forest for the early stages of nesting and incubation, moving to forest edges in the summer. Stepniski (1997) suggested that Great Gray Owls also use natural openings and muskeg for hunting. Indeed, Servos (1986) found high proportions of treed muskeg in Great Gray Owl home ranges in southeastern Manitoba. Although not statistically significant, treed muskeg did comprise a relatively large proportion of Great Gray Owl plots in this study.

Great Gray Owl plots also contained large amounts of hardwood-dominated mixedwood and, in this respect, more closely matched those of this species in Alberta than southeastern Manitoba, which were characterized by large proportions of conifer (Servos 1986, Stepnisky 1997). The reduced importance of conifer forest in Great Gray Owl plots in this study area was likely due to the fact that conifer forests are not available in the same amounts as in southeastern Manitoba (McCready *et al.* 1980).

In Wyoming, Whitfield and Gaffney (1997) found that Great Gray Owls used areas with dense canopy closure, which afforded better security cover for young from predators such as Great Horned Owls and Northern Goshawks (*Accipiter gentilis*). In this study, Great Gray Owl plots contained relatively large amounts of dense-canopied forest (crown closure class 4), but not out of proportion to what was randomly available in the study area. Although Great Gray Owls, like all secondary nest users, are restricted to some degree in habitat available for use by the preferences of the primary nest builders

Janes (1985) suggested that given an area supporting a sufficient prey population, a number of potential nest sites may be available and thus the owls must still select a preferred nesting habitat.

Barred Owls

The relatively low occurrence of unnatural clearings/burn areas and the predominance of older mixedwood forests in Barred Owl plots further supports the findings of several studies in Canada and northern United States and validates the Habitat Suitability Index (HSI) model derived for Manitoba (Bosakowski *et al.* 1987, Duncan and Kearns 1997, Mazur *et al.* 1997, Takats 1997, Mazur *et al.* 1998). Mainly secondary cavity nesters, Barred Owls require large-diameter trees that are primarily available in old mixedwood forests (Mazur *et al.* 1997). Older forests are considered more structurally diverse and often support larger prey densities (Roy *et al.* 1995, Schieck and Nietfield 1995). The relatively open understory of older forests may also allow for easier hunting (McGarigal and Fraser 1984). A study of Tawny Owls (*Strix aluco*) found that pairs inhabiting home ranges with relatively little ground cover, interspersed with clumps of understory vegetation were more productive than those that occupied areas with dense ground cover, or no ground cover, common in younger forests and open areas (Southern and Lowe 1968). In the present study, older aspen-dominated forest is often characterized by clumps of beaked hazelnut (*Corylus cornuta*), interspersed with open areas (McCready *et al.* 1980).

Water bodies made up a relatively large percentage of Barred Owl plots, as has been previously documented for Barred Owls (Bosakowski *et al.* 1987, Takats 1997).

Riparian forests are often skipped by fires and thus allow trees to grow large enough to provide cavities suitable for Barred Owl nests (Takats 1997). Wet areas have also been documented to contain greater abundance and diversity of animals (Bosakowski *et al.* 1987), a factor that may be important for a generalist predator such as the Barred Owl (Mazur and James 2000).

Barred Owl plots contained significantly greater proportions of the highest crown closure class than in random plots. This relationship was also found in Alberta (Takats 1997). Forests with a high crown density generally have cooler microclimates and selection for these habitats may be based on thermoregulation needs (Barrows 1981, Mazur *et al.* 1998). Barrows (1981) found that temperatures in a closed canopy forest in northern California were 3 to 5°C cooler than open areas. It has been suggested that Great Gray Owls likely suffer heat stress as a result of their thick plumage (Voous 1988) and thus would also benefit from closed canopy forest. However, the proportion of closed canopy forest in Great Gray Owl plots did not differ significantly from random.

Boreal Owls

Of the five species considered in the study, Boreal Owls have the most specific habitat associations in relation to different cover types. The abundance of over-mature mixedwood in Boreal Owl plots supports the findings of other studies of Boreal Owl habitat associations (Korpimäki 1988a, Hayward *et al.* 1993, Hayward 1997, Lane *et al.* 1997). In this study, Boreal Owl plots consisted mainly of old mixedwood forest and treed muskeg, interspersed with clearcut/burn areas and water. In Finland, Korpimäki (1988) found a similar pattern with Boreal Owl home ranges comprised of spruce

mixedwood forest with small patches of agricultural land. As opposed to the other species in the study, all Boreal Owls were located within the parks, thus agricultural land was not present in their plots.

Lane *et al.* (1997) found that male Boreal Owls in Minnesota used upland mixedwood forests for nesting and lowland conifer forests for diurnal roosting and nocturnal foraging, during the breeding season. Although deciduous forests were apparently avoided, hardwood-dominated mixedwood made up the largest proportion of the plots, which suggests a consistency of this trend.

Janes (1985) suggested that as part of predator-prey systems, raptor habitat associations can best be described through the habitat associations of their primary prey. As cavity-nesters however, Boreal Owls are likely limited, like Barred Owls and Northern Saw-whet Owls, by the availability of suitable nesting sites. Hayward *et al.* (1993) found that mixedwood forests contained a large number of potential nesting cavities, but that this habitat supported small numbers of its preferred prey species, the Red-backed Vole (*Clethrionomys gapperi*) and *Microtus* voles. Conversely, coniferous forest contained few cavities but large numbers of prey. In this study, the avoidance of deciduous forests and strong association with treed muskeg has not been documented previously and may reflect of the habitat preferences of the Boreal Owl's two main prey species. Red-backed Voles are found to be most abundant in older conifer-dominated forests in many geographical areas (Clough 1964, Millar *et al.* 1985, Roy *et al.* 1995). *Microtus* are abundant in conifer-dominated forests (Roy *et al.* 1995). In southeastern Manitoba, *Microtus* are also found in large numbers in treed muskeg (Servos 1986) and this may explain Boreal Owls' use of that cover type.

Although Boreal Owls used unnatural opening/burn areas in proportion to their availability in the study area, natural openings were avoided as inferred through Bonferroni confidence intervals. This pattern of use may be due to a combination of foraging preferences and interaction with other owl species. In southeastern Manitoba, clear-cut forests (cutting class 0) supported high numbers of *Microtus*. In this study area, Barred, Great Gray and Northern Saw-whet owls, potential competitors, avoided cleared forests. Hakkarainen and Korpimäki (1996) suggested that predation by and competition for nest sites with Ural Owls (*Strix uralensis*) reduced the breeding success of Boreal Owls nesting in the vicinity, but that Eagle Owls (*Bubo bubo*) did not directly compete and were not efficient predators of Boreal Owls. The latter two species thus coexisted. The apparent avoidance of deciduous forests by Boreal Owls may be a means of avoiding potential nest site competition and predation by the opportunistic and manoeuvrable Barred Owl. Competition for nest sites, and likely food, between Northern Saw-whet Owls (Lane 1988) is demonstrated in the vigorous responses of saw-whet owls to Boreal Owl playbacks (Duncan and Duncan 1997).

Northern Saw-whet Owls

Old, overmature hardwood dominated mixedwood comprised the bulk of Northern Saw-whet Owl plots, but this amount was a reflection of its availability in the study area. Saw-whet owls showed less specific habitat preferences than the Boreal Owl, except to avoid unnatural opening/burn areas and thus the associated cutting and crown closure classes 0. Although they did not show a preference for any specific cover type,

Northern Saw-whet Owl plots contained significantly greater proportions of cutting class 5 forests (overmature) than what was randomly available.

Cannings (1993) suggested that although Northern Saw-whet Owls occupied a wide variety of habitats in the southern boreal forest, they used mainly coniferous or mixed coniferous forests with a complex understory and middle canopy, especially riparian areas with large spruce across its range. These habitat preferences were not apparent in this study as there was not significantly more water or softwood-dominated forests in saw-whet owl plots.

Cannings (1993) also suggested that reports that the Northern Saw-whet Owl's apparent preference for dense forests with closed canopies is likely based on the analysis of daytime roosting locations rather than nesting locations. This is supported by this study as saw-whet plots contained significantly greater proportions of crown closure class 3. More open canopy forest is associated with the large proportion of old forests, which tend to have more gaps in the canopy (Hayward 1991, Stelfox 1995, Lee *et al.* 1995).

The association of Northern Saw-whet Owls with overmature forests in this study suggests that although they may not select for a specific cover type, individuals apparently use forests with more complex understories and a developed middle canopy, common in older mixedwood stands (Lee *et al.* 1995).

Competition between Boreal Owls and Northern Saw-whet Owls has been documented indirectly in a number of studies (Lane 1988, Lane and McKeown 1991, Duncan and Duncan 1997). It is also possible that the lack of an apparent selection for softwood-dominated mixedwood is a result of competitive exclusion by the larger Boreal Owl. Lane and McKeown (1991) observed a male Boreal Owl singing repeatedly from a

nesting cavity occupied by a Northern Saw-whet Owl and once attacked the male saw-whet. However, as the number of Northern Saw-whet Owls greatly exceeded that of Boreal Owls detected in this study, it is unlikely that they are being excluded from certain habitats.

Great Horned Owls

McInville and Keith (1974) found that the proportion of habitat types present in Great Horned Owl plots in Alberta did not differ from what was available; they concluded that in areas where prey is evenly distributed, Great Horned Owls did not appear to have specific habitat preferences. This is not the case in this study. Great Horned Owls in the parks of the Manitoba Escarpment were associated with overmature softwood-dominated mixedwood, as inferred from Bonferroni confidence intervals. However, Great Horned Owl plots contained both natural openings and unnatural opening/burn areas in proportion to what was available.

This pattern of habitat association has been documented in other studies (Baumgartner 1939, McGarigal and Fraser 1984, Johnsgard 1988). McGarigal and Fraser (1984) found that Great Horned Owls preferred stands of mature forest adjacent to agricultural areas and Baumgartner (1939) found that individuals preferred areas of mature forest bordering water and surrounded by open areas. Conversely, Johnson (1993) found a decrease in Great Horned Owl encounters with increasing amounts of old forest in the Pacific Northwest. This may be a result of the structural differences between old forests in eastern regions and western regions.

The lack of avoidance of natural openings and unnatural opening/burn areas by Great Horned Owls in this study area is likely a result of the species' preference to hunt from the edge of open areas (Johnsgard 1988, Houston *et al.* 1998). In the Rocky Mountains, Johnson (1993) found an increase in Great Horned Owl encounters in response to forest clearing. In Pennsylvania, Morrell and Yahner (1994) also concluded that the species preferred fragmented forested habitat.

Although not statistically significant, the relatively low amount of treed muskeg within Great Horned Owl plots has not been previously documented. As Great Horned Owls have been known to prey on Boreal and other owls (Hayward and Hayward 1993, Houston *et al.* 1998), this trend may further explain the high degree of association of Boreal Owls with treed muskeg habitat.

CONCLUSIONS AND RECOMMENDATIONS

All five owl species' plots varied from random with respect to cover type, suggesting that vegetation characteristics are an important proximal cue in raptor habitat selection. Forest age (cutting class) also appears to be an important selection factor as all but Boreal Owl plots differed significantly from random with respect to this variable. Both these variables affect the structure of habitat available and thus the availability of nest sites (Hayward *et al.* 1993, Takats 1997) and prey (Southern and Lowe 1968, Rohner and Krebs 1996). Crown closure, which may be influenced by forest age (Lee *et al.* 1995), appeared to be an important variable in the habitat selection of Barred and Northern Saw-whet owls. Caution must be exercised in the interpretation of results stemming from use

versus availability studies. It is important to remember that associations can only be inferred by way of such analyses (McCallum 1994).

The use of circular plots centred on estimated owl locations may introduce some level of bias into the results (Duncan and Kearns 1997). Owl home ranges are not naturally circular. Also, owls recorded during playback surveys may have been located at the edge of their home ranges, thus these circles may only represent a portion of the habitat used by an individual (Duncan and Kearns 1997, Mazur *et al.* 1998). Duncan and Kearns (1997) suggest that circular plots miss the complexity within and among stands and that the interaction between cover types within a home range may influence the habitat's suitability for that species. However, several studies have supported the use of circular plots as surrogate home ranges and suggest that this method is an efficient method in determining the landscape-level habitat associations of owl species (Lehmkuhl and Raphael 1993, Duncan and Kearns 1997, Mazur *et al.* 1998).

More detailed study at the stand and nest or roost site level would yield yet more information on the complex habitat associations of these species in this area of their geographical ranges, which could be compared with data gathered in other study areas. Ultimately, studies linking the variation in reproductive success with variations in habitat characteristics and prey availability would be useful in better quantifying the habitat requirements of forest owls in the Manitoba Escarpment (McCallum 1994, Janes 1985, Duncan and Kearns 1997).

CHAPTER 2: THE RELATIONSHIP BETWEEN FOREST FRAGMENTATION AND SLOPE AND THE DISTRIBUTION OF FIVE FOREST OWL SPECIES IN THE MANITOBA ESCARPMENT.

INTRODUCTION

The fragmentation of habitats is one of the greatest threats to the population viability of many species and species diversity (Noss and Csuti 1997). Fragmentation has been defined as the division of a continuous block of habitat into smaller, isolated patches (Noss and Csuti 1997) and can result from natural and unnatural means. The first chapter in this study examined the habitat associations of five forest owl species in the Manitoba Escarpment. Threats to these species may not be related solely to the effects of the loss of their associated habitat, but also to the spatial effects of forest fragmentation, such as edge effects (Schumaker 1996, Noss and Csuti 1997, Warnock and James 1997). Forest raptors are considered one of the most sensitive groups to habitat fragmentation because of their high trophic positions, low densities and large home range requirements (Newton 1979, Niemi and Hannowski 1997).

However, the impacts of forest fragmentation on a species may vary. Noss and Csuti (1997) suggested that nearly all landscapes are patchy at one or more spatial scales. Natural fragmentation by such things as water may benefit species as the natural gradation from forest interior to the adjacent water body may reduce edge effects (Noss and Csuti 1997). Some owl species, such as the Barred Owl, have been reported to be associated with forests bordering water (Carter 1925, Bosakowski *et al.* 1987).

The spatial effects of forest fragmentation may be further compounded by slope in this region of Manitoba, which is characterized by rolling hills. Owls may select certain

slope faces based on microclimate conditions that facilitate thermoregulation (Barrows 1981, Bull and Duncan 1993).

The objectives of this section of the study are: 1) To compare the home range plots centred on owl locations in relation to the amount of edge relative to forest area with that of random plots as this variable has been suggested to be a useful measure of forest fragmentation (Johnson 1993, Schumaker 1996), 2) To compare the amount of forest edge bordering water contained within owl plots with what occurs randomly. The amount and proximity of water within owl home ranges may affect microclimate characteristics and prey availability (Barrows 1981, Bosakowski *et al.* 1987) and 3) To compare owl and random plots locations with respect to elevation, slope aspect and gradient as topographic characteristics may influence owl distribution (Barrows 1981).

METHODS

Forest Fragmentation and Water Edge

Fragmentation may occur at many scales (Noss and Csuti 1997, Davidson 1998). Highly mobile, owls can travel between many forest patches therefore a home range level of spatial analysis was used for this study. The degree of fragmentation was measured as the ratio of edge to forest area, which increases as fragmentation increases (Johnson 1993). There has been no consensus on the most appropriate way to describe landscape patterns resulting from habitat fragmentation as it encompasses increased amount of edge, reduced size of habitat patches and increased isolation of remaining patches, among others (Davidson 1998). Some researchers have suggested that evaluating the various aspects of fragmentation separately is preferable to using indices such as edge-area ratios (Lawrence and Yensen 1991, Davidson 1998). However, as plots varied in size between

species, it was necessary to use a measure of fragmentation that was standardized across the different plot sizes. In this study, edge was defined as the transition between forest and non-forest habitats not including water bodies (cutting classes 0 and 1, and vegetation classes not containing forest cover). A species' association with water was approximated separately as the total amount of forest edge within a plot bordering a wetland.

Elevation and Slope Characteristics

Elevation and slope gradient were interpolated from contour lines on 1:50,000 topographic maps. Slope gradient values were grouped into six 3-degree intervals from 0 to 18 degrees (Forsman and Giese 1997). Slope aspect was measured using a compass to the nearest degree, for locations on slopes with gradients greater than 1.5 degrees.

Statistical Analyses

Data approached normality, as determined from graphical analysis of z-scores (Appendix 6, Zar 1984). Thus, a two-tailed student's t-test, with n_1+n_2-1 degrees of freedom and $\alpha=0.05$ was used to determine whether significant differences existed between owl and random plots with respect to edge-area ratio, total water edge and elevation. A student's t-test was used because of its robustness to even considerable departures from normality, especially if the hypothesis is two-tailed and the sample sizes are relatively large (Zar 1984), as in this study.

A chi-squared test, with $\alpha=0.05$, and Bonferroni confidence intervals were used to determine associations of owl and random plots with each slope gradient category (Neu *et al.* 1974, Byers *et al.* 1984, Forsman and Giese 1997). A Watson's U^2 test was used to test for differences between owl and random locations with respect to the mean angle of

slope aspect (Batschelet 1981). Although a non-parametric test, the Watson's U^2 is powerful at detecting differences between samples (Batschelet 1981).

RESULTS

Edge-to-area Ratios

The mean edge-to-area ratio for plots of all five species varied from 26.75 +/- 6.48 m/ha for Boreal Owls to 68.06 +/- 10.31 m/h for Great Horned Owls (Figs. 11-14). Barred Owl and Great Gray Owl plots had mean edge-to-area ratios of 42.55 +/- 6.32 m/ha and 40.23 +/- 8.18 m/ha respectively. Neither species' plots differed significantly from random 314-ha plots, which had a mean edge-to-area ratio of 49.81 +/- 9.67 m/ha ($t_{BAOW} = -0.946$, $p = 0.374$, $t_{GGOW} = -0.990$, $p = 0.257$, Fig. 11). Boreal Owl plots with an edge-to-area ratio of 26.75 +/- 6.48 m/ha contained significantly less forest edge relative to forested area than random 314-ha plots ($t_{BOOW} = -2.241$, $p = 0.006$, Fig. 11).

Northern Saw-whet Owl plots had a mean edge-to-area ratio of 40.42 +/- 5.12 m/ha, which did not differ significantly from random 160-ha plots, whose mean edge-to-area ratio was 54.62 +/- 11.62 m/ha ($t_{NSWO} = -1.75$ $p = 0.150$, Fig. 12). In contrast to the other four species' plots, Great Horned Owl plots had a mean edge-to-area ratio of 68.06 +/- 10.31 m/ha, which was significantly greater than that of random 500-ha plots at 47.39 +/- 9.27 m/ha ($t_{GHOW} = 1.97$ $p = 0.039$, Fig. 13).

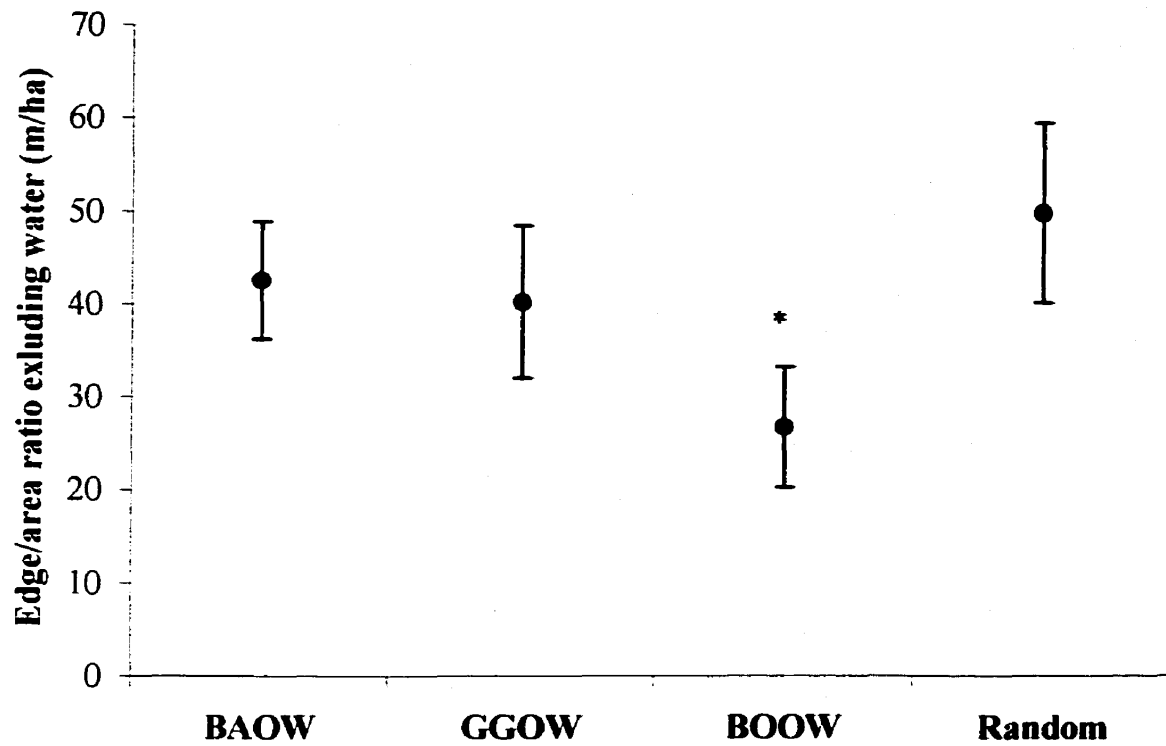


Fig. 11. Edge/area ratios for Boreal Owl ($n=30$), Great Gray Owl ($n=36$), Barred Owl ($n=77$) and random ($n=58$) 314-ha plots. * indicates a significant difference $\alpha < 0.05$ from random based on a two-sample t-test with n_1+n_2-2 degrees of freedom.

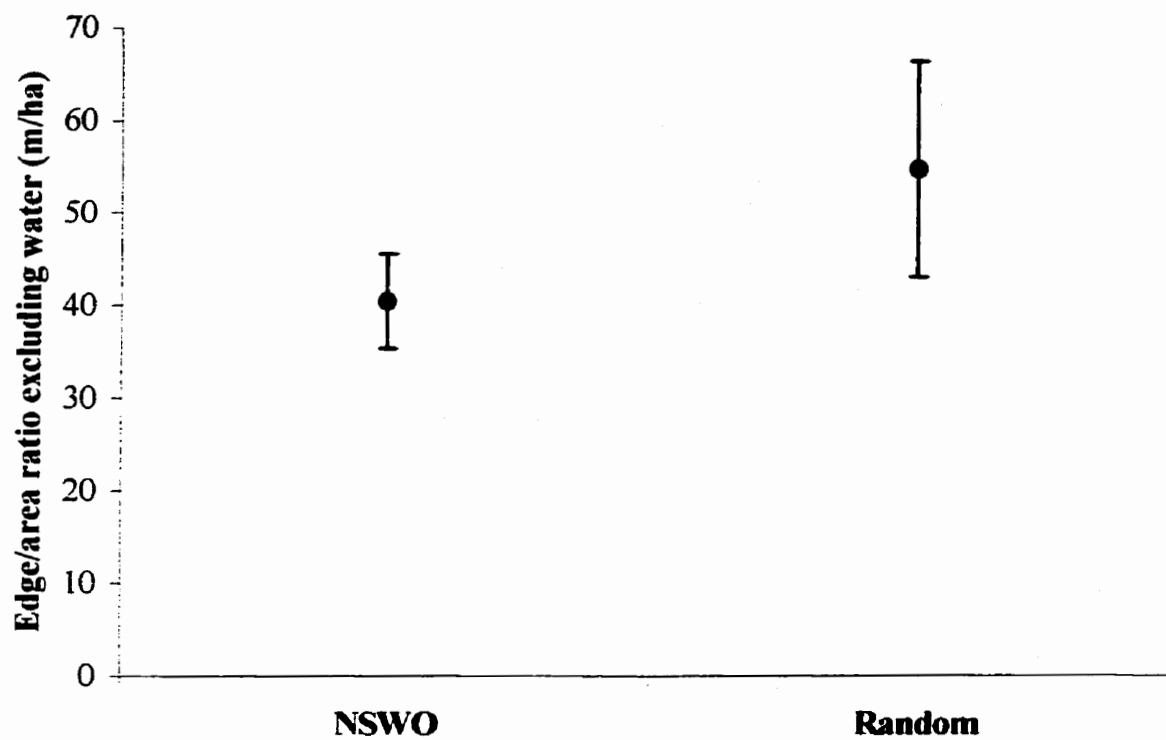


Fig. 12. Edge/area ratios for Northern Saw-whet Owl ($n=119$) and random ($n=58$) 160 ha plots. Northern Saw-whet Owl plots did not differ significantly ($\alpha < 0.05$) from random based on a two-sample t-test with n_1+n_2-2 degrees of freedom.

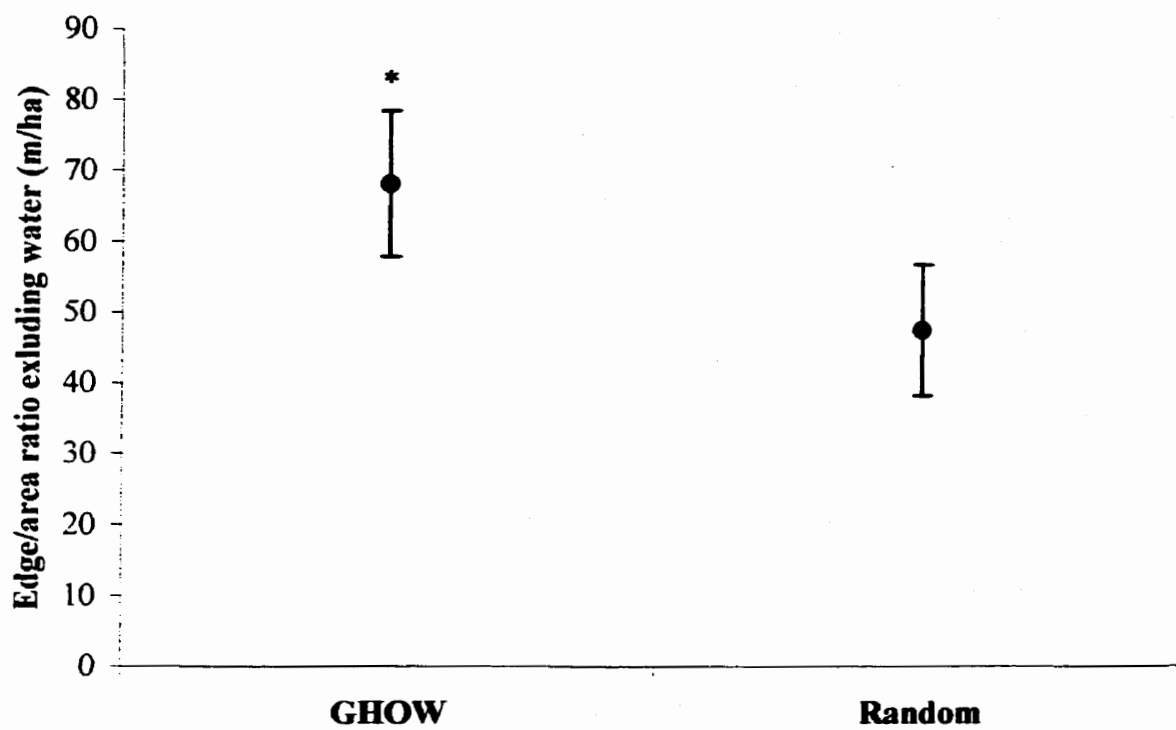


Fig. 13. Edge/area ratios for Great Horned Owl (n=85), and random (n=58) 500 ha plots.

* indicates a significant difference $\alpha < 0.05$ from random based on a two-sample t-test with n_1+n_2-2 degrees of freedom.

Water Edge

With means of 5.57 +/- 1.15 km and 5.22 +/- 0.22 km, respectively, only Boreal Owl contained significantly greater amounts of forest bordering water (water edge) than random 314-ha plots, which had a mean of 4.03 +/- 0.67 km ($t_{\text{BOOW}} = 2.07$, $p = 0.041$, Fig. 14). The amount of water edge within Barred Owl plots approached a significantly larger value than random 314-ha plots ($t_{\text{BAOW}} = 1.95$, $p = 0.050$, Fig. 14). Great Gray Owls had a mean of 4.91 +/- 0.94 km, which did not differ significantly from random 314-ha plots ($t_{\text{GGOW}} = 1.29$, $p = 0.189$, Fig. 14).

Northern Saw-whet Owl plots, with a mean water edge of 2.27 +/- 0.29 km, did not differ significantly from random 160-ha plots, which contained a mean of 2.11 +/- 0.37 km of water edge ($t_{\text{NSWO}} = 0.442$, $p = 0.645$). The Great Horned Owl plot's mean of 6.72 +/- 1.04 km of water edge also did not differ significantly from its associated random plots, which contained a mean 6.38 +/- 1.07 km of water edge ($t_{\text{GHOW}} = 0.369$, $p = 0.702$).

Elevation

Owl plot centres varied in mean elevation from 621.1 +/- 66.7 m above sea level for Great Horned Owls to 712.7 +/- 126.2 m for Boreal Owls (Fig. 15). Random plots were found at a mean elevation of 626.2 +/- 81.4 m (Fig 15). Only Boreal Owl plots differed significantly from random with respect to elevation and were significantly higher than random plots ($t_{\text{BOOW}} = 6.99$, $p < 0.0000$, Fig. 15).

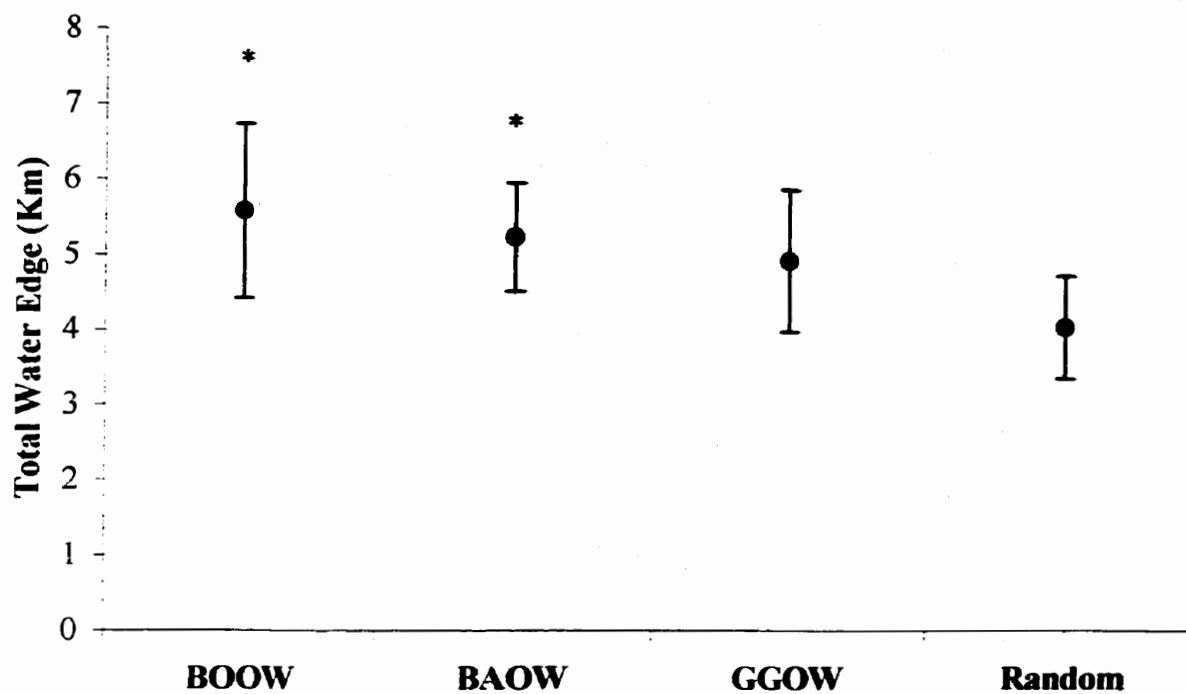


Fig. 14. Total amount of forest edge bordering water bodies within Boreal Owl ($n=30$), Barred Owl ($n=77$), Great Gray Owl ($n=36$) and random ($n=58$) 314 ha plots. * indicates a significant difference ($\alpha < 0.05$) from random based on a two-sample t-test with n_1+n_2-2 degrees of freedom.

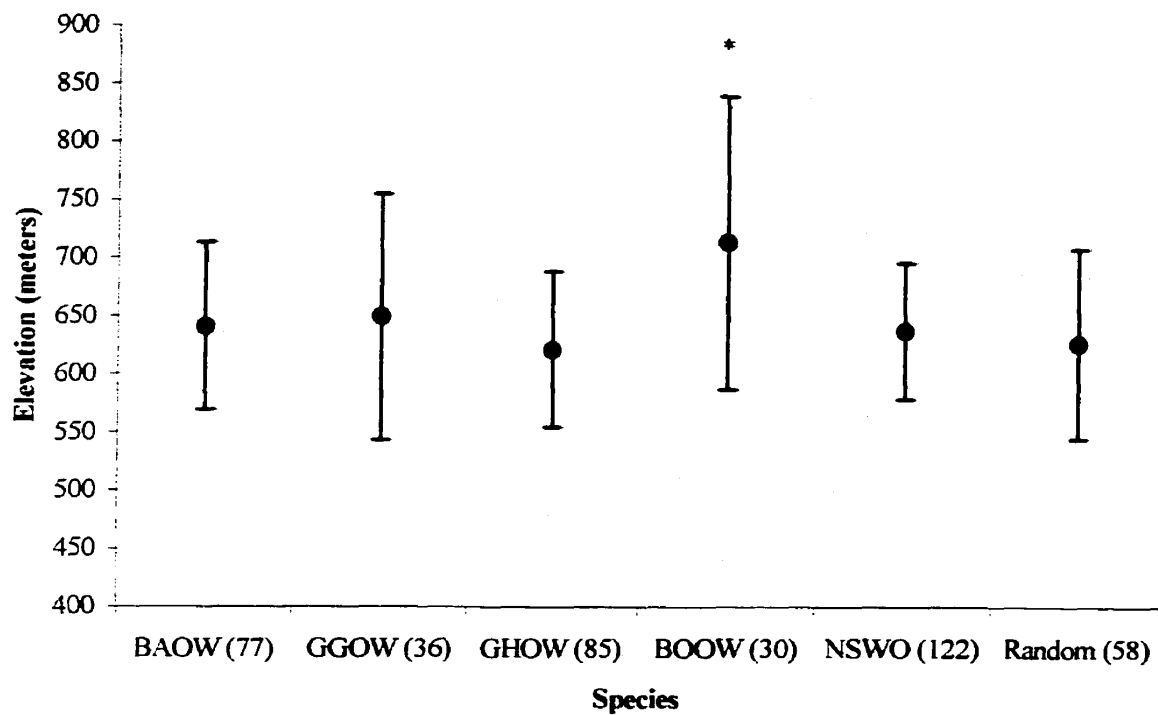


Fig. 15. Mean elevation \pm SE of owl and random locations (n). * indicates a significant difference from random ($\alpha < 0.05$) based on a two-sample t-test with $(n_1 + n_2) - 1$ degrees of freedom.

Slope Gradient and Aspect

Despite the rolling terrain of the Manitoba Escarpment, the bulk of owl and random locations were found on gentle to non-existent slopes. A small number of Northern Saw-whet Owl and Boreal Owl plots were found on steeper slopes (Fig 16). Only Great Horned Owl and Great Gray Owl plots differed significantly from random, with respect to slope gradient ($X^2_{\text{GHOW}} = 6.79$, $p = 0.034$, $X^2_{\text{GGOW}} = 8.88$, $p = 0.011$, $X^2_{\text{BAOW}} = 1.94$, $p = 0.379$, $X^2_{\text{NSWO}} = 5.54$, $p = 0.063$, $X^2_{\text{BOOW}} = 2.31$, $p = 0.314$, Fig. 16). Both were found significantly more often on slopes ranging from 0 to 3 degrees and avoided slopes between 9 and 15 degrees (Fig. 16). Great Gray Owl locations were also found significantly less often on slopes ranging from 3 to 6 degrees (Fig. 16).

Mean slope aspect angle for owl and random plots ranged from west (272.4° for Boreal Owls) to northeast (48.4° for Great Horned Owls, Table 2). Within species variation was very high as shown by the low r-values (Table 2). Only Northern Saw-whet Owl plots at 337.4° were significantly different from the mean aspect of random plots at 279.4 ($U^2 = 0.248$, $p < 0.05$, Table 2)

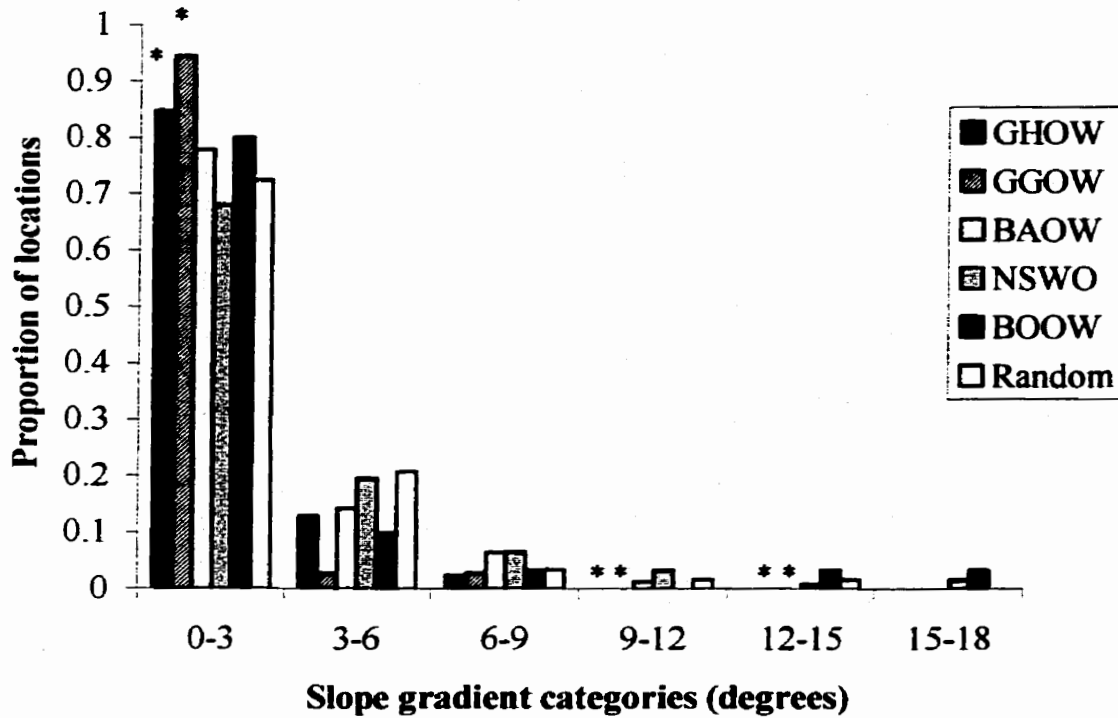


Fig. 16. Proportion of Great Horned Owl (n=85), Great Gray Owl (n=36), Barred Owl (n=77), Northern Saw-whet Owl (n=122), Boreal Owl (n=30) and random (n=58) plots within slope gradient categories. * indicates a significant difference from random ($\alpha < 0.05$) based on Bonferroni confidence intervals.

Table 1. Results of a Watson's U^2 test, with $\alpha=0.05$ between owl and random mean slope aspect angles. * indicates significant difference.

Species	Mean Slope aspect angle (degrees)	r	n	Watson's U2 Statistic	p
Barred Owl	320.5	0.132	31	0.152	> 0.05
Great Gray Owl	317.7	0.076	12	0.08	> 0.05
Great Horned Owl	48.4	0.175	29	0.058	> 0.05
Boreal Owl	272.7	0.099	18	0.119	> 0.05
Northern Saw-whet Owl	337.4	0.284	78	0.248	< 0.05 *
Random	279.4	0.115	31		

DISCUSSION

Forest Fragmentation

Boreal Owl and Great Horned Owl plots differed significantly from random with respect to the degree of forest fragmentation (Figs. 11 and 13). Although Barred Owl plots tended toward smaller edge-to-area ratios, the lack of any significant difference between Barred Owl plots and random is contrary to several studies that suggested Barred Owls are sensitive to forest fragmentation (Laidig and Dobkin 1995, Haney 1997, Takats 1997). There are no studies addressing the spatial effects of forest fragmentation on the occupancy or reproductive success of Barred Owls. A study of the Northern Spotted Owl (*S. occidentalis caurina*) found no relation between site selection and any indices of forest fragmentation (Meyer *et al.* 1998). Meyer *et al.* (1998) found that one of the major influences on Northern Spotted Owl site selection was the total amount of old growth forest. The results of the present study suggest a similar relationship, as shown by the significantly smaller amount of young open forest (Figs. 2, 5 and 8).

Great Gray Owl plots also did not differ significantly from random, but tended toward lower edge-to-area ratios (Fig. 11). In Alberta, Stepniski (1997) found that Great Gray owls occupied areas with less edge relative to forest area and that this ratio was highly correlated with the percent of forested area within owl territories. The Great Gray Owl is often considered an edge species, as its primary prey, *Microtus* spp. is most plentiful in open areas (Servos 1986, Roy *et al.* 1995). The species has been seen hunting in open areas, mainly from within 50 m of a forest edge (Sulkava and Huhtala 1997).

Forest management recommendations for the species include shaping small clearcuts with convoluted edges to increase areas for hunting and vole populations (Duncan

1997, Sulkava and Huhtala 1997). However, Whitfield and Gaffney (1997) suggested that highly fragmented areas may act as ecological traps for Great Gray Owls by providing ample prey, but insufficient cover for juveniles and dispersing adults, which may fall prey to Great Horned Owls, another edge species. In his recommendations for forest management for Great Gray Owls, Duncan (1997) suggested that the convoluted edges of clear-cuts may also serve to reduce predation by Great Horned Owls and Northern Goshawks (*Accipiter gentilis*).

Stepniski (1997) suggested that Great Gray Owl preferences regarding the degree of fragmentation might shift depending on the matrix of the overall landscape. In a matrix of agricultural land with patches of forest, owls may seek out areas with great proportions of forest cover, as it is the resource in demand (Stepniski 1997). Conversely, in areas where the overall matrix is forest, Great Gray Owls may seek areas with higher edge-to-area ratios than the landscape as a whole, as it is the edge that is in demand (Stepniski 1997). It is also important to note that, as secondary stick nesters, Great Gray Owls may be constrained in their habitat use by the habitat preferences of the primary stick nest builders, such as Northern Goshawks, which may have different tolerance ranges (Whitfield and Gaffney 1997).

Although Northern Saw-whet Owls did not show a significant pattern of occupation with regards to the degree of forest fragmentation, the species' plots tended toward smaller edge-to-area ratios than random (Fig. 12). Little is known of Northern Saw-whet Owl spatial responses to forest fragmentation. In his review of the literature, Cannings (1993) suggested that the species most likely would be negatively affected by

habitat loss due to logging, due to its preference for older coniferous forests, but he made no inferences regarding the potential effects of increased edge.

The slight trend toward less edge relative to area could be related to prey preferences. *Peromyscus* spp. make up the bulk of the saw-whet's diet throughout much of its range (Cannings 1993). These mice prefer areas with high amounts of downed woody material and an understory with relatively few shrubs and little litter (Roy *et al.* 1995), characteristics more consistent with forest interior.

The Boreal Owl showed a trend in occupancy with relation to forest fragmentation, with plots containing significantly less edge relative to forest area (Fig. 11), despite containing similar amounts of unnatural opening/burn area to random (Fig. 2). The current understanding of the Boreal Owl and its response to fragmentation is poor (Hayward 1997). However, the results of this study appear to contradict findings in Europe, which suggest that fledgling productivity for this species is higher in territories with a greater proportion of clear-cut (Hakkarainen *et al.* 1997). This apparent contradiction may be related to variation in preferred prey species between the two continents. In Europe, Boreal Owls prey predominantly on field voles (*Microtus* spp.), which are found in large numbers in clear-cuts and other open areas, thus individuals often forage from the forest edge (Korpimäki 1988b). Conversely, in North America, Red-backed Voles, a predominantly forest-dependent vole, makes up the bulk of the owl's prey (Hayward and Garton 1988).

Hayward (1997) suggested that forest edges would also be useful for foraging owls in North America. Sonerud (1986) found that Boreal Owls in Norway hunted mainly in mature coniferous forests during the winter and summer, as soft, crustless snow

in winter and minimal undergrowth in summer facilitated access to prey. However, in early spring, individuals took advantage of early snow melt conditions in clear-cuts to access the greater densities of voles in these areas, as access to the bare ground appeared earlier in these open areas than in forested stands (Sonerud 1986). In northwestern United States, Boreal Owls occupied old growth stands adjacent to clear-cuts, suggesting that stand structure plays a greater role in influencing owl occupancy than anything related to edge (Herren *et al.* 1996). In the present study, Boreal Owls apparently did not avoid clear-cuts or burn areas, but occupied plots containing openings in such a way to minimize the amount of edge relative to forest area within their home range. The apparent avoidance of edge by Boreal Owls in this study could be due in part to the large number of Great Horned Owls in the area and their apparent association with edge habitats. Hayward and Hayward (1993) suggested that the Great Horned Owl could be a significant predator on Boreal Owls, thus the avoidance of edge by the smaller species could be an anti-predator response.

Great Horned Owls showed an opposite response to forest fragmentation than the other four species, with plots containing significantly greater amounts of edge relative to forest area than randomly available (Fig. 13). Considered an edge species, the results of this study support other findings (Johnson 1993, Morrell and Yahner 1994, Laidig and Dobkin 1995).

Although no study has been conducted on the species' relationship to edge, a number of other studies suggest that an increase in forest fragmentation could lead to an increase in Great Horned Owl populations (Johnson 1993, Laidig and Dobkin 1995). Predominantly a perch and pounce predator, Great Horned Owls have been found to

associate strongly with forest edges when foraging. Several studies suggest that this may be related to the large size and relatively poor agility that limits the species' hunting ability in dense forest (Cottam *et al.* 1942, Baker 1962, Johnson 1993). Other studies have gone so far as to suggest that the quality of Great Horned Owl nesting territories is directly related to the proximity of edges along open areas for foraging (Baumgartner 1939, McInville and Keith 1974).

Throughout most of its range, the Great Horned Owl preys primarily on lagomorphs (Johnsgard 1988, Houston *et al.* 1998), a group of species found primarily along forest edges (Roy *et al.* 1995). Bosakowski *et al.* (1989) found that owls nesting in contiguous forest have lower productivity than individuals living in open areas and attributed this to the lack of its preferred prey species. This suggests that an increase in forest fragmentation may benefit Great Horned Owl reproductive success by providing more foraging opportunities.

Water Edge

Boreal Owl and Barred Owl plots contained significantly greater amounts of forest edge along water bodies than random, despite having similar amounts of water to random plots (Figs 2 and 14). Barred Owls have been found to be associated with riparian areas and wetlands in many other studies (Carter 1925, Smith *et al.* 1983, Bosakowski *et al.* 1987, Takats 1997, Mazur *et al.* 1998).

In Alberta, Takats (1997) found a large proportion of Barred Owl nests in stands bordering water and suggested that this was related to the distribution of its preferred nesting tree the Balsam Poplar (*Populus balsamifera*), which was common in wet areas.

Balsam Poplar is present in the Manitoba Escarpment (McCready *et al.* 1980), but its distribution relative to water is not known.

Often difficult to access, many riparian areas and wetlands are bypassed by forestry operations and other human intrusions (Bosakowski *et al.* 1987). Fire may also skip over wet areas, allowing for the growth of old large-diameter trees, suitable for nesting cavities (Bosakowski *et al.* 1987). It has also been suggested that riparian areas support a greater abundance and diversity of prey species than drier areas (Bosakowski *et al.* 1987). Barred Owls, an opportunistic predator, have also been observed dropping into small streams to catch fish and amphibians (Smith *et al.* 1983, Mazur and James 2000).

As a secondary cavity-nester, the Boreal Owl may also exploit similar aspects of riparian areas, however, Korpimäki (1988a) described poor nesting habitat for Boreal Owls as having greater amounts of wetlands. Baumgartner (1939) describes Great Horned Owl preferred nesting habitat as mature forest bordering water, surrounded by open areas. This association with water edge in Baumgartner's (1939) study may be a bias resulting from the bulk of uncleared forest edge existing in riparian areas. In this study no such association with water was observed.

Both Barred and Boreal Owls may benefit from a cooler microclimate that often results from proximity to water. Barrows (1981) found that forests bordering water were 2 to 5°C cooler than the surrounding interior forest. Barrows also recorded Spotted Owls (*Strix occidentalis*) moving to roost over water when ambient temperatures surpassed 30°C and Forsman and others (1984) found that 80% of Spotted Owl nests in their Oregon study area were within 300 m of permanent water. Although little is known about

temperature regulation in Barred Owls (Mazur and James 2000), Boreal Owls have been found to exhibit heat stress at temperatures about 20°C (Hayward *et al.* 1993).

Elevation and Slope Characteristics

Only Boreal Owls were found at higher elevations than random plots (Fig. 15). This supports results of other studies that describe Boreal Owl habitat as high elevation forests (Hayward 1993, Hayward 1997). As Boreal Owls appear to suffer from heat stress at temperatures as low as 20°C relative to other owl species (Ligon 1969, Barrows 1981, Hayward 1993), Hayward (1997) suggested that at least in summer Boreal Owl locations may be distributed in relation to an elevation gradient, which in turn influences the availability of cool microclimates, in an effort to avoid heat stress.

Although, the range of elevation is considerably greater in the Rock Mountains, the location of Hayward's (1993) study area, than that of the Manitoba Escarpment, temperatures on the escarpment tend to be 1 to 2°C cooler than the surrounding lowlands (McCready *et al.* 1980). It is also possible that Boreal Owls' apparent selection for higher elevations in this study may be attributed to their preference for treed muskeg and a trend towards greater proportions of softwood-dominated forests in their plots, as these habitat types tend to be found more frequently within the core of the Escarpment, at higher elevations. The other four species showed less specific habitat associations and thus may be found at a number of different elevations.

Great Gray Owls and Great Horned Owls avoided steeper areas (Fig. 16). Great Gray Owls' selection for flat locations may be related to the species' trend toward greater proportions of treed muskeg in its plots, a preferred habitat type elsewhere (Nero 1980, Duncan 1997). In Wyoming, Whitfield and Gaffney (1997) found that Great Gray Owls

tended to avoid steep slopes. The trend toward relatively larger amounts of open agricultural areas in Great Horned Owl plots may be related to the preference of this species for less steep slopes, as these areas are found at the base of the Escarpment.

Only Northern Saw-whet Owls showed a significant response in occupation of areas in relation to slope aspect (Table 2), with plots on more northerly slopes than random. Little is known of owl distribution with relation to slope aspect. Studies conducted on the Northern Spotted Owl found no significant pattern of occupation in relation to slope aspect (Blakesley *et al.* 1992, Forsman and Giese 1997). The occupation of significantly more northerly slopes than random by Northern Saw-whet Owls may be related again to microclimate variation. In ravines in northern California, Barrows (1981) found that north-facing slopes were 5 to 6°C cooler than slopes with a southern exposure. However the effects of the direction of slope may be confounded by the effects of the difference in vegetation found on each slope face (Barrows 1981). Slopes that do not receive direct midday sun, such as more northerly slopes, may retain greater moisture and thus produce larger trees and denser cover (Barrows 1981). If northern slopes provided significantly cooler microclimates, one would expect Boreal Owls, who suffer heat stress at lower temperatures than saw-whets (Ligon 1969, Hayward 1993), to occupy these slopes more often, however, this was not found in the present study. The effects of slope aspect on the spatial distribution of the other species, especially Boreal Owls, may have been affected by the small sample sizes of owl locations on slopes greater than 1.5 degrees. Great Horned Owls and Great Gray Owls, as they apparently avoided areas of steep slopes, would not be expected to show a preference with respect to slope aspect. It is difficult to separate the relationship between owl occurrences and topographic

characteristics and the variation in vegetation characteristics that go along with it (Barrows 1981). Studies at the roost or nest site level or using radio transmitter relocations may allow for the separation of these two factors.

CONCLUSIONS AND RECOMMENDATIONS

The five most common forest owl species in the Manitoba Escarpment did not distribute themselves spatially in a random pattern with respect to degree of fragmentation, elevation and to a much lesser extent, slope characteristics. Boreal Owls and Great Horned Owls exhibited each extreme in terms of occupancy patterns based on degree of forest fragmentation and few relationships were documented between owl occupancy and slope and elevation characteristics.

The effects of forest fragmentation on owl species are complex and dynamic. Forest edges are changing in size and shape each year with continued clearing and forest fires and succession of previously cleared areas. The FRI data used in this study are already over 10 years old and considered out of date and will be replaced by an updated set in the next few years (S. Frey pers. comm.). Once these data are updated, this study could be modified to reflect more current conditions. FRI data is recorded and presented at a broad level of detail and thus ignores within stand variation, increasing the potential for errors in stand descriptions (N. Kenkel, pers. comm.). However, in an effort to ground truth the FRI data for a study in southeastern Manitoba, Servos (1986) found that the classification polygons represented actual stand composition and density with sufficient accuracy for landscape-level and home range-level studies of habitat associations. This form of data has also been used in several other studies of owl habitat relationships

(Servos 1986, Bouchart 1991, Johnson 1993, Moen and Gutierrez 1997, Mazur *et al.* 1998)

Occupancy alone is not a sufficient measure of a species' response to forest fragmentation (Johnson 1993). Owls are highly mobile and the effects of fragmentation, such as increased distance between habitat patches, are likely greater than those of habitat loss alone (Noss and Csuti 1997). For forest owls, isolation of forest fragments may pose significant barriers to juvenile and adult movements and dispersal (Schumaker 1996, Meyer *et al.* 1998), an aspect of fragmentation not considered in this study. To create a more complete picture of the effects of forest fragmentation on owls, studies should focus on the survival, reproductive success and dispersal rates of owls in these fragmented habitats (Johnson 1993, McCallum *et al.* 1994).

Little work has been done on the effects of slope characteristics on the spatial distribution of raptors, despite the potential for great effects in areas of dramatic variation in topography. Even in areas of moderate elevation, changes in slope aspect and gradient can affect drainage, logging and burn patterns, and thus may be a covariate of stand age and tree size. Based on the owl-habitat relationship documented in this and other studies, these variables likely ultimately affect the distribution of owls.

Thus, despite the limitations of this study, the results indicated an association with edges in Great Horned Owls and the apparent avoidance of edges by Boreal Owls, the association with riparian forests in both Boreal and Barred owls and the indication that topographic features may influence owl distribution are useful as baseline data in the development of forest management protocols for this region so that the ecological integrity of these species may be better conserved.

SUMMARY

1. The objectives of this study were to describe the habitat associations of five owl species in the Manitoba Escarpment and to compare owl and random areas with respect to the degree of forest fragmentation, amount of water edge and elevation and slope characteristics.
2. A total of 264 owls in 1999 and 246 owls in 2000 were located through nocturnal surveys using taped playbacks of owl calls and through incidental encounters. Owl locations were digitized as UTM coordinates and overlaid on forest resource inventory maps.
3. Circular plots approximately equal in size to each species' published home range estimates were overlaid on each owl location. Habitat (cover type, cutting class and crown closure), edge, elevation and slope characteristics within were compared with a sample of stratified random plots of equal size in a use versus availability analysis.
4. Barred, Great Gray and Northern Saw-whet owl plots all contained significantly less unnatural opening/burn areas and the associated young open forest. These findings support those of other studies for Barred Owls and Northern Saw-whet Owls, both cavity nesters. This finding for Great Gray Owls differs from studies in southeastern Manitoba and may be related to the timing in the season of the study and/or the time of day of the surveys.
5. Boreal Owl plots contained significantly greater proportions of treed muskeg and smaller proportions of natural openings and deciduous forest, a trend possibly

related to a preference for Red-backed Voles and *Microtus*, which are often found in coniferous forest and treed muskeg.

6. All species showed some trend toward larger proportions of mature and old forest in their plots, and this trend was significant in Great Horned and Northern Saw-whet owls plot. Northern Saw-whet Owl plots contained greater amounts of forest with 51-70 % crown closure, whereas, Barred Owls preferred forest with high (71-100%) crown closure.
7. Only Boreal Owl and Great Horned Owl plots differed significantly from random with respect to degree of forest fragmentation. The smaller edge-to-area ratios with Boreal Owl plots may also be related to habitat preferences of prey species and possibly an avoidance strategy for one of its predators, the Great Horned Owl, whose plots contained significantly higher edge to area ratios than random.
8. The significantly larger amount of forest edge bordering water in Barred Owl and Boreal Owl plots could reflect an affinity of these species for wet areas due to the abundance of larger trees for nesting and possibly an increased abundance and diversity of prey species in riparian areas.
9. Boreal Owls were found at significantly higher elevations than random plots, thus supporting the hypothesis of an elevational distribution of this species in relation to summer temperatures. The avoidance of Great Gray and Great Horned owls of steeper slopes is likely due to the relatively large amount of treed muskeg and agricultural land found respectively in the plots of each species. The significantly greater amount of Northern Saw-whet Owl locations on northerly slopes may

reflect a preference by that species for cooler microclimates, which could facilitate thermoregulation.

10. Despite the potential biases of using circular plots centered on estimated owl locations, this study provides important baseline data in the development of management protocols for the forests inhabited by these species.

LITERATURE CITED

- Aebischer, N.J., P.A. Robertson, and R.E. Kenward. 1993. Compositional analysis of habitat use from animal radio-tracking data. *Ecology* **74**:1313-1325.
- Baily, R.H. 1968. Notes on the vegetation of Riding Mountain National Park. National Park Survey Report. No. 2. Department of Forestry and Rural Development, Forest Management Institute, Ottawa.
- Baker, J.D. 1962. The manner and efficiency of raptor depredations of bats. *Condor* **64**:500-503.
- Barrows, C.W. 1981. Roost selection by Spotted Owls: An adaptation to heat stress. *Condor*: **83**:302-309.
- Batschelet, E. 1981. *Circular Statistics in Biology*. Academic Press, Toronto.
- Baumgartner, F.M. 1939. Territory and population in the Great Horned Owl. *Auk* **56**: 274-282.
- Bibby, C.J., N.D. Burgess, D.A. Hill and S. Mustoe. 2000. *Bird Census Techniques*. 2nd Edition. Academic Press, Toronto.
- Blakesley, J.A., A.B. Franklin and R.J. Gutierrez. 1992. Spotted Owl roost and nest site selection in northeastern California. *J. Wildl. Manage.* **56**: 388-392.
- Bosakowski, T., R. Speiser, and J. Benzinger. 1987. Distribution, density and habitat relationships of the Barred Owl in northern New Jersey. In Nero, R.W., R.J. Clark, R.J. Knapton & R.H. Hamre, (*Editors*). *Biology and conservation of northern forest owls*. Symposium proceedings. Feb. 3-7, 1987. Winnipeg, Manitoba. Gen. Tech. Rep. RM-142. Fort Collins Co: USDA Forest Service Rocky Mountain Forest and Range Experiment Station. Pp 135-143.

- Bosakowski, T., R. Speiser, and D.G. Smith. 1989. Nesting ecology of forest-dwelling Great Horned Owls *Bubo virginianus* in the eastern deciduous forest biome. *Can. Field-Nat.* **103**:65-69.
- Bouchart, M.L. 1991. Great Gray Owl habitat use in southeastern Manitoba and the effects of forest resource management. MNRM Practicum. Natural Resources Institute. University of Manitoba. Winnipeg, Manitoba, Canada.
- Bull, E.L. and J.R. Duncan. 1993. Great Gray Owl (*Strix nebulosa*). In A. Poole and F. Gill (Editors). *The Birds of North America*. The Academy of Natural Sciences, Philadelphia, The American Ornithologists' Union, Washington D.C. No. 41.
- 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**:1050-1053.
- Cannings, R.J. 1987. The breeding biology of Northern Saw-whet Owls in southern British Columbia. In. Nero, R.W., R.J. Clark, R.J. Knapton and R.H. Hamre (Editors). *Biology and conservation of northern forest owls*. Symposium proceedings. Feb 3-7, 1987. Winnipeg, Manitoba. Gen. Tech. Rep. RM-142. Fort Collins Co: USDA Forest Service Rocky Mountain Forest and Range Experiment Station. Pp. 193-198.
- Cannings, R.J. 1993. Northern Saw-whet Owl (*Aegolius acadicus*). In A. Poole and F. Gill (Editors). *The Birds of North America*. The Academy of Natural Sciences, Philadelphia, The American Ornithologists' Union, Washington D.C. No.42
- Carter, J.D. 1925. Behavior of the Barred Owl. **42**: 443-444.
- Clark, K.A. and S.H. Anderson. 1995. Temporal, climatic and lunar factors affecting owl vocalizations in Wyoming. *J. Raptor Res.* **31**:358-363.

- Clough, C.G. 1964. Local distribution of two voles: evidence for interspecific interaction. *Can. Field-Nat.* **78**: 80-89.
- Cody, M.L. 1985. An introduction to habitat selection in birds. *In* M.L. Cody (*Editor*). *Habitat selection in birds*. Academic Press. Orlando. Pp. 4-56.
- Collins, K.M. 1980. Aspects of the biology of the Great Gray Owl. M.S. thesis, University of Manitoba, Winnipeg.
- Cottam, C, C.S. Williams, and C.A. Sooter. 1942. Flying and running speeds of birds. *Wilson Bull.* **54**:121-131.
- Davidson, C.1998. Issues in measuring landscape fragmentation. *Wildl. Soc. Bull.* **26**: 32-37.
- Davy, H.S. 1995. Porcupine Mountain - Eastern region preliminary 1994 botanical survey. Ecologically Significant Areas Program. Parks and Natural Areas Branch, Manitoba Department of Natural Resources, Winnipeg.
- Duncan, J.R. 1992. Influence of prey abundance and snow cover on Great Gray Owl (*Strix nebulosa*) breeding dispersal. Ph.D. dissertation. University of Manitoba. Winnipeg, Manitoba, Canada.
- Duncan, J.R. 1994. Habitat suitability index model for the Great Gray Owl (*Strix nebulosa*). Manitoba Forestry/Wildlife Management Project. Winnipeg, Manitoba, Canada.
- Duncan, J.R. 1996a. Conservation status ranks of the birds of Manitoba. Manitoba Conservation Data Centre MS Report Number 96-05, Winnipeg, Manitoba.

- Duncan, J.R. 1996b. An initial validation of a Barred Owl (*Strix varia*) habitat suitability index model for Manitoba. Manitoba Forestry/Wildlife Management Project. Winnipeg, Manitoba, Canada.
- Duncan, J.R. 1996c. Initial validation of a Great Gray Owl (*Strix nebulosa*) habitat suitability index model for Manitoba. Manitoba Forestry/Wildlife Management Project. Winnipeg, Manitoba, Canada.
- Duncan, J.R. 1997. Great Gray Owl (*Strix nebulosa*) and forest management in North America: A review and recommendations. *J. Raptor. Res.* **31**:160-166.
- Duncan, J.R. and P.A. Duncan. 1997. Increase in distribution records of owl species in Manitoba based on a volunteer nocturnal survey using Boreal Owl (*Aegolius funereus*) and Great Gray Owl (*Strix nebulosa*) playback. In J.R. Duncan, D.H. Johnson and T.H. Nicholls (*Editors*). *Biology and conservation of owls of the Northern Hemisphere. 2nd International Symposium Proceedings Feb 5-9, 1997.* Gen. Tech. Rep. NC-190. St Paul MN USDA Forest Service North Central Research Station. Pp. 519-524.
- Duncan, J.R. and A.E. Kearns. 1997. Habitat associated with Barred Owl (*Strix varia*) locations in southeastern Manitoba: A review of a habitat model. In J.R. Duncan, D.H. Johnson and T.H. Nicholls (*Editors.*) *Biology and conservation of owls of the Northern Hemisphere. 2nd International Symposium Proceedings Feb 5-9, 1997.* Gen. Tech. Rep. NC-190. St Paul MN USDA Forest Service North Central Research Station. Pp 138-145.
- Forbes, J.E. and D.W. Warner. 1974. Behavior of a radio-tagged Saw-whet Owl. *Auk* **91**: 783-795.

- Forsman, E., C. Meslow and H.M. Wight. 1984. Distribution and biology of the spotted owl in Oregon. *Wildl. Monogr.* **87**: 1-64.
- Forsman, E.D. and A.R. Giese. 1997. Nests of Northern Spotted Owls in the Olympic Peninsula, Washington. *Wilson Bull.* **109**:28-41.
- Fuller, M.R. and J.A. Mosher 1981. Methods of detecting and counting raptors, a review. Pp. 235-246 in Ralph, J.C. & J.M. Scott. (*Editors*) Estimating numbers of terrestrial birds. *Studies in Avian Biology* **6**: 235-46.
- Goldrup, C. 1992. An historic overview and analysis of consumptive uses of the resources in Duck Mountain Provincial Park. MNRM Practicum, University of Manitoba, Winnipeg.
- Gutierrez, R.J., J.E. Hunter, G. Chavez-Leon and J. Price. 1998. Characteristics of Spotted Owl habitat in landscapes disturbed by timber harvest in northeastern California. *J. Raptor Res.* **32**: 104-110.
- Hakkarainen, H and E. Korpimäki. 1996. Competition and predatory interactions among raptors: an observational and experimental study. *Ecology* **77**: 1134-1142.
- Hakkarainen, H., E. Korpimäki, V. Koivunen, and S. Kurki. 1997. Boreal Owl responses to forest management: a review. *J. Raptor. Res.* **31**:125-128.
- Haney, J.C. 1997. Spatial incidence of Barred Owls (*Strix varia*) reproduction in old growth forest of the Appalachian Plateau. *J. Raptor Res.* **31**:241-252.
- Hayward, G.D. 1991. Using population biology to define old-growth forests. *Wildl. Soc. Bull.* **19**:111-116.
- Hayward, G.D. 1997. Forest management and conservation of Boreal Owls in North America. *J. Raptor Res.* **31**:114-124.

- Hayward, G.D. and E.O. Garton. 1988. Resource partitioning among forest owls in the River of No Return Wilderness, Idaho. *Oecologia* **75**: 253-65.
- Hayward, G.D., P.H. Hayward, and E.O. Garton. 1993. Ecology of Boreal Owls in the northern Rocky Mountains, USA. *Wildl. Monogr.* **124**: 1-59.
- Hayward, G.D and P.H. Hayward. 1993. Boreal Owl (*Aegolius funereus*). In A. Poole and F. Gill (*Editors*). *The Birds of North America*. The Academy of Natural Sciences, Philadelphia, The American Ornithologists' Union, Washington D.C. No.63.
- Herren, V., S.H. Anderson, and L.F. Ruggiero. 1996. Boreal Owl mating habitat in the northwestern United States. *J. Raptor Res.* **30**:123-129.
- Houston, C.S., 1996. Great Horned Owl nest sites in Saskatchewan. *Blue Jay* **54**: 125-133.
- Houston, C.S., D.G. Smith, and C. Rohner. 1998. Great Horned Owl (*Bubo virginianus*). In A. Poole and F. Gill (*Editors*). *The Birds of North America*. The Academy of Natural Sciences, Philadelphia, The American Ornithologists' Union, Washington D.C. No.372.
- Janes, S.W. 1985. Habitat selection in raptorial birds. In M.L. Cody (*Editor*). *Habitat selection in birds*. Academic Press. Orlando. Pp. 159-188.
- Johnsgard, P.A. 1988. *North American Owls, Biology and Natural History*. Smithsonian Institution Press, Washington D.C.
- Johnson, D.H. 1993. Spotted Owls, Great Horned Owls and forest fragmentation in the central Oregon Cascades. M.Sc. Thesis. Oregon State University.

- Johnson, R.R., B.T. Brown, L.T. Haight and J.M. Simpson. 1991. Playback recordings as a special avian censusing techniques. *Studies in Avian Biology* **6**: 68-75
- Kirk, D.A. & C. Hyslop. 1998. Population status and recent trends in Canadian raptors: a review. *Biol. Conserv.* **83**: 91-118.
- Korpimäki, E. 1988a. Effects of territory quality on occupancy breeding performance and breeding dispersal in Tengmalm's Owl. *J. Anim. Ecol.* **57**:97-108.
- Korpimäki, E. 1988b. Diet of breeding Tengmalm's Owls *Aegolius funereus*: long-term changes and year-to-year variation under cyclic food conditions. *Ornis. Fenn.* **65**: 21-30.
- 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**: 151-157.
- Lane, B. 1988. 1988 Boreal Owl survey in Cook County. *Loon.* **60**: 99-104.
- Lane, B. and S. McKeown, 1991. Physical interactions between a male Boreal Owl and male Northern Saw-whet Owl. *Loon* **63**: 74-75.
- Lane, W.H., D.E. Andersen, and T.H. Nicholls. 1997. Habitat use and movements of male Boreal Owls (*Aegolius funereus*) in northern Minnesota as determined by radio telemetry. In J.R. Duncan, D.H. Johnson and T.H. Nicholls (*Editors*). *Biology and conservation of owls of the Northern Hemisphere. 2nd International Symposium Proceedings Feb 5-9, 1997. Gen. Tech. Rep. NC-190. St Paul MN USDA Forest Service North Central Research Station. Pp. 248-249.*
- Lawrance, W.F. and E. Yensen. 1991. Predicting the impacts of edge effects in fragmented habitat. *Biological Conservation.* **55**: 77-92.

- Lee, P.C, S. Crites, and J.B. Stelfox. 1995. Changes in forest structure and floral composition in a chronosequence of aspen mixedwood stands in Alberta. *In* J.B. Stelfox (*Editor*). Relationships between stand age, stand structure and biodiversity in aspen mixedwood forests in Alberta. Alberta Environmental Centre (AECV95-R1). Vegreville, Alberta. Canadian Forest Service (Project Number 0001A). Edmonton, Alberta. Pp. 29-48.
- Lehmkuhl, J.F. and M.G. Raphael. 1993. Habitat pattern around Northern Spotted Owl locations on the Olympic Peninsula, Washington. *J. Wildl. Manage.* **57**: 302-315.
- Ligon, J.D. 1969. Some aspects of temperature relations in small owls. *Auk* **86**: 458-472.
- Manly, B., L. McDonald, and D. Thomas. 1993. Resource selection by animals: Statistical design and analysis for field studies. Chapman and Hall, New York.
- Marcot, B.G. 1995. Owls of old forests of the world. October 1995. Gen. Tech. Rep. PNW-GTR 353, USDA Forest Service. Pacific Northwest Research Station, Portland, Oregon.
- Mazur, K.M., P.C. James, M.J. Fitzsimmons, G. Langen, and R.H.M. Espie. 1997. Habitat associations of the Barred Owl in the boreal forest of Saskatchewan, Canada. *J. Raptor. Res.* **31**: 253-259.
- Mazur, K.M., S.D. Frith, and P.C. James. 1998. Barred Owl home range and habitat selection in the boreal forest of central Saskatchewan. *Auk* **115**:746-745.
- Mazur, K.M. and P.C. James. 2000. Barred Owl (*Strix varia*). *In* A. Poole and F. Gill (*Editors*). The Birds of North America. The Academy of Natural Sciences, Philadelphia, The American Ornithologists' Union, Washington D.C. No.508.

- McCallum, D.A. 1994. Methods and terminology used with studies of habitat associations. In G.D. Hayward and J. Verner, (*Technical Editors*). Flammulated, boreal and great gray owls in the United States: A technical conservation assessment. Gen. Tech. Rep. RM-253. Fort Collins, CO: US Department of Agriculture, Forest Service, Rocky Mountain Forest Range and Experiment Station. Pp. 5-8
- McCready S., C. Rewcastle, D. Guinan, and L. L'Arrivee. 1980. Duck Mountain Resource Inventory. Manitoba Parks Branch, Department of Natural Resources. Winnipeg.
- McGarigal, K. and J.D. Fraser. 1984. Barred Owl responses to recorded vocalizations. *Condor*. **87**:552-553.
- McInville, W.B., Jr. and L.B. Keith. 1974. Predator-prey relations and breeding biology of the Great Horned Owl and Red-tailed Hawk in central Alberta. *Can. Field-Nat.* **88**: 1-20.
- Meyer, J.S., L.L. Irwin, and M.S. Boyce. 1998. Influence of habitat abundance and fragmentation on Northern Spotted Owls in Western Oregon. *Wildl. Monogr.* **139**: 1-51.
- Millar, J.S., D.G.L. Innes, and V.A. Loewen. 1985. Habitat use by non-hibernating small mammals in the Kananaskis Valley, Alberta. *Can. Field-Nat.* **99**:196-204.
- Moen, C.A. and R.J. Gutierrez, 1997. California Spotted Owl habitat selection in the central Sierra Nevada. *J. Wildl. Manage.* **61**: 1281-1287.
- Morrell, T.E. and R.H. Yahner. 1994. Habitat characteristics of Great Horned Owls in southcentral Pennsylvania. *J. Raptor Res.* **28**: 164-171.

- Morse, D.H. 1980. *Behavioral Mechanisms in Ecology*. Harvard Univ. Press, Mass.
- Mosher, J.A., M.A. Fuller, and M. Kopeny. 1990. Surveying woodland raptors by broadcast of conspecific vocalizations. *J. Field. Ornithol.* **61**: 453-461.
- Mount, D, C.E. Smith, D.S. Neufeld, J. Lettvenuk, D. Hunt, W.P. Mercer and W. J. Henderson. 1996. *Repap Manitoba 1997-2009 Forest Management Plan*. Repap Manitoba Inc., The Pas, Manitoba. October 1996.
- Natural Resources Manitoba. 1996. *Forest inventory field instruction manual*. Forest Resources Management, Winnipeg, Manitoba.
- Nero, R.W. 1980. *The Great Gray Owl. Phantom of the Northern Forest*. Smithsonian Institution Press, Washington D.C.
- Neu, C.W., R.C. Byers, and J.M. Peek. 1974. A technique for analysis of utilization-availability data. *J. Wildl. Manage.* **38**:541-545.
- Newton, I. 1979. *Population ecology of raptors*. Buteo Books, Vermillion, SD.
- Niemi, G.J. and J.M. Hanowski. 1997. Raptor responses to forest management: A holarctic perspective. *J. Raptor Res.* **31**:93-94.
- Noss, R.F. and B. Csuti. 1997. *Habitat Fragmentation*. In Meffe, G.K. and C.R. Carroll. *Principles of Conservation Biology*. 2nd Edition. Sinauer Associates, Inc. Massachusetts. Pp.269-304.
- Palmer, D.A. 1987. Annual, seasonal and nightly variation in calling activity of Boreal and Northern Saw-whet Owls. In Nero, R.W., R.J. Clark, R.J. Knapton, and R.H. Hamre, (*Editors*). *Biology and conservation of northern forest owls*. Symposium proceedings. Feb 3-7, 1987. Winnipeg, Manitoba. Gen. Tech. Rep. RM-142. Fort

Collins Co: USDA Forest Service Rocky Mountain Forest and Range Experiment Station. Pp. 162-168.

Parks Canada. 1997. Riding Mountain National Park Ecosystem Conservation Plan.

Unpublished Report. Wasagaming, Manitoba.

Ritchie, J.C. 1976. The late-Quaternary vegetational history of the western interior of Canada. *Can. J. Bot.* **54**: 1793-1818.

Rohner, C. 1997. Non-territorial 'floaters' in Great Horned Owls: space use during a cyclic peak of snowshoe hares. *Anim. Behav.* **53**: 901-912.

Rohner, C. and C.J. Krebs. 1996. Owl predation on snowshoe hares: consequences of antipredator behaviour. *Oecologia* **108**: 303-310.

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* J.B. Stelfox (*Editor*). Relationships between stand age, stand structure and biodiversity in aspen mixedwood forests in Alberta. Alberta Environmental Center (AECV95-R1). Vegreville, Alberta. Canadian Forest Service (Project Number 0001A). Edmonton, Alberta. Pp. 159-189.

Schieck, J. and M. Nietfield. 1995. Bird species richness and abundance in relation to stand age and structure in aspen mixedwood forests in Alberta. *In* J.B. Stelfox (*Editor*). Relationships between stand age, stand structure and biodiversity in aspen mixedwood forests in Alberta. Alberta Environmental Centre (AECV95-R1). Vegreville, Alberta. Canadian Forest Service (Project Number 0001A). Edmonton, Alberta. Pp. 115-157.

- Schumaker, N. H. 1996. Using landscape indices to predict habitat connectivity. *Ecology* 77:1210-1225.
- Servos, M.C. 1986. Summer habitat use of Great Gray Owls (*Strix nebulosa*) in southeastern Manitoba. MNRM Practicum. Natural Resources Institute, University of Manitoba.
- Smith, D.G., A. Devine, and D. Devine. 1983. Observations of fishing by a Barred Owl. *J. Field. Ornithol.* 54: 88-89.
- Sonerud, G.A. 1986. Effect of snow cover on seasonal changes in diet, habitat and regional distribution of raptors that prey on small mammals in boreal zones of Fennoscandia. *Holarctic Ecology* 9: 33-47.
- 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. (*Editor*). 1995. Relationships between stand age, stand structure and biodiversity in aspen mixedwood forests in Alberta. Alberta Environmental Centre (AECV95-R1). Vegreville, Alberta. Canadian Forest Service (Project Number 0001A). Edmonton, Alberta.
- Stepniski, D.P. 1997. Landscape features and characteristics of Great Gray Owl (*Strix nebulosa*) nests in fragmented landscapes of central Alberta. *In* J.R. Duncan, D.H. Johnson, and T.H. Nicholls, (*Editors*). *Biology and conservation of owls of the Northern Hemisphere. 2nd International Symposium Proceedings Feb 5-9, 1997.* Gen. Tech. Rep. NC-190. St Paul MN USDA Forest Service North Central Research Station. Pp. 601-607.

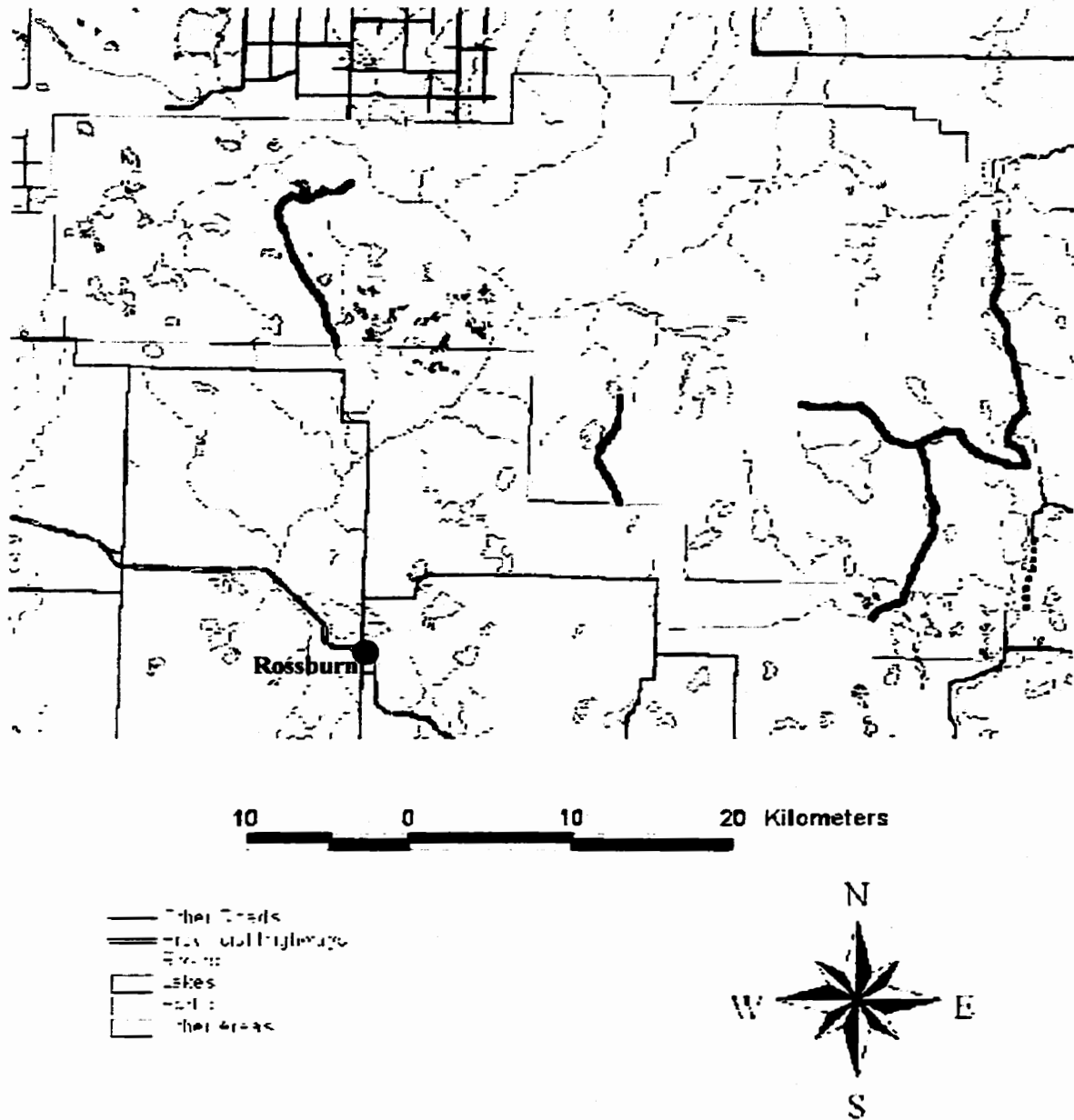
- Sulkava, S. and K. Huhtala. 1997. The Great Gray Owl (*Strix nebulosa*) in the changing forest environment of northern Europe. *J. Raptor Res.* **31**: 151-159.
- Takats, D.L. 1997. Barred Owl habitat use and distribution in the Foothills Model Forest. FMF Final Report. Department of Renewable Resources. University of Alberta, Edmonton.
- Takats, D.L. and G.L. Holroyd. 1997. Owl broadcast surveys in the Foothills Model Forest. In J.R. Duncan, D.H. Johnson, and T.H. Nicholls, (*Editors*). Biology and conservation of owls of the Northern Hemisphere. 2nd International Symposium Proceedings Feb 5-9, 1997. Gen. Tech. Rep. NC-190. St Paul MN USDA Forest Service North Central Research Station. Pp. 421-431.
- Walley, W.J. and C.F. Clyde. 1996. Occurrence and breeding of the Eastern Screech-owl north of the Riding Mountains, Manitoba. *Blue Jay* **54**: 89-100.
- Warnock, R.G. and P.C. James. 1997. Habitat fragmentation and Burrowing Owls (*Speotyto cunicularia*) in Saskatchewan. In J.R. Duncan, D.H. Johnson, and T.H. Nicholls (*Editors*). Biology and conservation of owls of the Northern Hemisphere. 2nd International Symposium Proceedings Feb 5-9, 1997. Gen. Tech. Rep. NC-190. St Paul MN USDA Forest Service North Central Research Station. Pp. 477-486.
- Whitfield, M.B. and M. Gaffney. 1997. Great Gray Owl (*Strix nebulosa*) breeding habitat use within altered forest landscapes. In J.R. Duncan, D.H. Johnson and T.H. Nicholls, (*Editors*). Biology and conservation of owls of the Northern Hemisphere. 2nd International Symposium Proceedings Feb 5-9, 1997. Gen.

Tech. Rep. NC-190. St Paul MN USDA Forest Service North Central Research Station. Pp. 498-505.

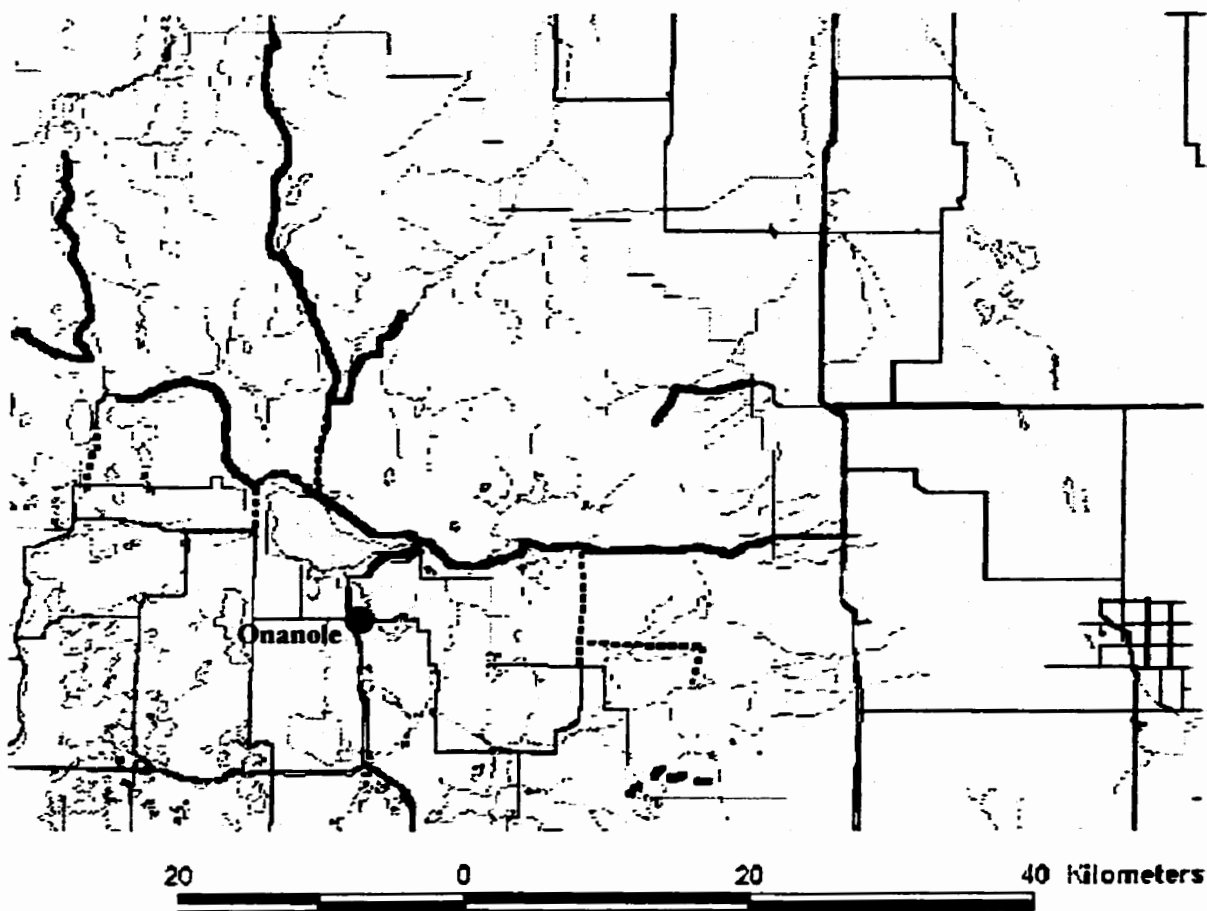
Voous, K.H. 1988. Owls of the northern hemisphere. The MIT Press, Cambridge, Massachusetts.

Zar, J.H. 1984. Biostatistical Analysis. 2nd edition. Prentice-Hall Canada Inc., Toronto.

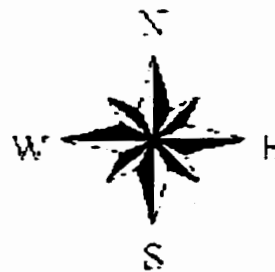
APPENDIX 1: Spatial Distribution of Survey Routes Within the Study Area



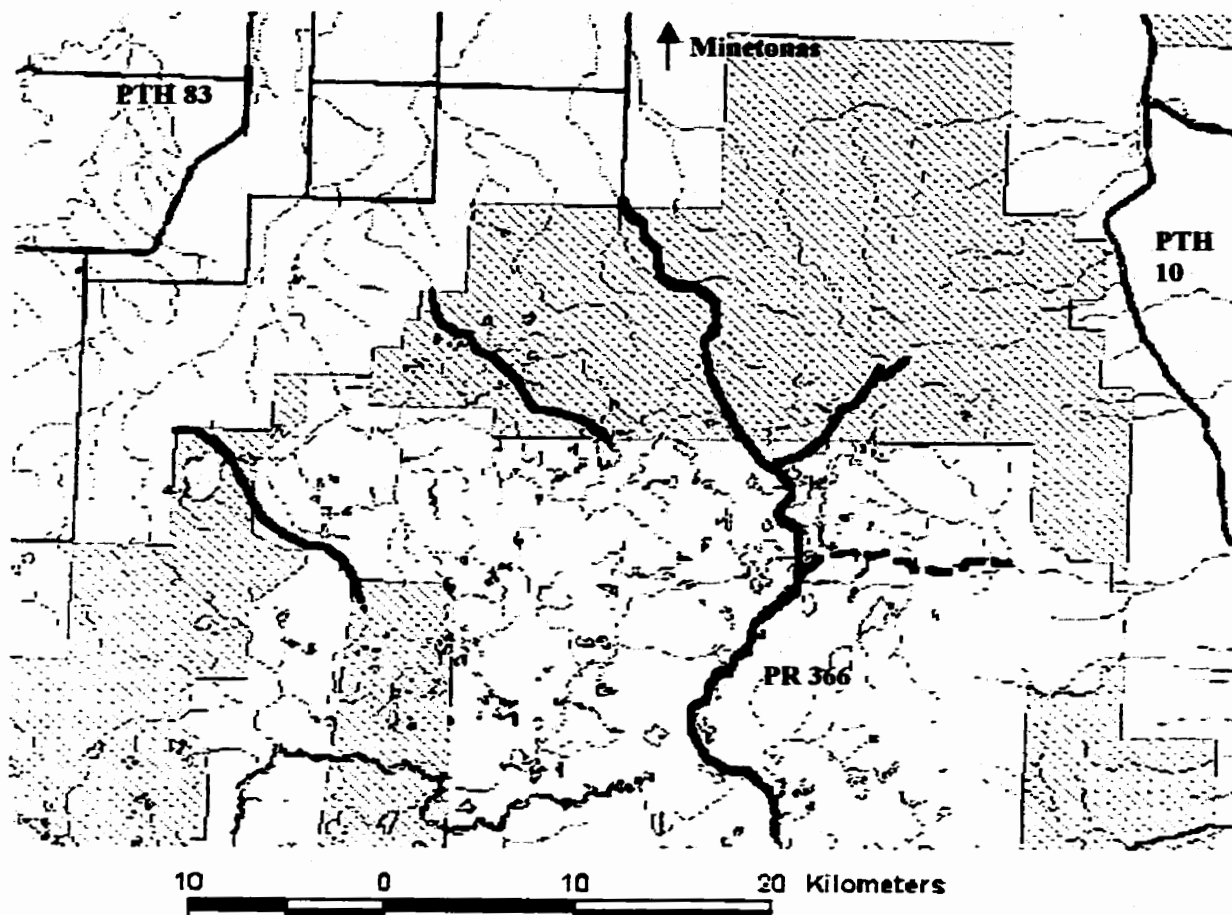
Riding Mountain National Park West: Bold solid lines represent routes surveyed in both 1999 and 2000. Bold dotted lines represent routes surveyed only in 1999.



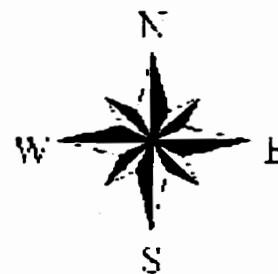
- Other Roads
- Provincial Highways
- Rivers
- ▭ Lakes
- ▭ Parks
- ▭ Other Areas



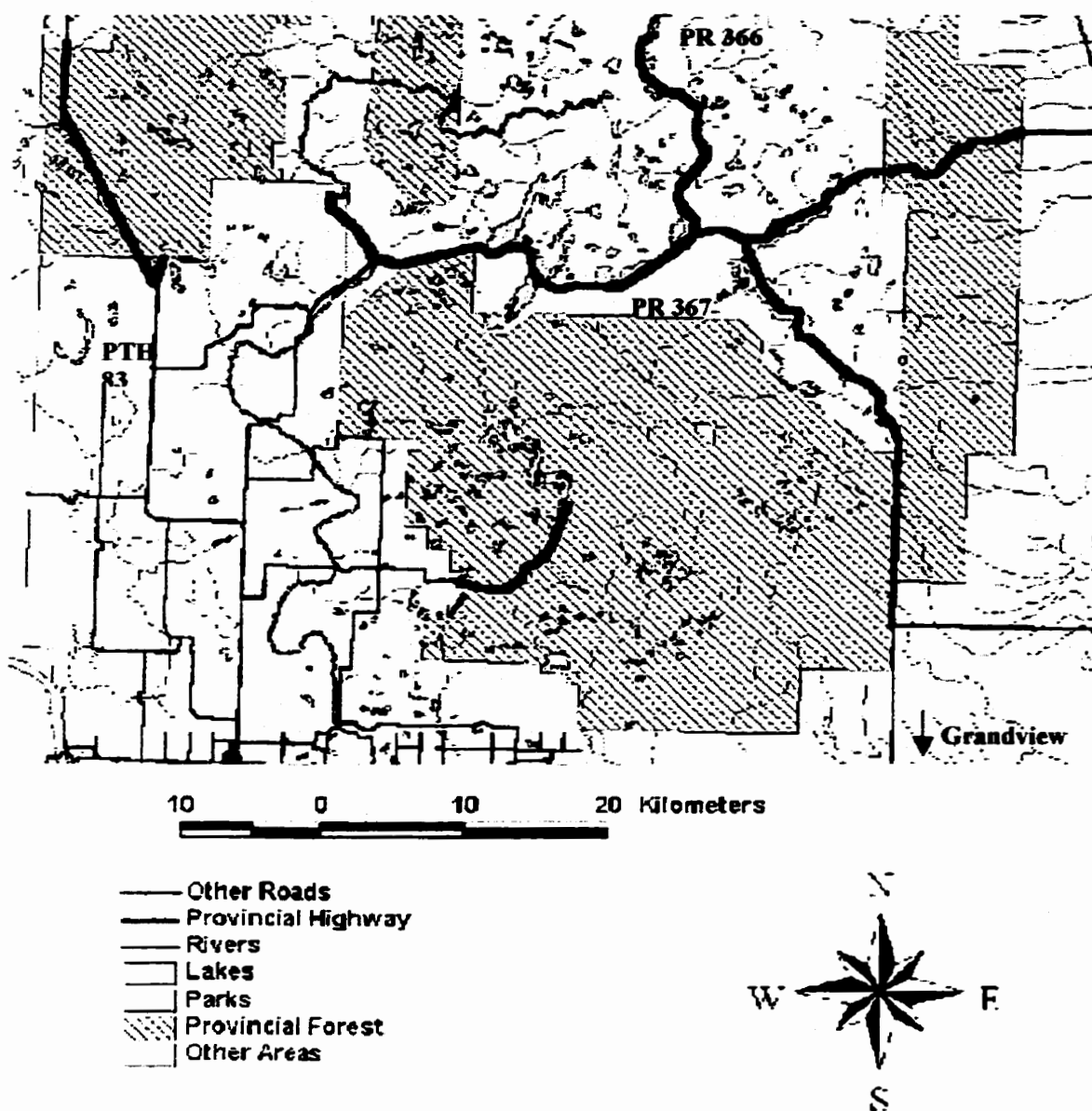
Riding Mountain National Park East: Bold solid lines represent routes surveyed in both 1999 and 2000. Bold dotted lines represent routes surveyed in 1999 only. Bold dashed lines represent routes surveyed in 2000 only.



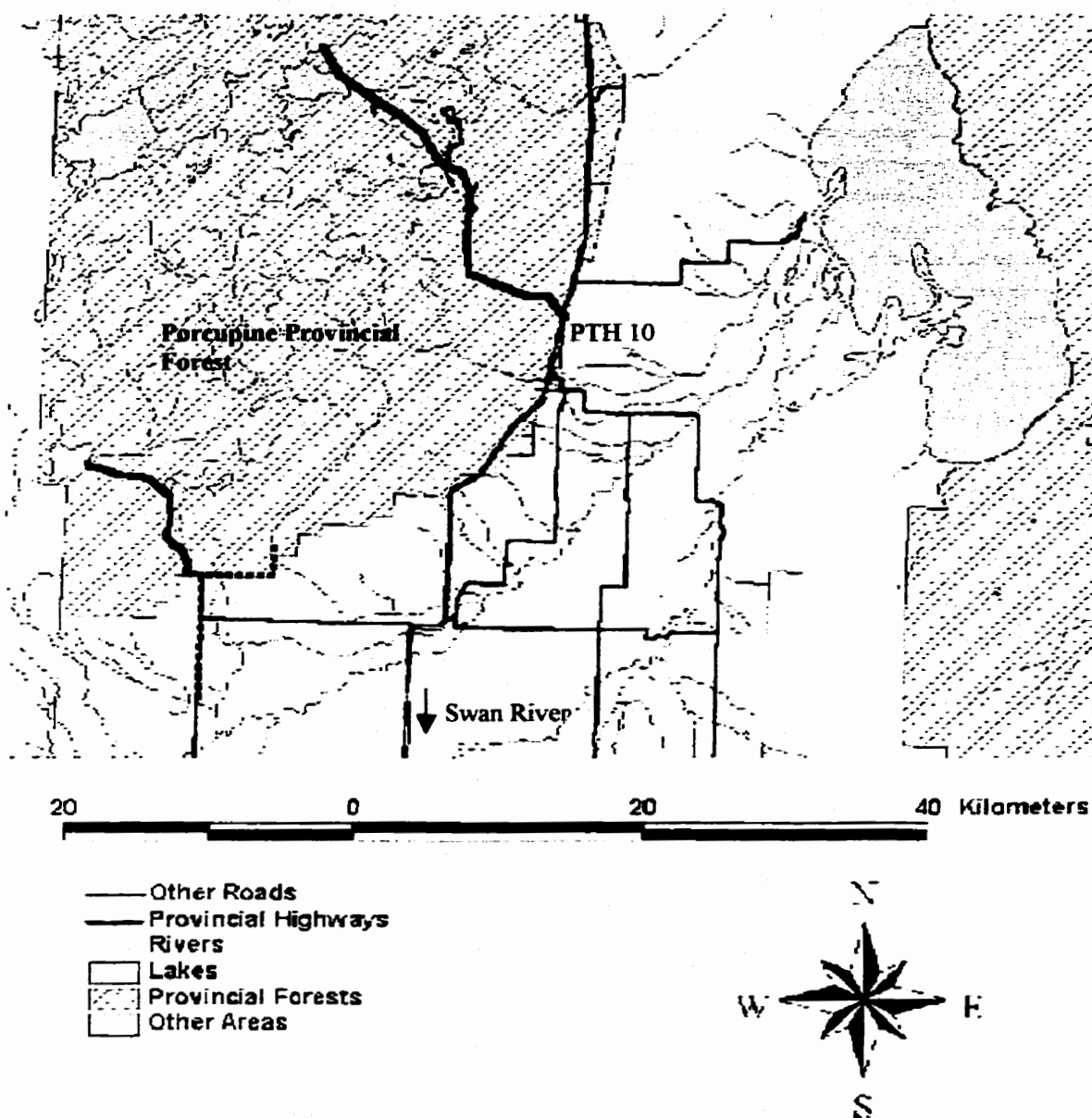
- Other Roads
- Provincial Highway
- - - Rivers
- ▭ Forest
- ▭ Park
- ▨ Provincial Forest
- ▭ Other Forest



Duck Mountain Provincial Park and Forest North: Bold solid lines represent routes surveyed in both 1999 and 2000. Bold dashed lines represent routes surveyed in 2000 only.



Duck Mountain Provincial Park and Forest South: Bold solid lines represent routes surveyed in both 1999 and 2000.



Porcupine Provincial Forest: Bold solid lines represent routes surveyed in both 1999 and 2000. Bold dotted lines represent routes surveyed in 1999 only.

APPENDIX 2. Cutting class category definitions (Natural Resources Manitoba 1996).

Class	Description
0	Forest land not restocked following fire, cutting, windfall or other major disturbances (hence potentially productive land). Some reproduction or scattered residual trees may be present.
1	Stands, which have an average height less than 3 meters. They may have been restocked either naturally or artificially and have scattered residual trees.
2	Advanced young growth of post size, with some merchantable volume. The average height of the stand must be over 3 meters.
3	Immature stands with merchantable volume growing at or near their maximum rate and should definitely not be cut. The average height of the stand should be over 10 meters and average diameter should be over 9.0cm at d.b.h.
4	Mature stands, which may be cut as they have reached rotation age.
5	Overmature stands, which should be given priority in cutting.

APPENDIX 3. Crown closure classes definitions (Natural Resources Manitoba 1996).

Class	Percentage canopy cover
0	0-20
2	21-50
3	51-70
4	71-100

APPENDIX 4. Number of individuals of each owl species detected in 1999 and 2000 through broadcast surveys in Riding Mountain National Park, Duck Mountain Provincial Park and Forest, and Porcupine Provincial Forest, as well as through incidental discoveries of nesting or calling birds within the study area.

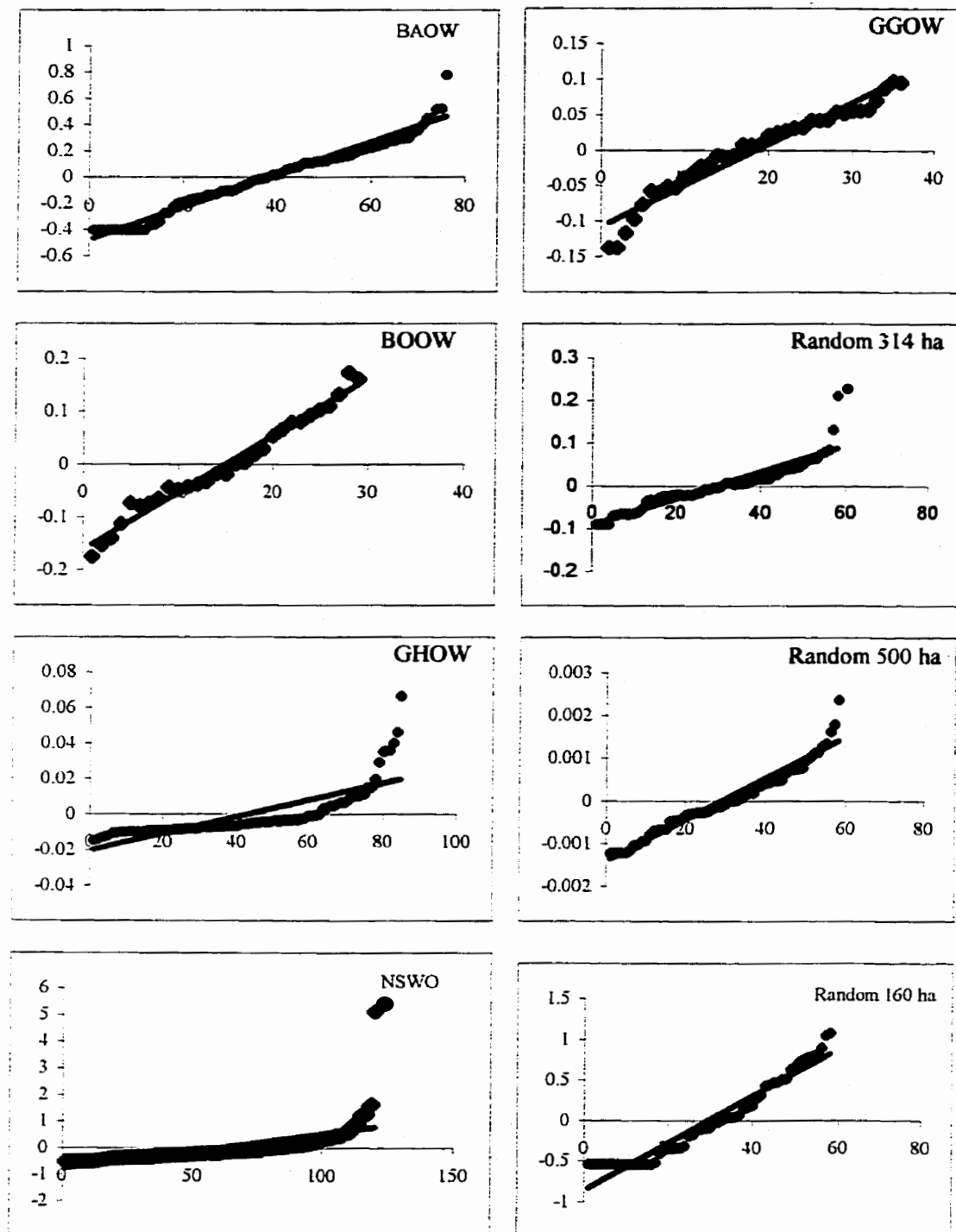
1999	Great Horned Owl	Great Gray Owl	Barred Owl	Long-eared Owl	Short-eared Owl	Boreal Owl	Northern Saw-whet Owl	Northern Hawk Owl	Total
RMNP	41	11	25	2	0	1	18	1	99
incidental	2	2	3	0	0	0	1	0	8
DMPP/ PPF	12	12	33	2	0	34	50	0	143
incidental	7	0	1	1	1	0	4	0	14
Total	62	25	62	5	1	35	73	1	264

2000	Great Horned Owl	Great Gray Owl	Barred Owl	Long-eared Owl	Short-eared Owl	Boreal Owl	Northern Saw-whet Owl	Northern Hawk Owl	Total
RMNP	48	6	24	2	0	0	67	0	147
incidental	3	2	5	1	0	0	0	0	11
DMPP/ PPF	17	6	17	1	0	17	23	0	81
incidental	5	1	0	0	1	0	0	0	7
Total	73	15	46	4	1	17	90	0	246

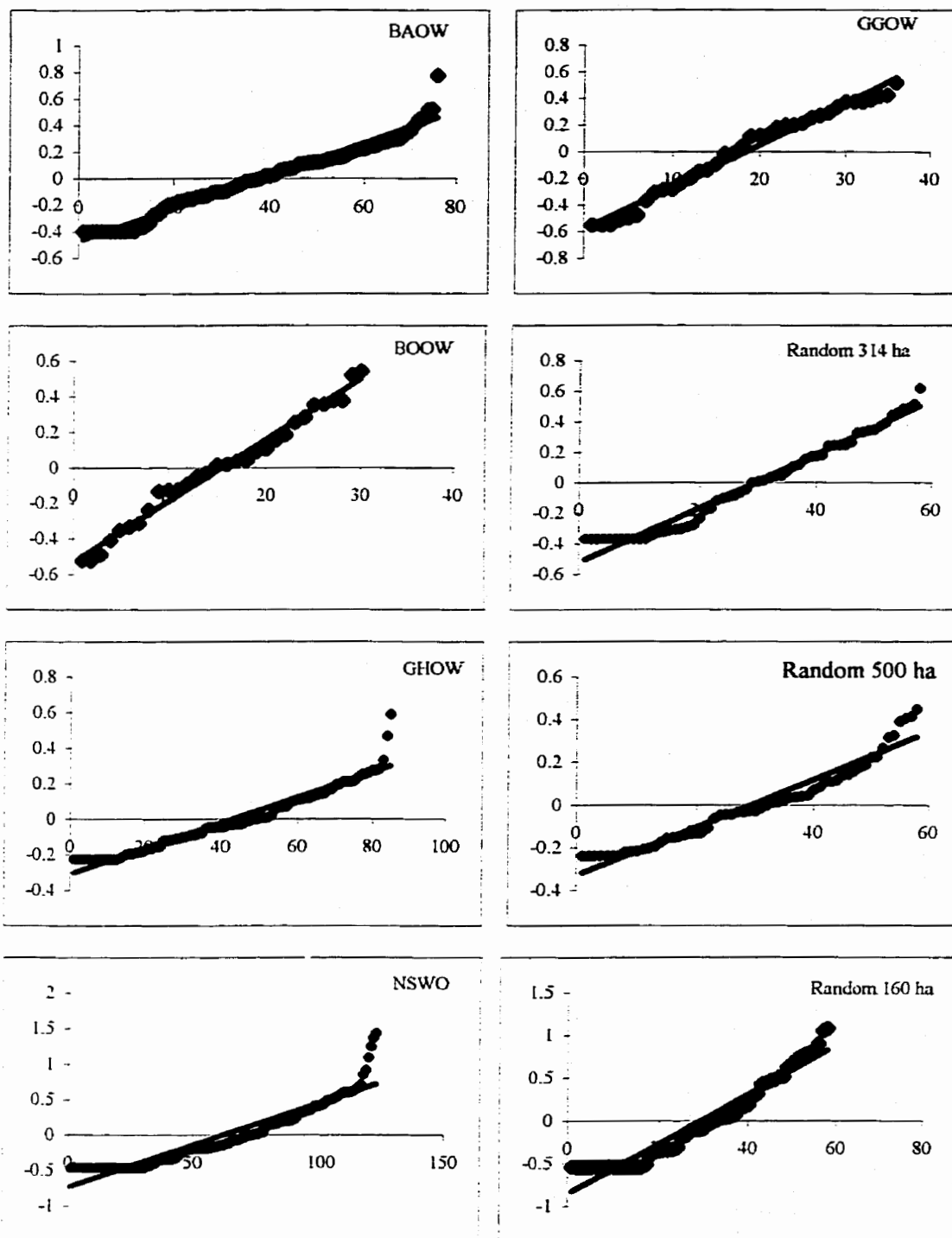
APPENDIX 5. Chi-square statistic for tests for differences in habitat variables between survey years.

Species	Stand Type			Cutting Class			Crown Closure		
	X ²	p-value	df	X ²	p-value	df	X ²	p-value	df
Barred Owl	12.46	0.03	5	0.90	0.97	3	1.93	0.59	2
Great Gray Owl	8.48	0.13	5	2.79	0.73	3	1.05	0.79	2
Great Horned Owl	14.91	0.04	7	7.15	0.21	3	19.87	0.00	3
Northern Saw-whet Owl	7.35	0.39	5	1.38	0.93	3	5.98	0.11	3
Boreal Owl	0.09	1.00	3	1.14	0.95	3	1.58	0.66	2

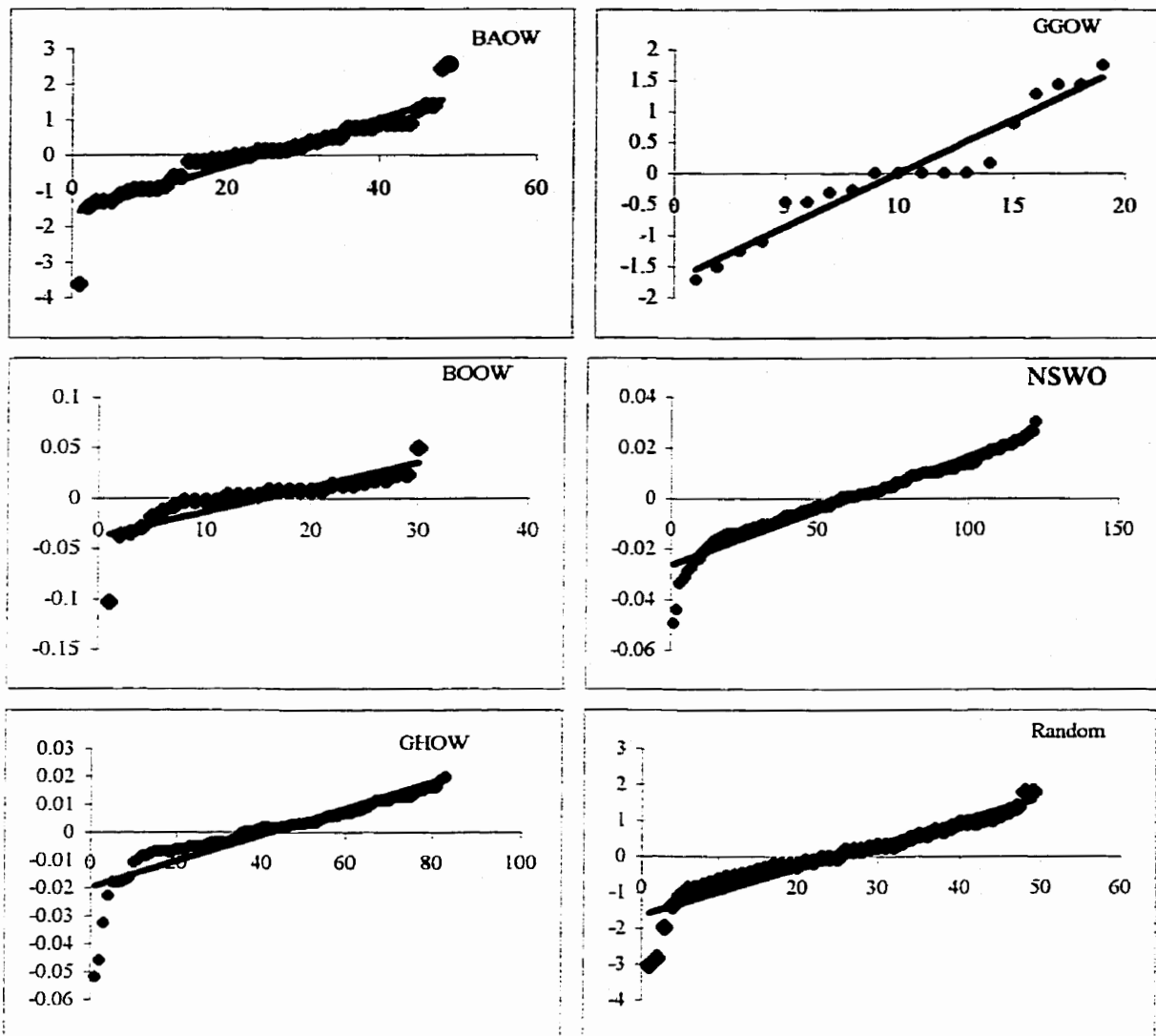
APPENDIX 6: Z-score charts for the variables edge-to-area ratio, water edge and elevation



Z-score charts for edge-to-area ratio values. Trend line represents a normal distribution.



Z-score charts for water edge. Trend line represents a normal distribution.



Z-score charts for elevation data. As elevation is not a function of plot size, only one set of random data was necessary. Trend line represents a normal distribution.