Influence of Prey Abundance and Snow Cover on Great Gray Owl Breeding Dispersal

by

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Doctor of Philosophy

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To Patsy,
Wise Owl!

Adult great gray owls exhibit a breeding dispersal pattern best described as a female-biased multi-annual calculated non-removal migration rather than nomadism. This pattern results from an interaction between two selective forces: the instability of *Microtus* biomass productivity in boreal regions and the advantages of breeding-site tenacity and fidelity. This interaction explains discrepancies in great gray owl breeding dispersal patterns described for populations elsewhere in its range.

Abstract

The influence of prey abundance and snow cover on the breeding dispersal of radio-marked adult great gray owls, *Strix nebulosa*, was investigated from 1984-90 in southeastern Manitoba and adjacent Minnesota. Of 2,004 prey items identified, 84% were meadow voles, *Microtus pennsylvanicus*. A great gray owl breeding density index fluctuated synchronously with multi-annual prey population changes.

During increase and peak vole population phases, adult owls remained on their breeding home ranges and did not disperse. Breeding dispersal was independent of snow cover and occurred following prey population crashes. There was no difference between male and female mean dispersal azimuths (14° versus 6°, $p=0.48$) and these were non-random ($p<0.01$) and significantly directed ($p<0.05$). Evidence of post-dispersal breeding-site fidelity was observed. On average, adult females dispersed farther (372 versus 235km, $p<0.05$) and earlier (October versus January/February, $p<0.05$) than adult males. A significant female-biased sex ratio was detected among winter-caught great gray owls (adults only, $p<0.05$).

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1. INTRODUCTION

Dispersal and migratory movements are recognized as important components of an organism's life history, especially with respect to population dynamics, social behaviour, and evolutionary processes (Lidicker and Caldwell 1982). Such movements represent a continuum, from the accidental and atypical dispersal of an individual of a sedentary species to annual round trip migrations of entire populations that span the earth's poles, with a range of intermediates in between. This variation is best thought of as a continuum of evolutionary solutions to different selective pressures. By virtue of their mobility, birds exhibit a rich and diverse variety of dispersal behaviour (Greenwood and Harvey 1982). Also, the study of bird dispersal strategies has received much attention owing to the relative ease with which birds can be observed. Comparisons of dispersal paradigms exhibited by avian species with varying degrees of shared life history traits illuminate selective pressures that have contributed to their evolution. In addition, within-species variation under different ecological conditions provides "natural experiments" (Diamond and Case 1986) from which limited conclusions can also be drawn.

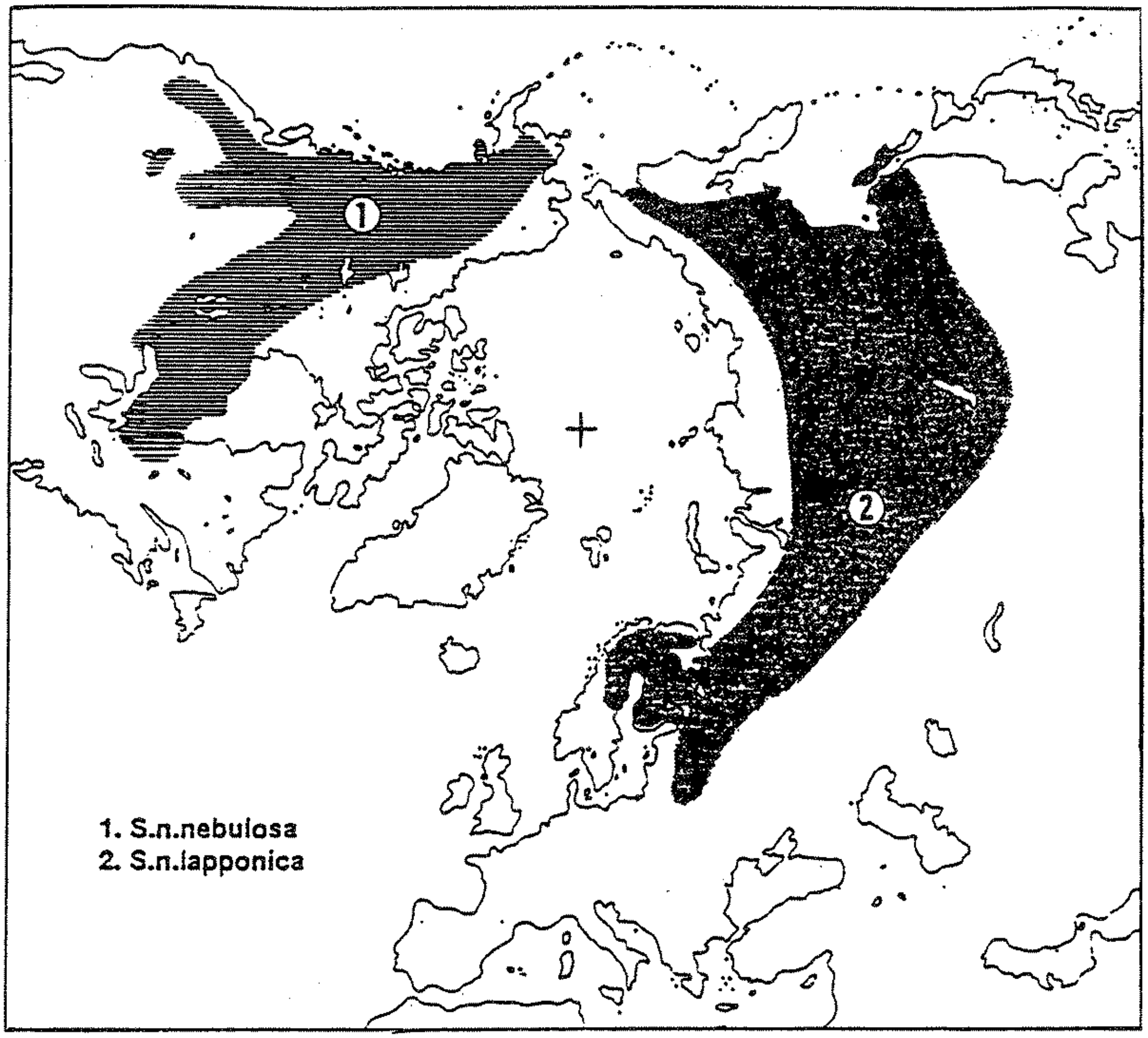
Natural selection has operated on northern forest owls to produce adaptations enabling their survival in boreal forest habitat. These include anatomical and behavioural adaptations resulting from interactions with prey populations over evolutionary time (Norberg 1987). Snow cover, which affects the mobility and foraging of organisms, is the most important selective force governing the historical and current distribution of vertebrates in northern latitudes (Formozov 1946). Formozov (1946:67) stated: "The glacial period was an epoch when the importance of the snow factor was singularly increased and when it played a decisive role in the ecology of the terrestrial biocenoses of many countries. During post-glacial time the importance of snowiness has become smaller, but it still remains quite influential and is deserving of detailed studies."

The thermal insulative value of snow cover is the reason why microtines flourish throughout the boreal forest region (Formozov 1946). Snow cover also decreases microtine availability to most predators (Hansson and Henttonen 1985). Small mustelids, however, are efficient subnivean microtine predators (King 1990). They possess characteristic adaptations perfected by the influence of snow cover as a selective force (Formozov 1946). Although snow does not hinder movements of avian microtine predators, most cannot capture microtines under thick snow (Sonerud 1986) and are forced to migrate annually to areas with less snow cover.

Throughout its circumpolar range (Fig. 1), the great gray owl (*Strix nebulosa*) specializes on microtines, especially *Microtus* species (Mikkola 1983, Johnsgard 1988, Voous 1988). Extreme ear asymmetry (Norberg 1987), relatively large size (Herrera and Hiraldo 1976), and especially snow-plunging behaviour (Godfrey 1967, Payne 1971, Salt and Salt 1976, Collins 1980, Nero 1980) enable the great gray owl to capture microtines under up to 45 cm of ice-crusted snow (Collins 1980, Nero 1980, Hildén and Helo 1981). The great gray owl's distribution lies almost completely in regions of severe and continuous winters with much snow. Thus, annual or multi-annual breeding dispersal patterns are likely exhibited by great gray owls only when their limits of tolerance for snow thickness are surpassed, or when prey populations decline.

Multi-annual microtine population fluctuations have been well documented (Delaney 1974, Krebs and Myers 1974, Golley et al. 1975, Finerty 1980, Lidicker 1988). Great gray owls are thought to disperse nomadically in search of food when faced with a declining prey base, rather than to switch to different prey species (Newton 1979, Nero 1980, Mikkola 1981). However, no study to date has monitored snow cover, prey use, prey abundance, and great gray owl breeding dispersal simultaneously over one or more vole cycles.

Figure 1. Distribution of the great gray owl (modified from Mikkola 1981).


①
②
1. S.n.nebulosa
2. S.n.lapponica

1.1 Definitions

The haphazard use of dispersal terminology has resulted in unnecessary confusion in the literature (Baker 1978, Belthoff and Ritchison 1989, Warkentin and James 1990). The original terminology of Greenwood (1980) will be used herein unless otherwise indicated. Two types of dispersal are generally recognized; natal dispersal and breeding dispersal. **Natal dispersal** involves "a permanent movement of juveniles from birth (or hatch) site to first breeding or potential breeding site,.." and **breeding dispersal** is "the movement of individuals, which have reproduced, between successive breeding sites" (Greenwood 1980:1141). If the dispersal is reproductively successful it is referred to as **effective.** If unsuccessful, or if the outcome is unknown, the dispersal is deemed **gross.** Dispersal does not imply a two-way movement by an individual or its progeny. Migration traditionally implies the return to the original breeding area (Lidicker et al. 1982, but see Baker 1978).

Andersson (1980:175) defined **nomadism** as "a tendency of adults as well as juveniles to move widely in search of food, and to settle and breed where it is locally abundant." This corresponds to Baker's (1978:25-26) **non-calculated removal migration.** Non-calculated denotes that, at the time of dispersal initiation, the animal has no information, either memorized or through social communication, about its destination. Removal defines a dispersal away from an area which is not followed by a return to that area. While published data suggest that numerous species may be nomadic, Andersson (1980:176) noted that "absolute proof of adults changing breeding areas over longer distances is difficult to obtain....further ringings of breeding adults are needed in species suspected of adult nomadism." While banding studies have provided valuable insight into the nature of avian movements and breeding ecology, results are limited and biased towards shorter distances, and in directions where recaptures or recoveries are more likely to occur (Greenwood and Harvey 1982). Although costly, marking and monitoring great gray owls with radio-transmitters largely eliminates these biases.

1.2 Hypotheses and Predictions

Lundberg (1979) noted that nest-site availability, food, clutch size, mate- and nest-territory fidelity, sexual size dimorphism and longevity all contribute to shaping the pattern of mobility and wintering strategies of northern owls. Of these, food abundance and nest-site availability are considered the most prominent (Lundberg 1979, Mikkola 1983). Lundberg (1979) and others have proposed hypotheses to explain observed owl dispersal phenomenon.

In light of these hypotheses great gray owls have been described as being nomadic (Newton 1979, Nero 1980, Mikkola 1981), nest-site tenacious (Stefansson 1985, Hilden and Solonen 1987), and annual migrants (Lundberg 1979). In addition, different sex- and age-biased dispersal regimes have been proposed. The results of this study are considered in light of three hypothesized factors believed to influence dispersal.

1.2.1 *Nest-site Availability*

Lundberg (1979) considered assured access to nest-sites the most fundamental factor governing dispersal by northern forest owls. He predicted:

> Both sexes (of food specialists) should disperse annually if nest-sites are abundant (stick nests) when prey availability decreases due to snow cover (Lundberg 1979).

1.2.2 *Prey Availability*

Andersson (1980) predicted that species dependent on cyclic food production should exhibit nomadic breeding dispersal. More specifically:

A. Breeding density will fluctuate in response to prey availability.

B. Individuals will remain site tenacious while prey availability is high and will disperse when it is low.

C. Individual breeding dispersal direction will be random or non-calculated.

D. Individuals will not likely return to former breeding sites.

1.2.3 *Age and Sex*

The costs and benefits of breeding dispersal are thought to vary according to the age and sex of an individual. Age- and sex-biased mobility predictions resulting from three "single-factor" hypotheses (Myers 1980, Ketterson and Nolan 1983, Byrkjedal and Langhelle 1986) are:

A. Juveniles and adult males should disperse earlier and travel farther than adult females. Dominance Hypothesis: Subdominant birds are the first to relocate when conditions get harder due to intraspecific and intersexual competition (Gauthreaux 1978, Ketterson 1979, Ketterson and Nolan 1979).

B. Males should disperse earlier than females. Body Size Hypothesis: Larger birds endure fasting better and have greater cold tolerance than smaller ones and therefore are able to winter under more rigorous conditions (Ketterson and Nolan 1979).

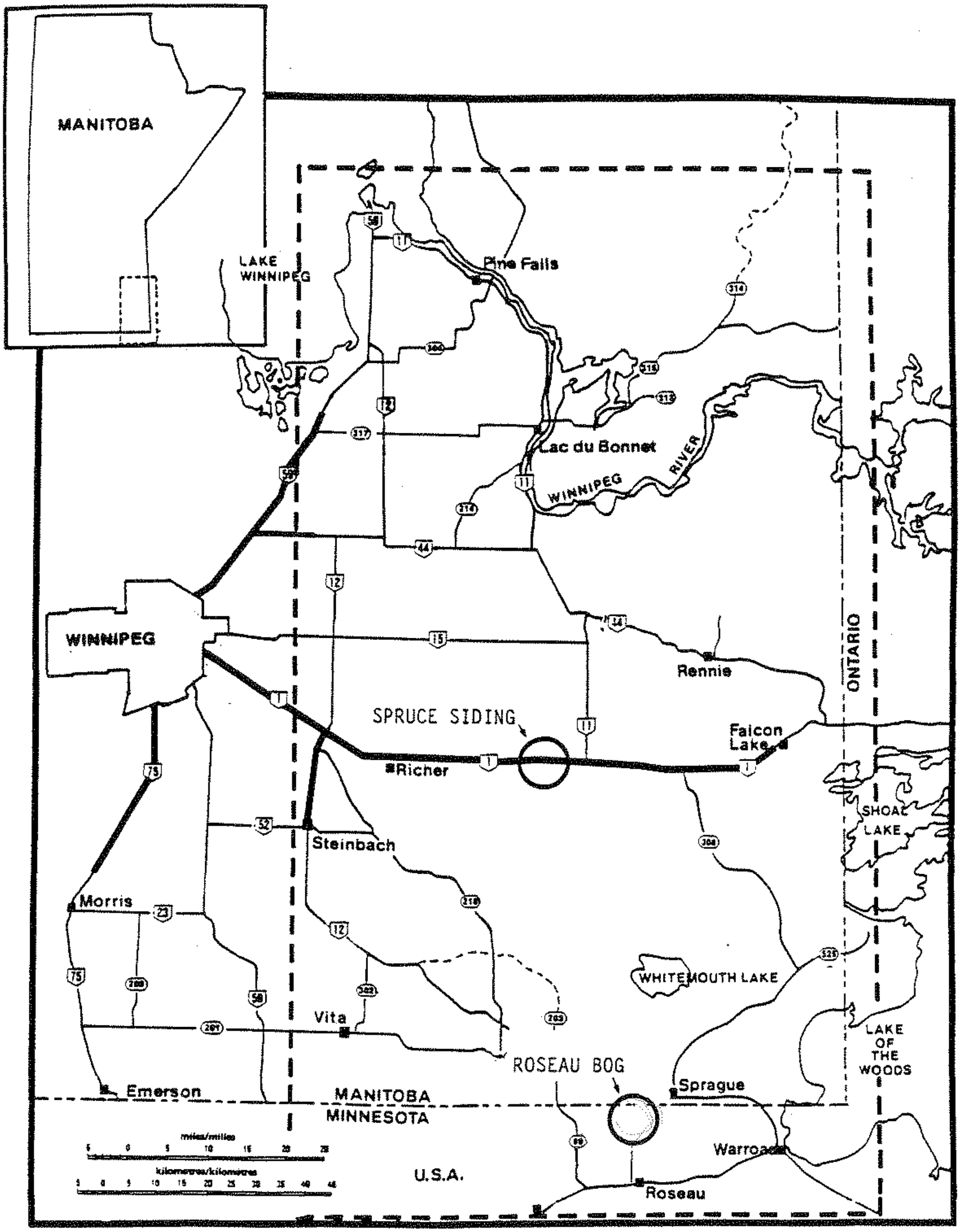
C. Females and juvenile males should disperse earlier and travel farther than adult males. Arrival-time Hypothesis: Males establish the breeding territory and should migrate the shortest distance in order to get early access to a territory in spring (Ketterson and Nolan 1979).

Because this study considers only breeding dispersal, hypotheses 1.2.3.A and 1.2.3.B are not mutually exclusive.

2. STUDY AREA

The study area (Fig. 2), covering 25,100 km^2, is ecologically diverse with a complicated geological history. Both ground moraine from Pleistocene glaciers and lacustrine deposits of Glacial Lake Agassiz have resulted in a variety of soil conditions and habitats (Teller 1984). Glacial Lake Agassiz is thought to have drained into Hudson Bay, following the retreat of the most recent ice sheet, about

Figure 2. The study area including two locations: Spruce Siding and Roseau Bog.


MANITOBA
LAKE WINNIPEG
Pine Falls
Lac du Bonnet
WINNIPEG RIVER
WINNIPEG
Rennie
ONTARIO
SPRUCE SIDING
Falcon Lake
Richer
Steinbach
SHOAL LAKE
Morris
WHITEMOUTH LAKE
Vita
LAKE OF THE WOODS
ROSEAU BOG
Sprague
Emerson
MANITOBA
MINNESOTA
Warroad
U.S.A.
Roseau
miles/milles
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23
201
203

7,500 years ago.

Typical of boreal forest regions, the study area is flat, poorly drained, with the predominant vegetation consisting of patches of black spruce (*Picea mariana*) and tamarack (*Larix laricina*) interspersed with swamps and meadows (Rowe 1972). Jack pine (*Pinus banksiana*) and trembling aspen (*Populus tremuloides*) occur in drier areas. Prior to 1958, fires burned large areas annually. Today, logging and smaller, less frequent fires perpetuate this vegetation type. Monospecific forestry plantations occur in some areas and a network of fireguard roads have rendered many areas accessible to human activity. Demands for pulpwood, firewood, fenceposts and peat for mulch and energy have increased dramatically in recent years (Nero et al. 1984). In spite of this, there remain large tracts of undisturbed habitat.

Climate is boreal continental. The mean values ± s.d. for climate data from seven Environment Canada climate stations (Appendix A) located throughout the study area (Environment Canada 1982) are:

- January and July temperatures, -19.4 ± 0.5^{0}C and 19.1 ± 0.4^{0}C, respectively.
- Snowfall, 128 ± 11.1 cm/year, and rainfall, 41.1 ± 3.2 cm/year.
- Total annual precipitation, 54 ± 3.9 cm/year of which 24 ± 3.6% falls as snow.

2.1 Forest Classification

The Boreal and Great Lakes-St. Lawrence Forest Regions (Rowe 1972) are represented within the study area. These regions are further divided into sections based on the presence/absence of specific tree species.

The northeastern corner of the study area is representative of the Northern Coniferous Section of the Boreal Forest Region and is dominated by Precambrian outcrops with interspersed poorly drained areas and small lakes (Rowe 1972). Black spruce is the most common tree species in this section with jack pine, tamarack and some white birch (*Betula papyrifera*) present.

The Manitoban Lowlands Section (northwest and west in the study area) and the Lower English River Section (north-central part of the study area), also of the Boreal Forest Region, are of rather low relief owing to the post-glacial lake deposition of lacustrine sands and clays (Rowe 1972). Additional common tree species found here include white spruce (*Picea glauca*), trembling aspen, balsam poplar (*Populus balsamifera*) and balsam fir (*Abies balsamea*).

The east-central and southeastern portions of the study area are representative of the Quetico and Rainy River Sections of the Great Lakes-St. Lawrence Forest Region.

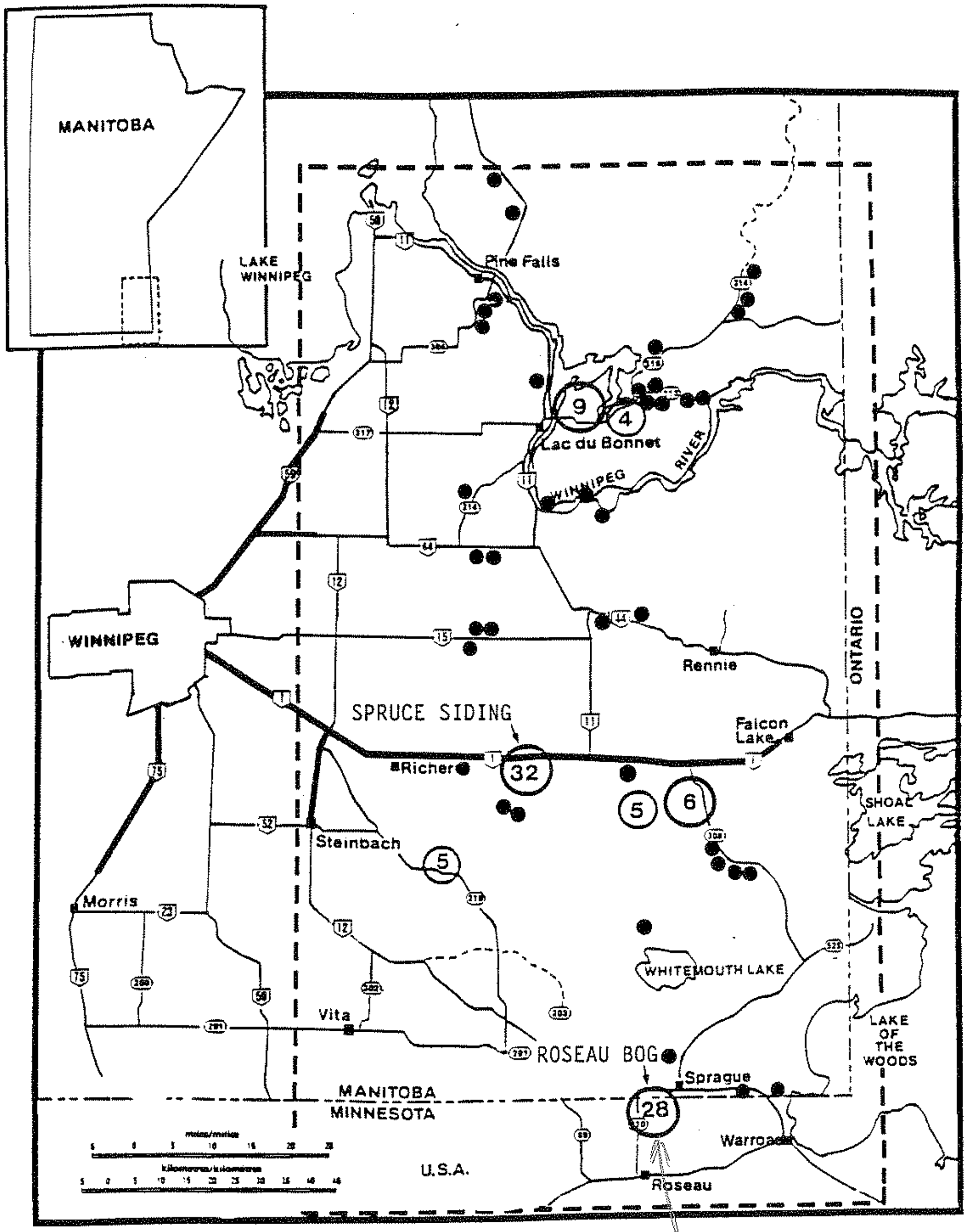
While boreal tree species predominate, eastern white pine (*Pinus strobus*)and eastern white cedar (*Thuja occidentalis*) are also diagnostic of these sections. Glacial lake beach deposits, mixed with patches of glacial till, form small discontinuous elevated patches amidst areas of low relief in these areas (Rowe 1972).

3. METHODS

3.1 Nest Surveys

Great gray owls rely on old hawk and raven stick nests, or natural depressions on broken-topped dead trees, for nest-sites (Nero 1980, Mikkola 1981). Hence, they readily accept man-made structures placed in trees in suitable habitats. The provision of man-made structures, coupled with the monitoring of known natural nest-sites, provides the most efficient means of determining the presence of nesting owls (Collins 1980, Nero 1980, Bohm 1985, Bull and Henjum 1990). Approximately 130 man-made and natural nest structures were checked for nesting owls two to three times each spring (April, May and June) from 1984 to 1991. These were distributed throughout the study area, with some clumping in areas under intensive study (Fig. 3). An index of nest use [(# occupied/# checked) X 100] eliminated bias due to small annual variation in the number of nest-sites checked.

Figure 3. Distribution of nest structures surveyed (1984-91). Dots represent single nest-sites. Circles represent an area containing the indicated number of nest-sites.


MANITOBA
LAKE WINNIPEG
Pine Falls
9
4
Lac du Bonnet
WINNIPEG RIVER
WINNIPEG
Rennie
ONTARIO
SPRUCE SIDING
Falcon Lake
Richer
32
5
6
SHOAL LAKE
Steinbach
5
Morris
WHITEMOUTH LAKE
Vita
ROSEAU BOG
Sprague
LAKE OF THE WOODS
MANITOBA
MINNESOTA
28
Warroad
U.S.A.
Roseau
miles/milles
kilometres/kilomètres

EO #1

3.2 Diet

Pellet analysis is a reliable technique for determining the diet of raptors, especially owls (Errington 1932, Glading et al. 1943, Marti 1987). Pellets were collected from in and around the nest-sites and, less frequently, from hunting radio-marked great gray owls in all seasons. Additional information was obtained from prey remains in and around nest-sites, observations of prey capture and from the stomach contents of road-killed owls. A fast pellet dissection technique using a NaOH solution (Marti 1987) resulted in severe tooth loss from microtine skulls and dentary bones. This made identification of prey species extremely difficult and time consuming. Therefore, the prey species and number of prey consumed was determined by careful dissection of pellets. Skeletal remains from pellets or stomach contents were identified using mammalian and avian specimen collections at the Zoology Department, University of Manitoba.

Prey diversity indices have been widely used as quantitative measures of food niche breadth (Pielou 1972, Hurtubia 1973) and to characterize and compare raptor diets (Herrera and Hiraldo 1976, Jaksic and Marti 1981, Jaksic et al. 1982, Jaksic and Marti 1984). The selection of one of the many measures of diet overlap is a subjective decision. Marti (1987) reviewed the shortcomings and advantages of various indices. Krebs (1989) reviewed studies where indices were applied to artificial populations with known overlaps to investigate biases and sensitivity to sample size, changing number of resources (i.e. prey species), and evenness of resource use. Morisita's measure (Krebs 1989) was chosen as it was found to have nearly zero bias as the abovementioned conditions were experimentally manipulated. This measure varies from 0 (no similarity) to 1 (complete similarity).

Other diet indices were calculated to compare study locations within the present study, and to compare this study with results from others. Pianka's Index measures the percentage of diet overlap and is a modification of the MacArthur-Levins measure (Krebs 1989). Percent similarity (Krebs 1989) is considered the simplest index to interpret because it measures the actual area of overlap. It is also analytically robust to grouping together prey types if the sample size is large. Formulae used to calculate indices are found in Krebs (1989).

Samples of pooled diet data were quantified as percent number and percent biomass of each prey species, or higher taxonomic grouping when appropriate. For each species, mean prey mass was estimated as the average weight of at least 10 locally-collected specimens when possible. Otherwise, Burt and Grossenheider (1976) was used for mammals and Dunning (1984) for birds. Percent biomass is a better indicator of a prey species' relative importance to the predator whereas percent number provides a better indication of the impact a predator may have on prey species. However, percent biomass and percent number were 92.5 percent similar (Percent Similarity Measure, Krebs 1989). Therefore, given the error likely associated with prey biomass estimations, prey similarity indices (see above) were calculated with either actual prey numbers or percent number.

Because the frequency of estimated great gray owl prey weights in the sample was negatively skewed (Rankit Plot) and was non-normal (Wilk-Shapiro statistic = 0.2235, Shapiro and Francia 1972), and because the arithmetic mean prey weight is sensitive to infrequent large or small prey weights, the geometric mean prey weight was calculated (Sokal and Rohlf 1981). However, because other studies often reported only arithmetic mean prey weight, this value was also calculated for comparative purposes.

3.3 Prey Abundance

In order to detect spatial-temporal patterns of microtine population abundance fluctuations, microtine density must be sampled at regular intervals and concurrently at a number of locations over at least one multi-annual cycle. Although microtine abundance cannot be measured reliably (Pearson 1985 *in* Anderson 1987), a reasonably accurate method exists (Mihok et al. 1985). Typically, the number of voles captured per standard number of trap-nights serves as a numerical index of population density. Year-to-year comparisons of density indices within sample sites have revealed four demographic phases of multi-annual cycles: increase, peak, decrease and trough. Saitoh (1987) offered the following unbiased classification scheme for these phases:

> *Increase phase*: a year in which the numerical index was higher than in the previous year and lower than the following year.
>
> *Peak phase*: a year in which the index was higher than those in the previous and the following year.
>
> *Decline phase*: a year in which the index was lower than that in the previous year and was higher than that in the following year.
>
> *Trough phase*: a year in which the index was lower than those in the previous and the following years.

If an index for a given year is the same as that in the previous or the following year, the index is compared with that in an earlier or later year.

Prey abundance was monitored at two locations, Spruce Siding (SS) and Roseau Bog (RB), 90 km apart (Fig. 2). A standardized small mammal snap-trap census (Schwartz 1985) was conducted biannually, in mid-May and mid-October, from 1986 to 1991. Mihok et al. (1985) determined that this method accurately estimated small mammal abundance for nine of the 10 years of his study. The census at each location consisted of six lines, in three pairs, of 50 stations per line. Stations were located at 10-m intervals along each line. A pair of census lines ran parallel and 50 m apart. One Museum Special snap-trap (Woodstream Corp., Lititz, Pennsylvania, USA) baited with peanut butter, rolled oats and bacon fat was set at each station for three nights. The lines were checked each morning, trapped mammals removed and traps reset or re-baited as required. In each location a pair of census lines sampled a tamarack stand, while the other two pairs sampled open areas with numerous hunting perches. Earlier studies revealed that these areas were used by hunting great gray owls (Servos 1986, J.R. Duncan unpubl. data). An index, I = (100 * # mammals caught)/(# traps * # nights), was used to estimate prey abundance for each area and for each year. Numerical index values were used for correlation analyses. Saitoh's (1987) phase states were used for qualitative association between breeding dispersal and prey population states.

Ivlev's selectivity index (Krebs 1989) was used to compare prey availability to prey use by great gray owls. This measure ranges from -1 to +1 and can only compare one species at a time. A value close to +1 indicates that a species is used in greater proportion than it is available and a value of 0 indicates that a species is consumed in proportion to its availability. An index close to -1 indicates that a species is eaten less frequently than it is available.

3.4 Snow Cover

Monthly snow thickness for the Roseau Bog and Spruce Siding study areas was estimated as the average of data from four Environment Canada weather stations (Winnipeg Climate Centre, Atmospheric Environment Service, 266 Graham Avenue, Winnipeg, Manitoba, R3C 3V4) near the study areas. Actual snow thickness at these two study areas was measured (J.R. Duncan, unpubl. data) in January, February and March of 1987 and 1989. Measurements agreed to within 12 cm of the estimated values (mean difference=5.15 cm, s.d.=4.6, n=60). Therefore, estimated snow thickness data were considered adequate for subsequent analysis with respect to great gray owl breeding dispersal. The importance of snow surface crusts and hardness will be discussed below.

For each radio-marked adult great gray owl that dispersed, the snow thickness at the time of dispersal was recorded as the estimated monthly maximum for the relevant study area. This biased estimates towards thicker snow cover. In light of the results presented below, this is not a problem in this analysis. The difference between estimated snow thickness at dispersal and an 8-year averaged monthly maximum value was also tabulated. This was done for the study area from which an owl dispersed (defined below) as well as for the closest Environment Canada weather station to where the owl settled (see below).

3.5 Radio-telemetry

Owls were snared from perches near their nest-sites using a modified hand-held fibreglass telescoping fishing pole. Occasionally, mist nets were used with a captive, unreleasable great horned owl (*Bubo virginianus*) or northern raven (*Corvus corax*) as a "lure bird." In winter, owls were lured close enough for capture in a large, hand-held fish-landing net using either an artificial or live mouse (Nero 1980). Verbail, bal-chatri and Cooper traps were infrequently used to catch owls in all seasons (Bull 1987).

Radio-transmitters (Lotek Engineering Inc., 34 Berczy St., Aurora, Ontario L4G 4J9) measured 8 cm long by 1.5 cm in diameter and averaged 35 g, complete with harness. A 28-cm long whip antenna extended posteriorly from each unit. Each transmitter was powered by a 2000 mA, 3.9 V lithium battery; current drain ranged from 0.1 to 0.19 mA/h. Frequencies were separated by at least 15 kHz within the 164 mHz band. A modified "back-pack-type" harness, consisting of a plastic coated wire running through 6 mm (diameter) teflon tubing, was used to attach transmitters to owls. Properly fitted, the transmitter and harness lay adjacent to the owl's skin and was completely covered by its plumage. Only the antenna protruded out over the bird's tail.

From the ground, three compass bearings for an individual radio-marked owl enabled its location to be plotted on a map or air photo. Bearings were obtained with a three or four-element, directional hand-held yagi antenna connected to a radio-receiver via a RG-59/U coaxial cable. Radio-signals were detected from as far as 10 km with factors such as perch height, local topography, signal interference and seasonal changes of deciduous vegetation affecting detection range and accuracy (Cochran 1980). When radio-contact from the ground was lost, indicating an owl may have moved out of radio-reception range, it was relocated by aircraft. A four-element directional yagi antenna was mounted to each wing of a fixed wing monoplane. The antenna's elements were positioned vertically and the antennas pointed outward, perpendicular to the flight path. A right-left switch box connected both antennas to the receiver via RG-59/U coaxial cables. Search patterns were determined by the last known location of the missing owl, topography and aerial reception range (55 to 135 km at 2500 m above ground level). Areas in all directions from an owl's last known location were searched. When a signal was detected, the owl's location was determined to within 50 m by a number of low level (40 m above ground) passes. When weather or fuel constraints prohibited the above, the owl's approximate location and/or bearing was obtained to facilitate relocation, either by aircraft or from the ground at a later date (Mech 1983).

The locations of radio-marked birds were obtained at varying intervals until their transmitters expired, they died, or radio-contact was lost. When possible, owls were recaptured to remove or replace transmitters about to expire. Signal changes, such as decreased reception range, frequency drift, and best-signal orientation of the yagi antenna, indicated possible mortality. Prompt recovery of the transmitter and owl remains was required to determine the cause of death, but was not always possible. The cause of mortality was a subjective decision based on evidence such as tracks, feces, feathers, pellets and teeth marks. Owls with whom radio-contact was lost were searched for on all subsequent search flights until their transmitter's expected expiry date.

3.6 Breeding Dispersal

An owl's movements are herein defined as the Euclidean or linear distance between relocations, as determined by the radio-telemetry techniques described above. These distances represent minimal values as the owls may have meandered to varying degrees while en route between relocations.

Andersson (1980) defined breeding dispersal distances greater than 100 km as adult nomadism. However, Greenwood and Harvey (1982) suggested that the number of territories crossed has more biological relevance as an index of dispersal than distance alone. Great gray owls defend a relatively small mating and nesting territory (cf. Nice 1941) centered at the nest-site, but forage on neutral ground (Wahlstedt 1974, Nero 1980, Bull 1987, Duncan 1987). Therefore, home ranges of adjacent breeding pairs may overlap extensively. Great gray owl home range diameters were estimated at 3 km (J.R. Duncan, unpubl. data), which agrees with other published estimates (Nero 1980, Bull and Henjum 1990).

Breeding dispersal occurred when an owl left its breeding home range after nesting and travelled more than 30 km (Euclidean distance), or more than 10 breeding home range diameters, to its subsequent summer and/or breeding home range (Sonerud et al. 1988). Breeding dispersal direction was recorded as the azimuth, in degrees, between an owl's breeding home range to its subsequent summer and/or breeding home range. Similarly, breeding dispersal date was recorded as the midpoint date in the time interval, in days, when an owl was last relocated on its breeding home range to when it was next relocated at least 30 km en route to its subsequent summer and/or breeding home range. Breeding dispersal distance was the Euclidean distance between an owl's breeding home range to its subsequent summer and/or breeding home range (Gross breeding dispersal if nesting status was unknown versus Effective breeding dispersal if nesting, cf. Greenwood 1980). The occurrence of breeding dispersal was related to prey population phase states (see above) and to snow thickness. Circular statistical test procedures followed Batschelet (1981).

4. RESULTS

4.1 Nest Surveys

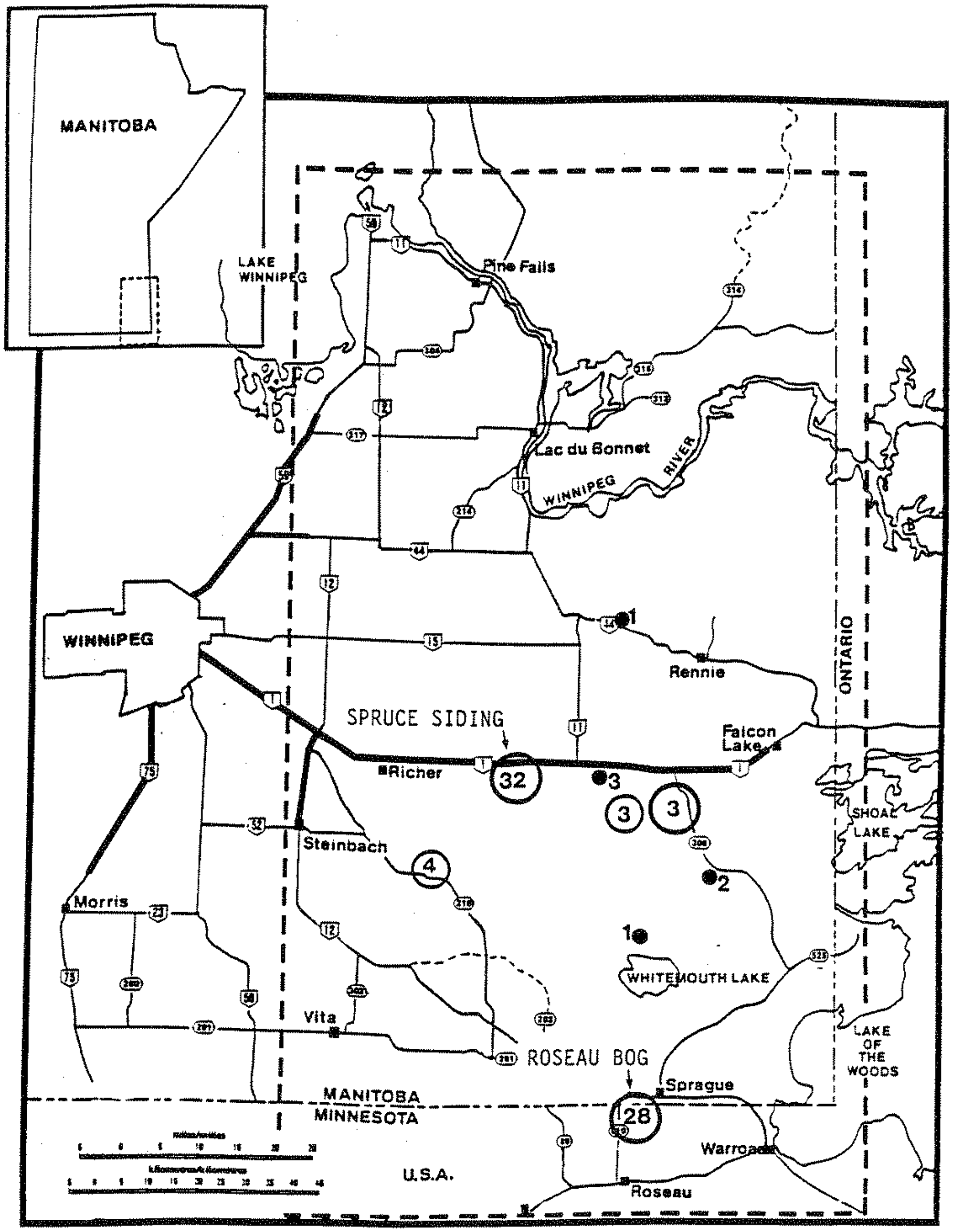
The number of occupied nests fluctuated greatly, ranging from 0 to 26, with peaks occurring in 1984 and 1987 (Table 1). In both these years the distribution of occupied nests was clumped in two areas, Roseau Bog and Spruce Siding, 90 km apart (Appendix B). Seventy-four percent of the total number of nesting great gray owl pairs occurred in these two areas containing only 32% of the total nest structures surveyed (Figs. 3, 4). Breeding densities as high as 1.6 nesting pairs/km^2 were recorded. While some isolated nest-sites were occupied, the distribution of breeding great gray owls in the nest-sites surveyed appeared non-random (Chi-square=112.5, d.f.=12, p<0.001, Appendix C).

TABLE 1. Annual fluctuations of nest structure use.

Year	# Occupied	# Checked	Index[1]
1984	19	122	15.57%
1985	0	148	0.00%
1986	4	135	2.96%
1987	26	137	18.98%
1988	13	140	9.29%
1989	1	142	0.70%
1990	4	145	2.76%
1991	10	137	7.30%
Total	77	1106	6.96%

1 Index = (# Occupied/# Checked) x 100

Figure 4. Distribution of occupied nest structures. Numbers equal the frequency with which great gray owls nested at single nest-sites (dots) and in areas containing more than one nest-site (circles) over an 8-year period (1984-91).


MANITOBA
LAKE WINNIPEG
Pine Falls
Lac du Bonnet
WINNIPEG RIVER
WINNIPEG
Rennie
ONTARIO
SPRUCE SIDING
Falcon Lake
Richer
32
3
3
3
1
2
1
4
Steinbach
SHOAL LAKE
Morris
WHITEMOUTH LAKE
Vita
LAKE OF THE WOODS
ROSEAU BOG
Sprague
MANITOBA
MINNESOTA
28
Warroad
U.S.A.
Roseau
59
11
12
317
214
44
15
1
75
52
216
23
201
302
203
308
313
315
314
89

4.2 Diet

Pairwise comparisons of the diet of three groups within the study area (Table 2) yielded high values for Pianka's index of percent diet overlap, Percent Similarity, and Morisita's Index (Krebs 1989, Appendices D, E). Therefore, the diets of the three groups were virtually identical and were pooled (Table 3) for comparison with great gray owl diets from Eurasia and other North American studies.

Percent Similarity Index values between winter and summer great gray owl diets ranged from 66% (Alaska, Appendix F) to 81% (this study, Appendix G), with data from Fennoscandia yielding an intermediate value of 75% (Appendix H). Morisita's Index values for the three winter-summer diet comparisons were 0.85, 0.98 and 0.98, respectively.

Meadow voles (*Microtus pennsylvanicus*) constituted 84% of 2004 prey items identified from pellets. Comparing prey use to the snap-trap survey results revealed that meadow voles were used in proportion greater than their availability (Table 4), while red-backed voles (*Clethrionomys gapperi*) and shrews (Soricidae) were underutilized (Table 4).

TABLE 2. Prey items identified from pellets from nest-sites at Roseau Bog (RB), Spruce Siding (SS) and other (O) locations in southeastern Manitoba and adjacent Minnesota (1986-90).

	RB	SS	O
Prey Species	% Number (n)	% Number (n)	% Number (n)
Mammalia	97.7 (721)	96.9 (682)	100 (565)
Condylura cristata			0.2 (1)
Microtus pennsylvanicus	84 (620)	79 (554)	88.5 (500)
Synaptomys borealis	6.6 (49)	10 (70)	6.4 (36)
Clethrionomys gapperi	3.5 (26)	3 (23)	2.1 (12)
Peromyscus maniculatus	0.3 (2)	0.3 (2)	
Phenacomys intermedius			0.2 (1)
Tamiasciurus hudsonicus	0.3 (2)	1.3 (9)	
Eutamias minimus		0.4 (3)	
Sorex cinereus	0.7 (5)	1.6 (11)	0.7 (4)
Blarina brevicauda	1 (7)	0.4 (3)	1.1 (6)
Sorex arcticus	0.8 (6)	0.3 (2)	0.2 (1)
Microsorex hoyi	0.1 (1)	0.1 (1)	0.4 (2)
Mustela rixosa	0.1 (1)	0.1 (1)	
Mustela erminea	0.3 (2)		
Lepus americanus (juveniles)		0.4 (3)	0.4 (2)
Aves	2.1 (16)	2.7 (19)	0 ()
Accipiter striatus		0.3 (2)	
Buteo platypterus	0.1 (1)	0.1 (1)	
Perisoreus canadensis	0.3 (2)	0.6 (4)	
Turdus migratorius	0.3 (2)		
Dendragapus canadensis	0.1 (1)		
Anas spp.	0.1 (1)		
Sparrow-sized birds	1.2 (9)	1.7 (12)	
Amphibia			
Rana sylvatica	0.1 (1)		
Total # Prey Items	738	701	565
# Nests	20	16	13
# Pellets	133	160	131
# Prey Species	18	16	10
# Prey/Pellet	5.5	4.4	4.3

TABLE 3. Percent number and percent biomass of prey items identified from pellets from nest-sites in southeastern Manitoba and adjacent Minnesota (1986-90).

Prey Species	n	% Number	% Biomass	Mean Wt.(g)[1]
Mammalia	1968	98.2	96.19	
Condylura cristata	1	0.04	0.06	56
Microtus pennsylvanicus	1674	83.53	85.12	45
Synaptomys borealis	155	7.73	4.20	24
Clethrionomys gapperi	61	3.04	1.79	26
Peromyscus maniculatus	4	0.19	0.11	24
Phenacomys intermedius	1	0.04	0.03	28
Tamiasciurus hudsonicus	11	0.54	2.67	215
Eutamias minimus	3	0.14	0.15	44
Sorex cinereus	20	0.99	0.09	4
Blarina brevicauda	16	0.79	0.40	22
Sorex arcticus	9	0.44	0.09	9
Microsorex hoyi	4	0.19	0.02	4
Mustela rixosa	2	0.09	0.11	49
Mustela erminea	2	0.09	0.22	97
Lepus americanus (juveniles)	5	0.24	1.13	200
Aves	35	1.74	3.79	
Accipiter striatus	2	0.09	0.31	139
Buteo platypterus	2	0.09	1.03	455
Perisoreus canadensis	6	0.29	0.50	73
Turdus migratorius	2	0.09	0.17	77
Dendragapus canadensis	1	0.04	0.54	474
Anas spp.	1	0.04	0.77	678
Sparrow-sized birds	21	1.04	0.47	20
Amphibia				
Rana sylvatica	1	0.04	0.01	8
Total # Prey Items	2004			
# Nests	49			
# Pellets	424			
# Prey Species	23			
# Prey/Pellet	4.72			

[1] Estimated as per methods.

TABLE 4. Ivlev's (1961) selectivity index[1] values for prey items. Data from nest-sites and snap-trap surveys at Roseau Bog (RB) and Spruce Siding (SS).

Study Area	Prey Group[2]	Proportion[3] Eaten	Proportion[3] Available	Ivlev's Index
RB	*Microtus*	0.906	0.14	0.732
	Clethrionomys	0.035	0.66	-0.899
	Shrews	0.017	0.18	-0.827
SS	*Microtus*	0.89	0.27	0.534
	Clethrionomys	0.03	0.54	-0.895
	Shrews	0.024	0.17	-0.753
All[4]	*Microtus*	0.913	0.18	0.671
	Clethrionomys	0.03	0.62	-0.908
	Shrews	0.024	0.17	-0.753

[1] Ivlev's Index = (Pe-Pa)/(Pe+Pa).

[2] *Microtus* includes *Microtus pennsylvanicus* and *Synaptomys borealis*, *Clethrionomys* is *C. gapperi*, Shrews includes *Sorex cinereus*, *Microsorex hoyi*, *Blarina brevicauda* and *Sorex arcticus*.

[3] Proportions do not add up to one because other preys items are not included in the analysis.

[4] Data from all nest sites combined.

4.3 Prey Abundance

The results of the snap-trap surveys are presented in Appendix I. Table 5 shows the small mammal data indices and the concurrent number of great gray owl breeding pairs at each study location, as well as combined data for the whole study area. No consistent relationships between mammal groups trapped were detected.

The number of breeding great gray owls correlated significantly with the number of *Microtus* (r_s=0.9 and 0.87, Spruce Siding and Roseau Bog, respectively, $p<0.05$, Table 5) but not with the total number of small mammals caught or with any other subgroup (Table 5). However, this relationship did not remain significant when the data were pooled (Table 5) because *Microtus* populations fluctuated asynchronously in the two study locations (Fig. 5).

4.4 Breeding Dispersal

Thirteen of 27 (48%) adult male and 23 of 39 (59%) adult female radio-marked great gray owls were tracked for at least one year following radio-tagging on breeding home ranges in southeastern Manitoba and adjacent Minnesota (Table 6). These proportions were not significantly different (Chi-Square=0.75, d.f.=1, p=0.39). When adult great gray owls abandoned their breeding home ranges

TABLE 5. Average[1] annual snap-trap results and great gray owl breeding fluctuations.

A. Spruce Siding

Year	MV[2]	RBV[2]	S[2]	Other[2]	Total	# Nests Occupied
1986	12.5	71	27.5	1	112	0
1987	17	48.5	1.5	4	71	5
1988	25	19.5	16.5	0	61	7
1989	13.5	6.5	5	0	25	1
1990	19	13	12.5	0	44.5	3
Spearman Rank Correlations with # Nests	0.9 $p<0.05$	-0.1 $p>0.1$	-0.3 $p>0.1$	-0.11 $p>0.1$	-0.1 $p>0.1$	

B. Roseau Bog

Year	MV	RBV	S	Other	Total	# Nests Occupied
1986	68.5	102	56.5	6	233	4
1987	23	41	6.5	6.5	77	15
1988	0.5	68.5	12	3.5	84.5	0
1989	6	80.5	11.5	5	103	0
1990	11.5	102.5	17.5	3	134.5	1
Spearman Rank Correlations with # Nests	0.87 $p<0.05$	-0.15 $p>0.1$	-0.05 $p>0.1$	0.67 $p>0.1$	-0.05 $p>0.1$	

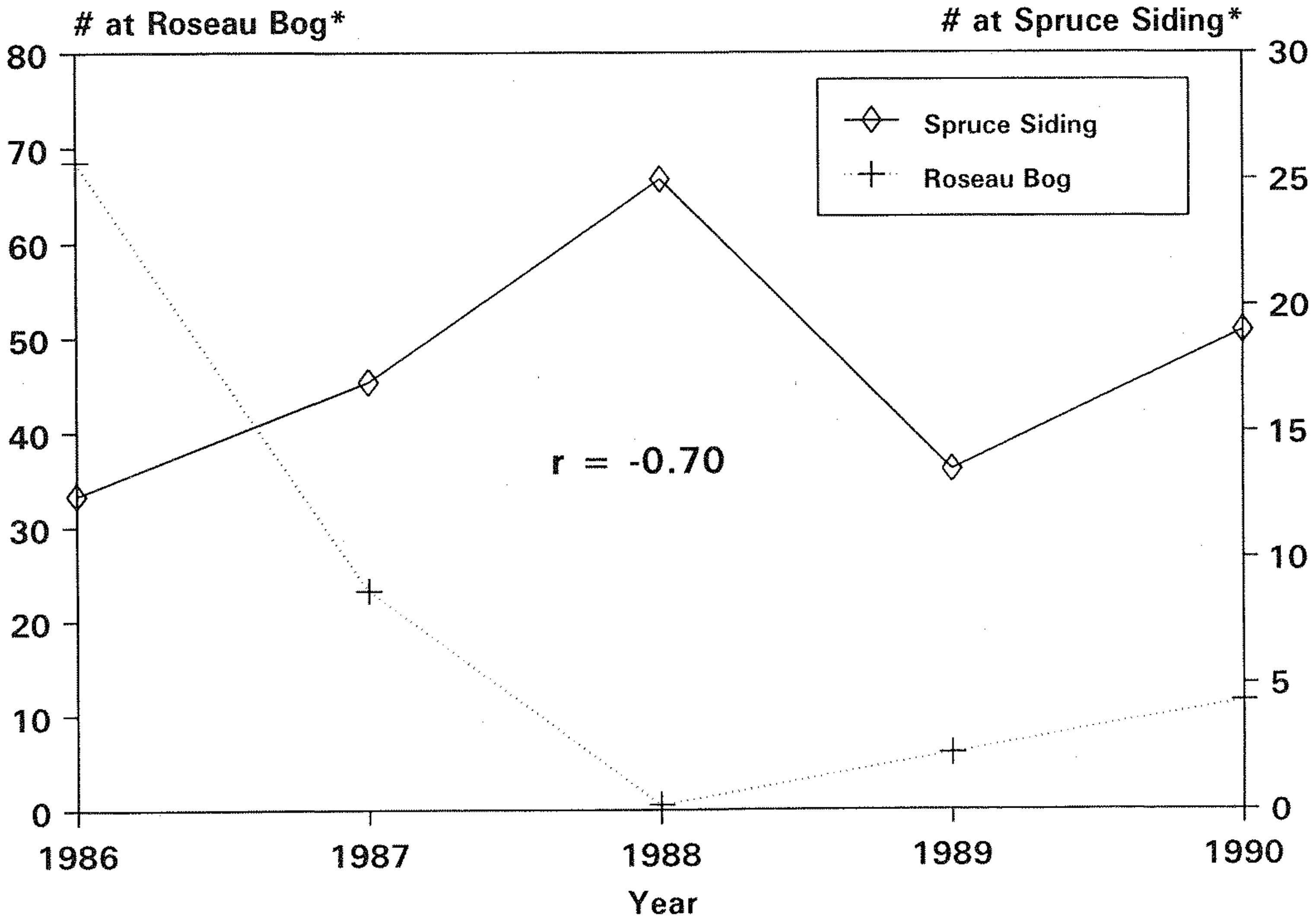
C. Combined Data from all Southeastern Manitoba

Year	MV	RBV	S	Other	Total	# Nests Occupied
1986	81	173	84	7	345	4
1987	40	89.5	7	10.5	147	26
1988	25.5	88	28.5	3.5	145.5	13
1989	19.5	87	16.5	5	128	1
1990	30.5	115.5	30	3	179	4
Spearman Rank Correlations with # Nests	0.41 $p>0.1$	0.15 $p>0.1$	-0.36 $p>0.1$	0.36 $p>0.1$	0.153 $p>0.1$	

1 Average result for year calculated from data in Appendix I as: (# caught in spring + # caught in fall)/2

2 MV = *Microtus pennsylvanicus* and *Synaptomys borealis*
RBV = *Clethrionomys gapperi*
S = *Sorex cinereus, S. hoyi, S. arcticus* and *Blarina brevicauda*
Other = *Peromyscus maniculatus* and *Napaeozapus insignis*

Figure 5. *Microtus* census data: Spruce Siding versus Roseau Bog. r = Spearman rank correlation coefficient.



* Averaged Data: Table 5

TABLE 6. Fate of radio-marked great gray owls (1984-90).

	Adults			
Fate[1]	Males	Females	Fledglings	Total
D/SHR	10	15	3	28
D/BHR		2		2
D/R	1			1
R/SHR	1			1
R/BHR	1	6		7
D/L		4	2	6
D/M	4		3	7
M/SHR	6	5	26	37
L/SHR	4	7	1	12
Total	27	39	35	101

[1] D/SHR = dispersed (D) to another summer home range (SHR): breeding status unknown.
D/BHR = dispersed to another breeding home range (BHR).
D/R = dispersed & returned to former BHR, but did not renest.
D/L = dispersed but lost (L) before establishing a SHR.
D/M = dispersed and found dead (M) prior to establishing a SHR
R/SHR = remained resident on previous BHR, but did not renest.
R/BHR = remained resident on previous BHR and renested.
M/SHR = found dead on SHR prior to next breeding season.
L/SHR = lost while on SHR prior to next breeding season.

following prey population declines, their dispersal was characterized in terms of distance and direction to their subsequent summer and/or breeding home range. Dispersal date was estimated as the midpoint in the interval, in days, when an owl was last relocated within 30 km of its breeding home range and subsequently relocated en route to its subsequent summer and/or breeding home range (Tables 7, 8).

4.4.1 *Distance*

This linear measure is summarized in Tables 7 and 8 and displayed in Figures 6 and 7. Adult females dispersed significantly farther than adult males ($p<0.05$, Mann-Whitney U Test). Female dispersal distances were non-normally distributed while those of males were ($p<0.05$ and $p>0.5$, $n=16$ and 11, Wilk-Shapiro statistic=0.88 and 0.97, respectively, Shapiro and Wilk 1965). This was due to a bimodal distribution of seven females dispersing from the Roseau Bog study area following prey population declines in 1987-88. Four of these females settled on summer home ranges within 35, 25, 21 and 14 km of an area known to be experiencing a prey population high with numerous breeding pairs present (Table 7). The other three females dispersed past this same area and continued hundreds of kilometres north. Excluding this group of "short" dispersing females from the sample, female distribution distances become normally distributed ($p>0.05$, $n=12$, Wilk-Shapiro

TABLE 7. Breeding dispersal data and concurrent prey population phase state for adult female great gray owls.

Year	ID	Area[1]	Fate[2]	A	B	C	D	E
1984	279	SS	D/SHR	360	2	11-Dec-84	21	Decrease
1984	103	SS	D/SHR	684	26	01-Nov-84	63	Decrease
1984	255	SS	D/SHR	521	41	17-Nov-84	28	Decrease
1984	643	SS	D/SHR	494	35	31-Oct-84	61	Decrease
1984	15	SS	D/SHR	416	356	15-Jan-85	53	Decrease
1986	557	RB	R/BHR	0				Peak
1987	602	RB	D/SHR	488	8	19-Nov-87	2	Decrease
1987	672	RB	D/SHR	544	4	18-Nov-87	0	Decrease
1987	759	RB	D/SHR	548	8	21-Jul-87	59	Decrease
1987	702	RB	D/BHR	58	21	23-Aug-87	11	Decrease
1987	640	RB	D/SHR	69	28	27-Oct-87	6	Decrease
1987	632	RB	D/SHR	67	6	05-Oct-87	29	Decrease
1987	712	RB	D/BHR	42	0	30-Jul-87	7	Decrease
1987	660	SS	D/SHR	352	13	19-Oct-87	13	Increase
1987	231	SS	R/BHR	0				Increase
1987	271	SS	R/BHR	0				Increase
1987	592	SS	R/BHR	0				Increase
1987	621	SS	R/BHR	0				Increase
1987	671	O	R/BHR	0				Increase
1987	612	O	D/SHR	405	347	29-Jul-87	42	Decrease
1988	480	SS	D/SHR	330	32	30-Oct-88	13	Decrease
1988	621	SS	D/SHR	448	10	25-Jul-88	0	Decrease
1988	702	O	D/SHR	472	343	13-Oct-88	3	Decrease

Adult Females that Dispersed but Died, or were Lost, Prior to Establishing a Subsequent Summer Home Range.

Year	ID	Area[1]	Fate[2]	A	B	C	D	E
1984	132	SS	D/L			01-Nov-84	63	Decrease
1987	532	O	D/L			29-Oct-87	2	Decrease
1988	271	SS	D/L			30-Sep-88	6	Decrease
1988	640	O	D/L			12-Oct-88	55	Decrease

1 Roseau Bog (RB), Spruce Siding (SS) and other (O) locations in southeastern Manitoba and adjacent Minnesota.

2 D/SHR = dispersed (D) to another summer home range (SHR):breeding status unknown.
D/BHR = dispersed to another breeding home range (BHR).
D/R = dispersed and returned to former BHR, but did not renest.
D/L = dispersed but lost (L) before establishing a SHR.
D/M = dispersed and found dead (M) prior to establishing a SHR.
R/SHR = remained resident on previous BHR, but did not renest.
R/BHR = remained resident on previous BHR and renested.

A. Dispersal distance (km) between subsequent summer home ranges.
B. Azimuth between subsequent summer home ranges.
C. Midpoint in time interval in which owl emigrated (>30 km) its breeding home range.
D. Time interval (in days) in which owl emigrated.
E. Prey population phase state (see methods).

TABLE 8. Breeding dispersal data and concurrent prey population phase state for adult male great gray owls.

Year	ID	Area[1]	Fate[2]	A	B	C	D	E
1984	295	SS	D/SHR	398	1	19-Jan-85	61	Decrease
1984	842	SS	D/SHR	325	34	19-Jan-85	47	Decrease
1984	347	SS	D/SHR	141	8	20-Jan-85	56	Decrease
1984	44	SS	D/SHR	172	53	17-Oct-84	33	Decrease
1984	209	O	D/SHR	41	263	14-Feb-85	9	Decrease
1984	435	SS	D/R	0		15-Jan-85	53	Decrease
1986	143	RB	R/BHR	0				Peak
1987	848	RB	D/SHR	230	349	13-Apr-88	14	Decrease
1987	581	RB	D/SHR	53	21	15-Jul-87	28	Decrease
1987	830	O	D/SHR	291	10	10-Mar-88	8	Decrease
1987	680	SS	R/SHR	0				Increase
1988	970	O	D/SHR	480	350	09-Sep-88	2	Decrease
1988	680	SS	D/SHR	448	10	10-Sep-88	103	Decrease

Adult Males that Dispersed but Died, or were Lost, Prior to Establishing a Subsequent Summer Home Range.

Year	ID	Area[1]	Fate[2]	A	B	C	D	E
1984	229	SS	D/M			06-Mar-85	25	Decrease
1984	407	SS	D/M			11-Feb-85	1	Decrease
1985	435	SS	D/M			10-Oct-85	0	Trough
1988	581	O	D/M			09-Jan-89	8	Decrease

1 Roseau Bog (RB), Spruce Siding (SS) and other (O) locations in southeastern Manitoba and adjacent Minnesota.

2 D/SHR = dispersed (D) to another summer home range (SHR): Breeding status unknown.
D/BHR = dispersed to another breeding home range (BHR).
D/R = dispersed and returned to former BHR, but did not renest.
D/L = dispersed but lost (L) before establishing a SHR.
D/M = dispersed and found dead (M) prior to establishing a SHR.
R/SHR = remained resident on previous BHR, but did not renest.
R/BHR = remained resident on previous BHR and renested.

A. Distance (km) between successive summer home ranges.
B. Azimuth between successive summer home ranges.
C. Midpoint date in time interval in which owl emigrated from (more than 30 km) its breeding home range.
D. Time interval (in days) in which owl emigrated.
E. Prey population phase state (see methods).

Figure 6. Post-vole crash dispersal direction/distance histogram for adult female radio-marked great gray owls. Dots denote the location of post-dispersal summer home range.

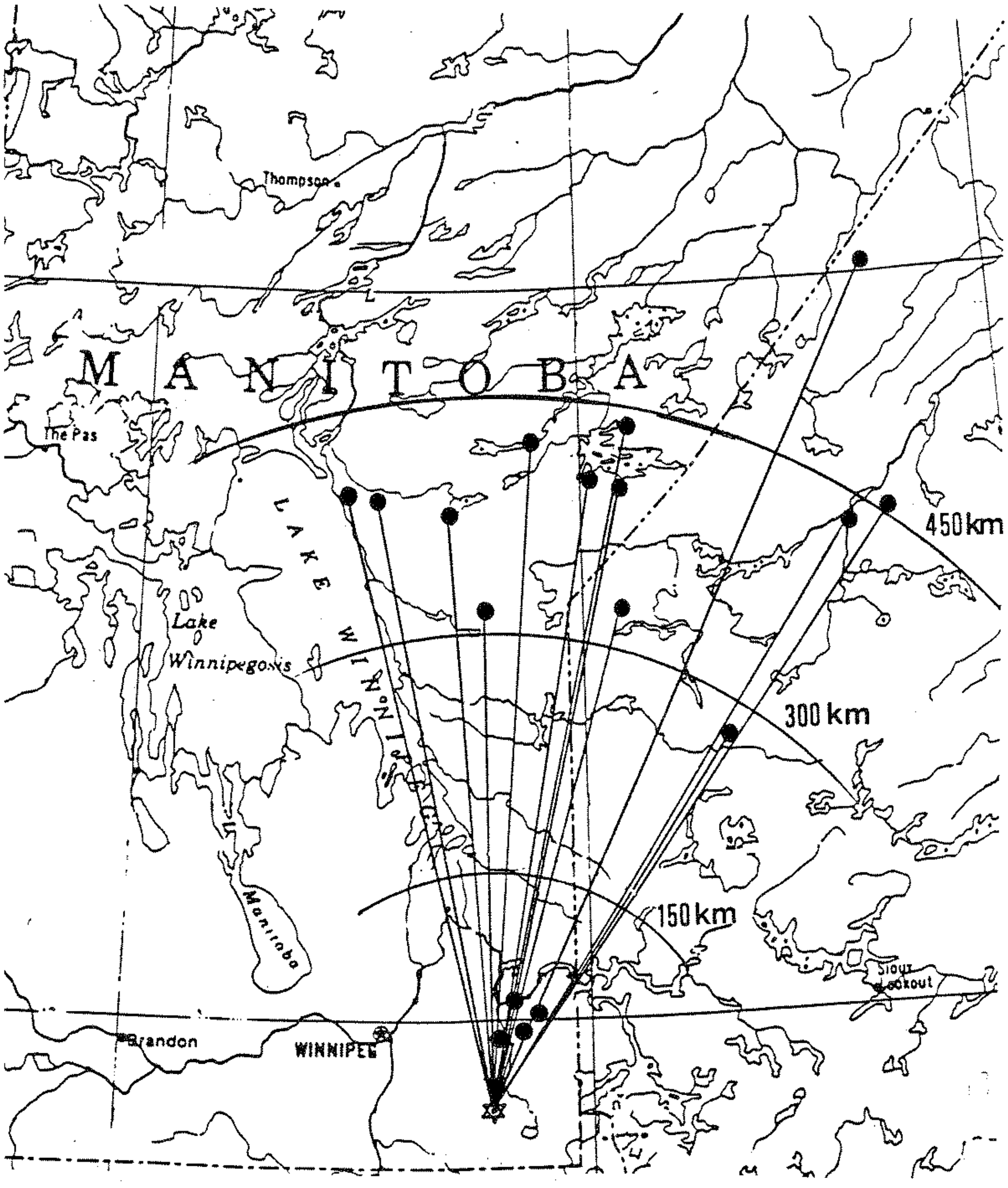
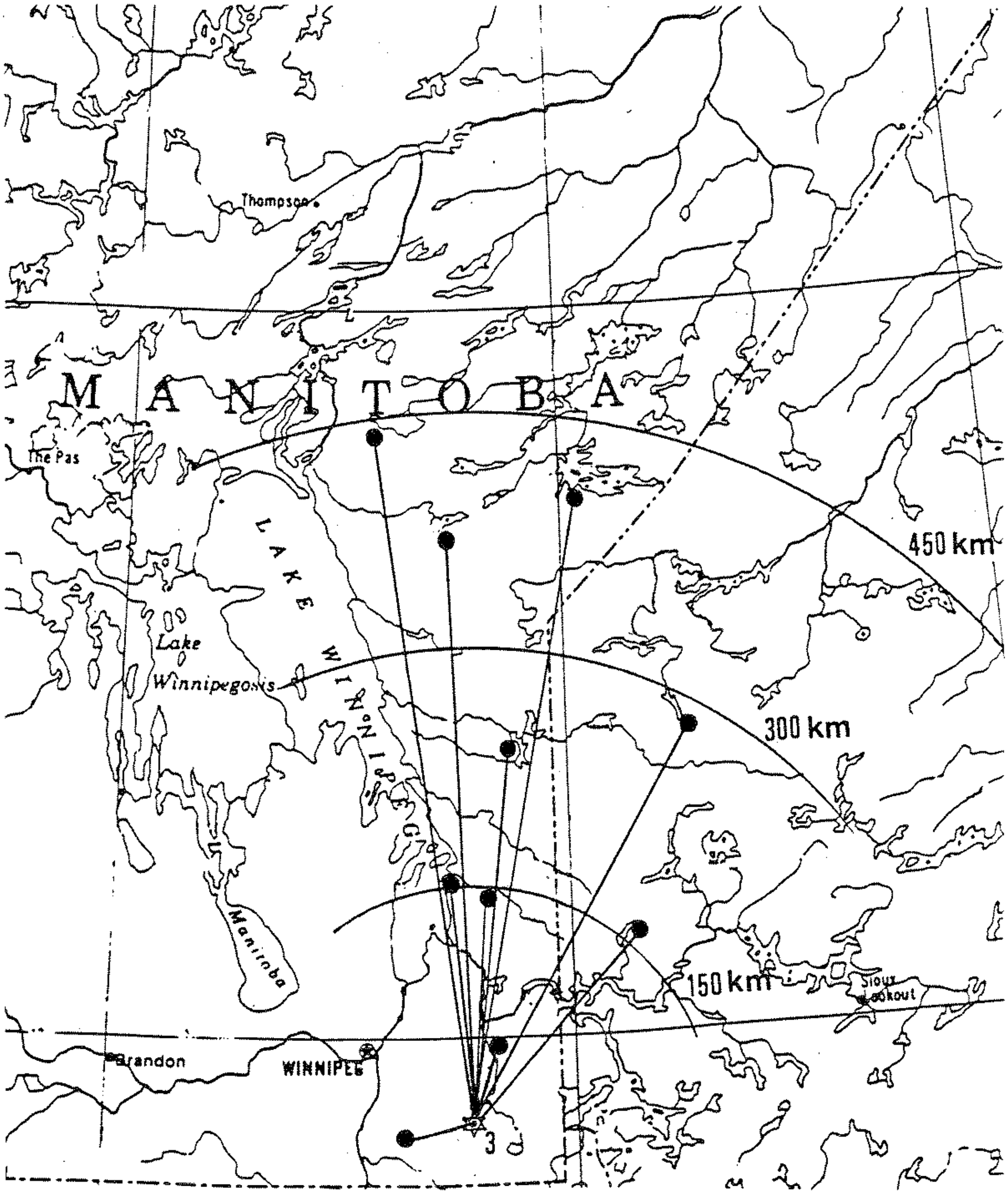

Thompson
MANITOBA
The Pas
LAKE WINNIPEG
Lake Winnipegosis
Manitoba
450km
300 km
150km
Sioux Lookout
Brandon
WINNIPEG

Figure 7. Post-vole crash dispersal direction/distance histogram for adult male radio-marked great gray owls. Dots denote the location of post-dispersal summer home range.


Thompson
MANITOBA
The Pas
LAKE WINNIPEG
Lake Winnipegosis
Manitoba
450 km
300 km
150 km
Sioux Lookout
Brandon
WINNIPEG
3

statistic=0.96, Shapiro and Wilk 1965), and the difference between male and female dispersal distances is enhanced ($p<0.001$, two sample t test).

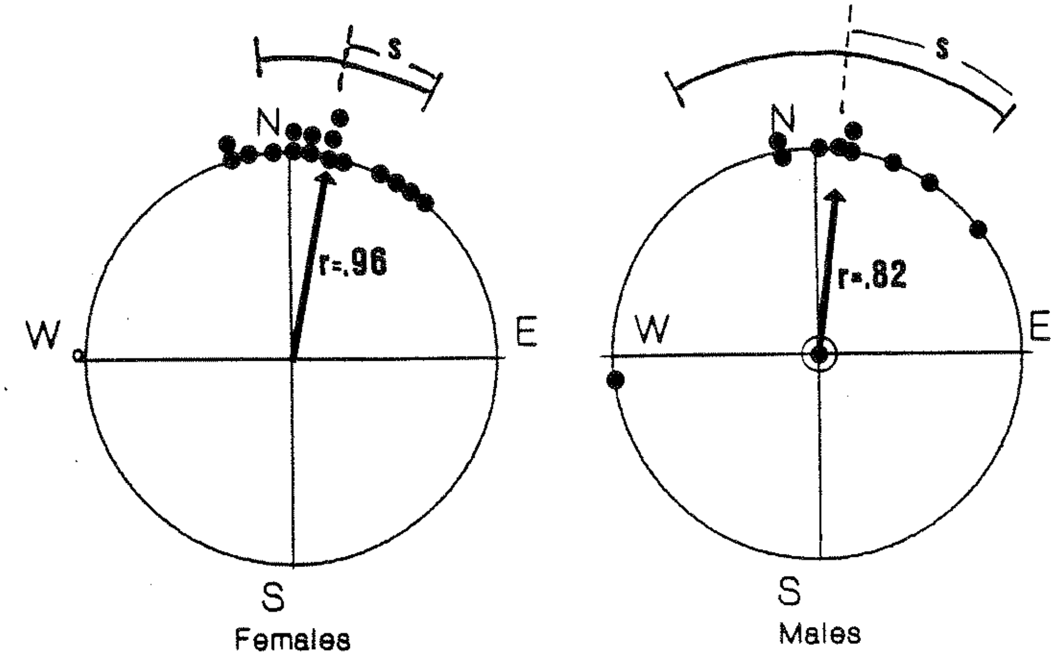
4.4.2 *Direction*

Breeding dispersal directions (azimuth) were significantly non-random for adult males and adult females ($p<0.001$, Rayleigh test, Fig. 8, Tables 7, 8, Appendix J) and their directedness was significant ($p=0.02$ and $p<0.001$, males and females respectively, Hodges' and Ajne's test). Mean female (14^0) and male (6^0) dispersal azimuths were not significantly different ($p=0.48$, Watson-Williams test, Appendix J).

4.4.3 *Chronology*

The timing of adult female breeding dispersal was significantly non-random ($p<0.001$, Rayleigh test) and significantly directed ($p<0.001$, Hodges' and Ajne's test). The mean dispersal date for females was mid-October and ranged from July to January (Fig. 9, Tables 7, 8, Appendix K). Male dispersal dates, however, were random ($p=0.129$, Rayleigh test) and were not significantly directed ($p=0.583$, Hodges' and Ajne's test). The mean dispersal date for adult males was late-January and ranged from as early as July (the only recorded case in this study of a male deserting its mate and fledged young) to April. On average, females departed earlier than males (Fig. 9, $p<0.05$, 95% Confidence

Figure 8. Great gray owl dispersal direction (azimuth).

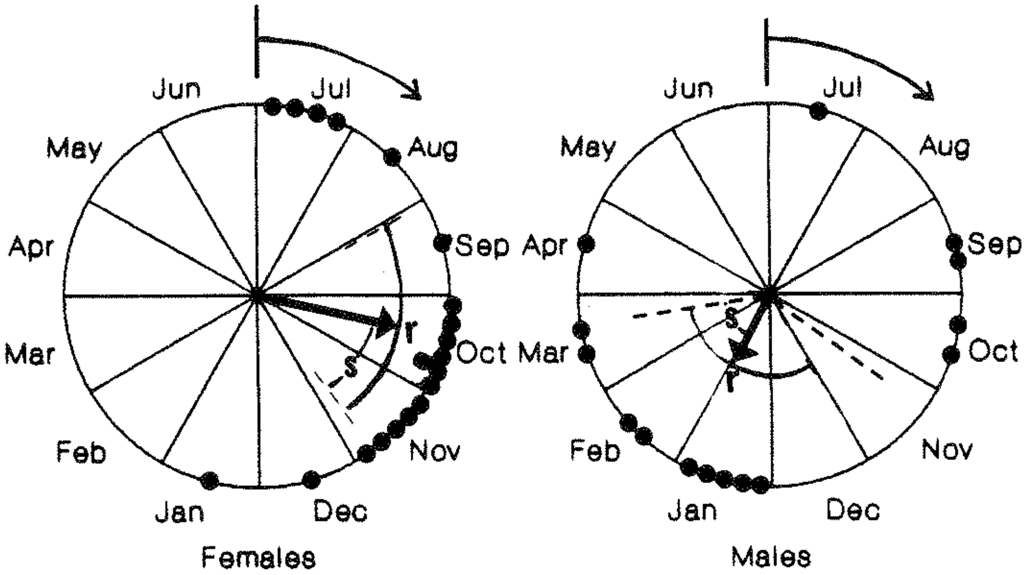


● = DISPERSAL AZIMUTH OF AN OWL

r = LENGTH OF MEAN VECTOR

s = MEAN ANGULAR DEVIATION

Figure 9. Great gray owl dispersal date.



● = DISPERSAL DATE OF AN OWL
r = LENGTH OF MEAN VECTOR
s = MEAN ANGULAR DEVIATION

Coefficient Interval, Batschelet 1981).

4.4.4 *Influence of Prey Abundance*

Three of 13 adult males (ID#'s 680, 435, and 143) either remained on, or returned to, their former breeding home range (Table 8). Two of these males (680 and 143) did not disperse during the intervening winter. They experienced peak and/or increasing *Microtus* populations (Table 8). Male 143 renested with the same female at their former nest-site. Male 680 wandered through the breeding territories of five nesting pairs, but did not nest. Coincidentally, this male's mate (660, Table 7) was the only one of six females to disperse in this interval. Male 435 experienced a prey population decline, dispersed and overwintered 42 km north of its former breeding home range. It was the only one of six concurrently dispersing males that returned to its former breeding home range the following summer. It occupied an expanded version of its former home range, but did not nest.

Six of 27 adult females (22%) nested at the same nest-site they used the preceeding year (five females) or one within 200 m (Table 7). These females experienced either peak or increasing prey populations and did not disperse between breeding seasons. As mentioned above, a seventh female (660) dispersed to a different summer home range under similar conditions.

Twenty-six of 27 adults dispersed when prey populations were either decreasing or low (Tables 7, 8). Conversely, eight of nine adults remained on their former breeding home ranges when prey populations were increasing or at a peak. The interaction between dispersal strategy and prey population phase state was significant (Chi-Square=26.1, d.f.=1, p<0.001).

4.4.5 *Influence of Snow Cover*

There was no consistent relationship between snow thickness and dispersal of radio-marked adults. During the winter of 1986-87, when maximum snow thickness reached almost 80 cm (twice the eight-year average snow thickness), great gray owls at Roseau Bog overwintered and renested the following spring (Tables 7, 8, 9). Owls at Spruce Siding experienced similar conditions during the winter of 1988-89 and dispersed. Conversely, when below-average maximum snow thickness (20 cm) occurred during the winter of 1987-88 (Table 9), great gray owls at the Spruce Siding study area overwintered and nested while owls at Roseau Bog dispersed (Tables 7, 8). As shown in section 4.2.2, these discrepancies are consistent with asynchronous prey population fluctuations.

TABLE 9. Estimated monthly snow thickness[1] (cm) at Roseau Bog and Spruce Siding (1983-90).

A. Roseau Bog

	Oct	Nov	Dec	Jan	Feb	Mar
1983				31.5	14	0
1983-84	0	18.5	16	16	15	6
1984-85	6	2	18	29	47.5	0
1985-86	0	34	42.5	38.5	35	0
1986-87	0	20	31.5	51.5	74	7.5
1987-88	0	4.5	11.5	19	7.5	24
1988-89	9	21.5	55.5	78	70	42.5
1989-90	0	6	24	41	54	0
Average	2.14	15.21	28.43	38.06	39.63	10.00

B. Spruce Siding

	Oct	Nov	Dec	Jan	Feb	Mar
1983			18	19	0	
1983-84	0	15	20.5	32	29	0
1984-85	4.5	0.5	25.5	38	43.5	0
1985-86	0	29	39	38	44	0
1986-87	0	21	34	31	47	21.5
1987-88	0	0	15.5	22	19	17.5
1988-89	10.5	15.5	38	77.5	74.5	51
1989-90	0	7	24	34.5	41.5	11.5
Average	2.14	12.57	28.07	36.38	39.69	12.69

[1] Data from Environment Canada.

Thirteen (62%) adult females and four (27%) adult males dispersed before snow accumulated (Table 10). Almost all adult females (90%) dispersed when snow was less than 11 cm thick. One-half of the adult males dispersed prior to snow accumulations greater than 20 cm. All 37 adults dispersed when snow was less than 45 cm thick (Table 10). Four (19%) adult females and six (40%) adult males dispersed when snow thickness exceeded 8-year monthly averages (Table 10).

Great gray owls dispersed to home ranges that were at a relatively lower elevation and that received greater total annual snowfall (Appendix A, Figs. 6, 7). Radio-marked owls that had dispersed were observed hunting successfully on northern home ranges where snow thickness exceeded 70 cm (J.R. Duncan, unpubl. data).

4.4.6 *Effectiveness*

Dispersal was effective (sensu Greenwood 1980) in that at least two radio-marked females nested successfully following emigration from southeastern Manitoba or adjacent Minnesota (Table 6). An additional female nested 2 years after emigrating from southeastern Manitoba (J.R. Duncan, unpubl. data). Eight other females were observed at least once during post-dispersal breeding seasons; courtship behaviour was observed but no nests were found. It is easier to detect nesting than to prove that it had not occurred, or

TABLE 10. Estimated snow thickness (cm) and dispersal date.

Adult Females							Adult Males						
No.	ID	Mon	Yr	A	B	A-B	No.	ID	Mon	Yr	A	B	A-B
1	621	JUL	88	0	0	0	1	970	SEP	88	0	0	0
2	271	SEP	88	0	0	0	2	229	MAR	85	0	14.5	-14.5
3	632	OCT	87	0	2.1	-2.1	3	581	JUL	87	0	0	0
4	711	JUL	87	0	0	0	4	848	APR	88	0	0	0
5	255	NOV	84	0	12.6	-12.6	5	44	OCT	84	4.5	2.1	2.4
6	702	AUG	87	0	0	0	6	435	Oct	85	10.5	2.1	8.4
7	640	OCT	87	0	2.1	-2.1	7	682	OCT	88	10.5	2.1	8.4
8	132	NOV	84	0	12.6	-12.6	8	830	MAR	88	17.5	14.5	3
9	532	OCT	87	0	2.1	-2.1	9	581	JAN	89	29	39	-10
10	660	OCT	87	0	2.1	-2.1	10	347	JAN	85	38	39	-1
11	759	JUL	87	0	0	0	11	842	JAN	85	38	39	-1
12	103	NOV	84	0	12.6	-12.6	12	295	JAN	85	38	39	-1
13	612	JUL	87	0	0	0	13	435	JAN	85	38	39	-1
14	602	NOV	87	4.5	15.2	-10.7	14	407	FEB	85	43.5	42.6	0.9
15	672	NOV	87	4.5	15.2	-10.7	15	209	FEB	85	43.5	42.6	0.9
16	643	OCT	84	4.5	2.1	2.4							
17	702	OCT	88	9	2.1	6.9							
18	480	OCT	88	10.5	2.1	8.4							
19	640	OCT	88	10.5	2.1	8.4							
20	279	DEC	84	25.5	28.1	-2.6							
21	15	JAN	85	38	39	-1							

A Estimated snow thickness (see methods).
B Average estimated snow thickness (see methods).

that it had been initiated and failed.

5. DISCUSSION

5.1 Factors Influencing Breeding Dispersal

Of all factors thought to influence northern forest owl breeding dispersal patterns, nest-site and prey availability are considered the most important (Lundberg 1979, Mikkola 1981). However, the age and sex of an individual are also thought important. These factors are discussed below in the context of the hypotheses presented in section 1.2.

5.1.1 *Nest-site Availability*

Lundberg (1979) considered assured access to nest-sites the most fundamental factor governing dispersal by northern forest owls. He predicted that both sexes (of food specialists) should disperse annually if nest-sites are abundant (stick nests) when prey availability decreases due to snow cover (Lundberg 1979). Great gray owls frequently nest in old stick nests (Nero 1980), but occasionally use decayed concavities atop broken tree stumps, cliff ledges, and will even nest on the ground (Mikkola 1983, J.R. Duncan, unpubl. data). They are a small mammal specialist and are therefore similar to the long-eared owl (*Asio otus*) (Collins 1980, Nero 1980, Mikkola 1983, Cramp 1985, Korpimäki 1986, Johnsgard 1988). According to Lundberg's (1979) hypothesis, the great gray owl should disperse each year to areas with greater prey availability (thinner snow cover) because nest-sites are not limited. The results of this study were not consistent with this prediction. Nest-sites were either less available than Lundberg hypothesized or they were less influencial in moulding great gray owl breeding dispersal.

Sonerud (1986) argued that given adequate prey, the great gray owl should exhibit year-round residency since, like boreal (*Aegolius funereus*) and northern hawk owls (*Surnia ulula*), it can hunt within forest habitat. He contended that feeding ecology and snow cover are more important than nest-site availability in determining the pattern of mobility and wintering strategies of owls.

While all owls can hunt by the energetically inexpensive sit-and-wait method, some, like the long-eared owl, use the energetically more expensive quartering (flying) hunting method (Wijnandts 1984). During snow-free periods both hunting methods can take advantage of prey occurring in clear-cuts or natural openings. However, microtine populations are less vulnerable in open, snow-covered areas (Korpimäki 1986, Sonerud 1986). This is due to increased supranivean and snow-tunnelling activity of small mammals in forested habitat resulting from the lack of a well developed, continuous pukak layer (Sonerud 1986). Habitat-related subnivean CO_2 accumulations in some forested areas may also play an important role in microtine vulnerability to predation (Penny and Pruitt 1984).

Short, broad wings, providing greater maneuverability among vegetation, are an adaptation enabling certain owls to capture prey in wooded areas (Norberg 1987). The relatively long and narrow wings of the long-eared owl renders it less able to capture prey in forest habitat. It must migrate to snow-free areas and return to northern breeding areas only when open areas are partially snow-free (Sonerud 1986).

5.1.2 *Snow Cover*

Snow cover significantly alters microtine prey availability to many predators (Formozov 1946). It is therefore an important potentially confounding factor in detecting the influence of prey abundance on great gray owl breeding dispersal. However, during this study breeding dispersal was not measurably influenced by snow cover. This does not preclude that snow cover could not directly affect great gray owl dispersal at other times or elsewhere in its circumpolar range, especially in mountainous regions. For example, Bull and Henjum (1990) concluded that most radio-marked great gray owls they monitored in Oregon underwent altitudinal migrations. The owls travelled no more than 43.2 km (average 13.4 km) to lower elevations with less snow and, they presumed, greater prey availability. Bull and

Henjum (1990) incorrectly concluded that great gray owls in southeastern Manitoba and adjacent Minnesota accomplished the same by dispersing up to 700 km north (Duncan 1987). While it is true that the owls in Manitoba did relocate at lower elevations, they experienced winters with greater snowfall (Appendix A). Perhaps the best example of the great gray owl's tolerance of thick snow comes from Oregon. One adult female great gray owl radio-tracked in mountainous terrain spent two winters at a high elevation with snow thickness in excess of 150 cm (Bull and Henjum 1990).

Great gray owls locate prey concealed beneath snow using auditory cues (Norberg 1987). They typically hover above the snow, plummet head first, break through the snow cover with clenched feet, and attempt to grasp prey with their feet and talons. This behaviour is called "snow-plunging" (Law 1960, Godfrey 1967, Collins 1980, Nero 1980, Hilden and Helo 1981). While snow-plunging, great gray owls are often described as hitting the snow face first (Nero 1980, Mikkola 1983), with the feet being brought forward at the last instant in a fashion characteristic of raptors in general (Johnsgard 1988). This can be accomplished in milliseconds (Goslow 1971).

Norberg (1987:40) stated that "even though the great gray owl does not appear to use its large size to take big prey, it obviously benefits from its size in other ways." Snow-plunging allows great gray owls to capture prey in open habitat where prey is less vulnerable to other northern forest owls (Sonerud 1986). The great gray owl's weight (700 to 1600 g, Appendix N) is important to the owl's success in breaking through hard crusted snow. Great gray owls achieve this by dropping as much as 7 m from either a perch or from a hover above the suspected prey. A biophysical analysis of great gray owl snow-plunging is presented in Appendix M. Small changes in variables such as velocity at impact or contact surface area can easily account for a great gray owl's ability to penetrate and catch prey through hard-crusted snow. Consider a 1000 g great gray owl hitting a 1 cm thick snow crust at 5 m/s. With a contact surface of 50 cm^2, it hits with a pressure force of 2500 g/cm^2. By decreasing its contact surface to 30 cm^2, i.e. by clenching its feet more tightly, the owl increases the pressure force to 4167 g/cm^2 (Appendix M).

Collins (1980) found that great gray owls penetrated hard snow (3000 to 3500g/cm^2) as much as 30 cm to capture prey. He found that plunge hole depth was independent of snow hardness. I measured snow hardness at fresh plunge holes until I found that great gray owls captured prey through snow crusts in excess of 10,000 g/cm^2. Others have reported great gray owls catching prey under snow crusts able to support a 80 kg person (Hildén and Helo 1981), and plunging down as far as 45 cm below the snow surface (Nero 1980).

Collins (1980) estimated a 22% success rate for snow-plunging great gray owls based on nine observations. I observed 26 plunges involving nine different owls in which I could determine the outcome. Seventeen were successful (65%). The relationship of prey capture success rate to snow conditions warrants further study, but it is clear that great gray owls are well adapted to capturing prey under hard, thick snow. Great gray owls have also been observed breaking through soil and capturing pocket gophers (*Thomomys talpoides*) in their underground tunnels (Tryon 1943).

Snow cover likely affects great gray owl dispersal indirectly through its powerful influence on small mammal survival during the fall and spring critical periods (Pruitt 1978). A snow thickness of 10 to 15 cm is required to moderate the subnivean bio-climate of microtines, insulating them from severe low ambient temperatures and radiant heat energy loss (Pruitt 1978).

5.1.3 *Prey Availability*

The literature is replete with suggestions that great gray owl breeding dispersal is related to prey population declines (Cramp 1985). However, empirical data are largely lacking (Mikkola 1983). The general consensus is that as long as prey populations remain adequate, most great gray owls stay on their breeding areas or perhaps move only short distances (Hildén and Solonen 1987). Conversely, when prey populations crash, great gray owls are believed to move nomadically in search of food rather than take alternative prey (Newton 1979, Mikkola 1983).

Great gray owl breeding density and dispersal were strongly associated with local *Microtus* population declines. Therefore, great gray owls were indeed nomadic as Andersson (1980) predicted (see section 1.2.2, A and B). Andersson (1980) compared the relative merits of adult avian nomadism to site tenacity based on a model relating the fitness of an individual to its clutch size, mortality rate, and pattern of food production.

Great gray owls that did not disperse following prey declines did not survive over winter to the next breeding season (Table 6). Little or no breeding was detected in southeastern Manitoba or adjacent Minnesota following prey declines. At least three great gray owls reproduced following breeding dispersal. These factors increased the relative merits of nomadism over site-tenacity in Andersson's (1980) model.

Geographic asynchronous food production fluctuations, a central assumption of Andersson's (1980) model, was observed during this study (Fig. 5). However, the extent to which asynchrony occurs over larger geographic areas is not clear. Small mammal populations frequently exhibit geographically asynchronous (both within and between species) multiannual cycles (Hagen 1956, Pruitt 1968, 1972, Hansson 1969, Mysterud 1970, Myrberget 1973, Saitoh 1987, Krohne and Burgin 1990). This does not imply that "cosmic" or extrinsic factors do not occasionally synchronize microtine populations, but that numerous other factors, both intrinsic and extrinsic, often function to disrupt any synchronizing effects they may have (Pruitt 1968, Lidicker 1988). Similarities between the behaviour of even simple non-linear models and long-term microtine population studies suggest that small mammal population fluctuations are chaotic and unpredictable (May and Oster 1976, Gleik 1987). Interestingly, Andersson (1980) concluded that cyclic rather than random food fluctuations favoured nomadism.

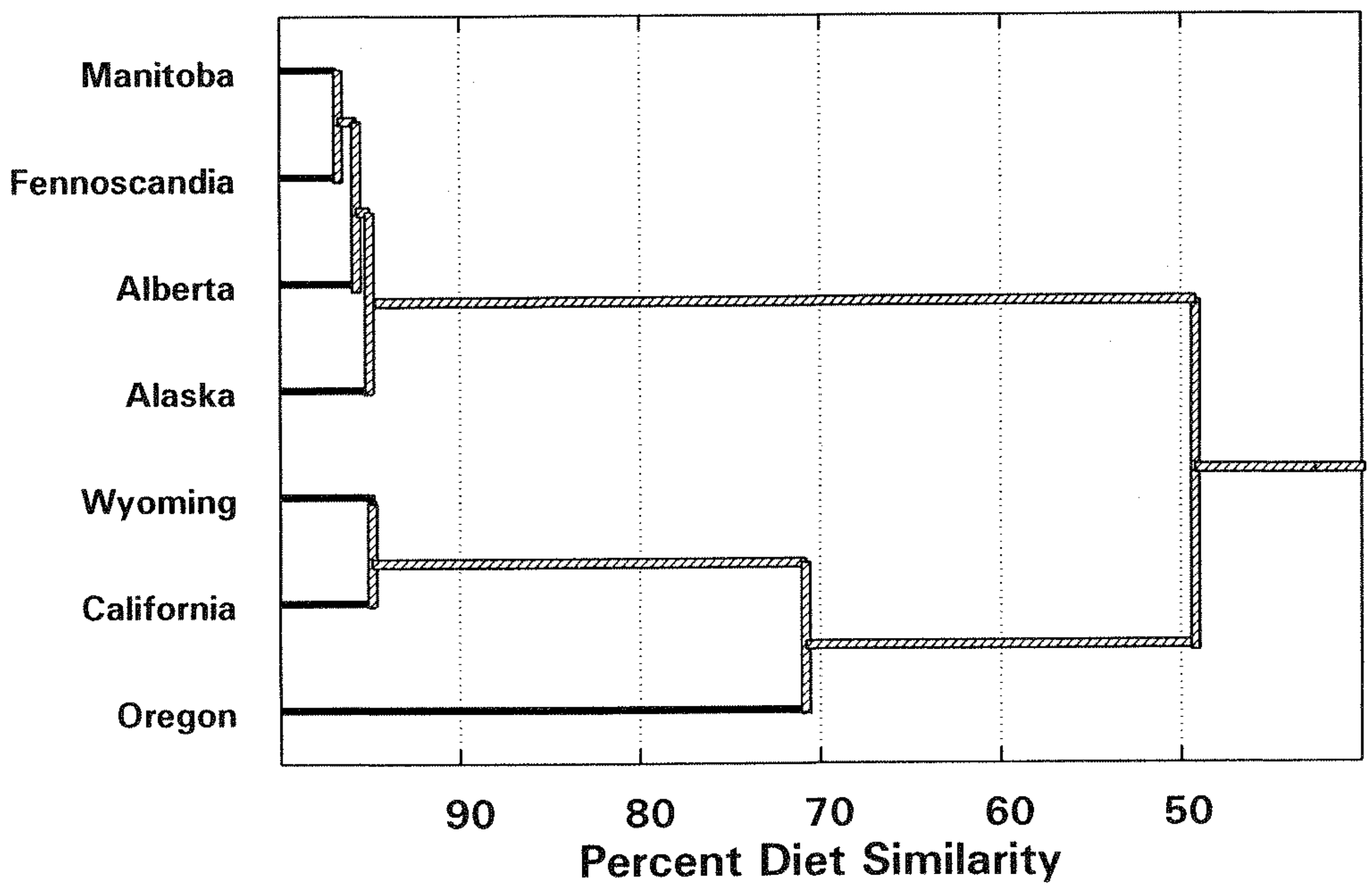
5.1.3.1 *Intraspecific Variation*

Comparisons of within-species variation in dispersal strategies are useful in understanding the selective pressures resulting in the observed dispersal pattern. Breeding dispersal distances of adult great gray owls observed in this study and by Nero (1980) and Nero et al.

(1984) were comparable to those obtained from Fennoscandia (Cramp 1985, Hildén and Solonen 1987). Great gray owls in Oregon (Bull and Henjum 1990), Idaho and Wyoming (Franklin 1987) and California (Winter 1986) moved much shorter distances than great gray owls at higher latitudes. In Oregon, the maximum distance 16 adult great gray owls ranged from their nests, over a 3-year period, averaged 13 km. The same value for 19 juveniles after 1 year was 18 km (Bull and Henjum 1990).

A cluster analysis, based on percent diet similarity indices (Appendix L), revealed that great gray owl populations at southern latitudes are distinct from populations in Fennoscandia and North American boreal forest regions (Fig. 10). At lower latitudes in North America, great gray owls use pocket gophers as alternate buffer prey species when faced with microtine population declines (Winter 1986, Franklin 1987, Reid 1989, Bull and Henjum 1990). Pocket gopher populations are not known to fluctuate cyclically (Chase et al. 1982, Teipner et al. 1983), whereas northern microtine populations are low in diversity and fluctuate multi-annually (Henttonen 1986). This natural experiment (Diamond and Case 1986) emphasizes the importance of food biomass production instability to the expression of great gray owl nomadism.

Figure 10. Average linkage cluster tree diagram created using the unweighted pair-group method on great gray owl prey data in Appendix L.

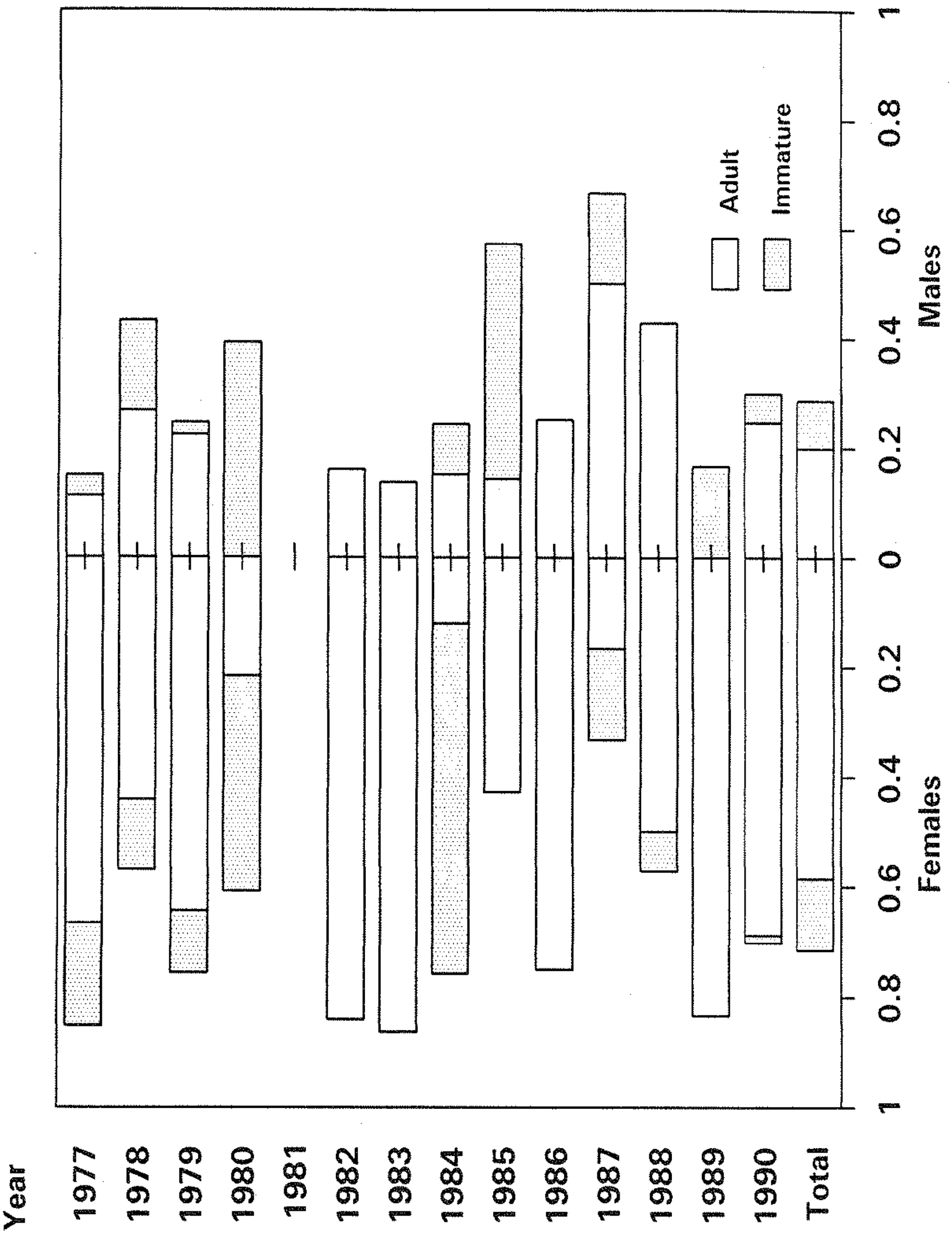

Manitoba
Fennoscandia
Alberta
Alaska
Wyoming
California
Oregon
90
80
70
60
50
Percent Diet Similarity

5.1.4 *Age and Sex*

When prey populations increased or peaked, radio-marked adult great gray owls were site-tenacious and used the same nest or one close by (see also Wahlstedt 1976, Mikkola 1981). When prey populations declined, adult females dispersed farther (Figs. 6, 7) and earlier (Fig. 9) than adult males. Therefore, assuming equal catchability and mortality, one would predict a female-biased sex-ratio for live winter-caught adult owls and for adult specimens. Among 87 adult winter specimens (dated 1977 to 1991; from collections at the Manitoba Museum of Man and Nature and the Zoology Department, University of Manitoba, Winnipeg) there were significantly more females (59) than males (one-tailed Binomial, $p<0.005$). Collins (1980) tabulated data on museum great gray owl specimens for North America from 1890 to 1976. The sex was reported for 387 of 687 winter-killed specimens, but no information on age was given. There were significantly more females (229) than males (one-tailed Binomial, $p<0.001$).

The sex-ratio of winter-captured adult great gray owls in Manitoba was significantly female-biased (Fig. 11, Appendix N), but that of juveniles was not. Other studies found great gray owl natal dispersal distances ranged from 1.6 to 753 km (Nero 1980, Mikkola 1981, Cramp 1985, Bull and Henjum 1990) and are comparable to those of adults. Surviving

Figure 11. Annual fluctuations of age-sex class proportions of winter-caught great gray owls (1977-90).


Year
1977
1978
1979
1980
1981
1982
1983
1984
1985
1986
1987
1988
1989
1990
Total
Females
Males
1
0.8
0.6
0.4
0.2
0
0.2
0.4
0.6
0.8
1
Adult
Immature

juvenile radio-marked great gray owls in southeastern Manitoba and adjacent Minnesota dispersed earlier than adult males and concurrently with adult females following prey population declines (Duncan 1987).

Age and sex differences in great gray owl dispersal are consistent only with the arrival-time hypothesis (section 1.2.3). Adult male dispersal is perhaps influenced by competition for breeding territories with suitable nest-sites. Similar results were found for adult northern hawk owls (Byrkjedal and Langhelle 1986) and boreal owls (*Aegolius funereus*) (Lundberg 1979, Löfgren et al. 1986, Sonerud et al. 1988). Snowy owls and female and juvenile northern hawk owls were found to be more influenced by social dominance (Nagell and Frycklund 1965, Byrkjedal and Langhelle 1986, Kerlinger and Lein 1986).

5.2 Are adult great gray owls nomadic?

It makes intuitive sense that nomadism would have great survival and reproductive value to a specialist predator dependant on an irregularly fluctuating prey population. However, nomadic breeding dispersal direction is characterized as being non-calculated or random. This was not observed in this study (Fig. 8). Another prediction of the hypothesis that great gray owls are nomadic is that individuals would not be faithful to their former breeding sites following gross or effective breeding dispersal (section 1.2.2.D). If great gray owls are completely nomadic, we would not expect evidence of natal or breeding philopatry between vole population peaks, especially given the dispersal distances observed in this study. Individual owls likely would encounter a prey population peak (given asynchronous food fluctuations) and stop en route prior to arriving at their former nest-site. However, is non-calculated or random dispersal the only logical consequence of natural selection under these circumstances? If food resources fluctuate unpredictably, should individuals of an irruptive species drift aimlessly in search of food? Andersson (1980) noted that factors other than food availability also influence the relative merits of nomadism versus site-tenacity or fidelity to former nesting sites.

Boreal, northern hawk and great gray owls exhibit female-biased breeding dispersal in northern forest regions as predicted by the arrival-time hypothesis. The benefits of site-tenacity to an individual adult male owl include access to scarce suitable nest-sites, especially considering that polygyny has been reported for the first two species and suspected on more than one occasion for great gray owls (Mikkola 1983, Lehtoranta 1986, J.R. Duncan, unpubl. data). While stick nests are thought to be relatively common compared to nest cavities, their distribution in suitable habitat is not necessarily uniform. In addition, site-tenacious birds are thought to benefit from a knowledge of food resources and shelter locations within their home range (Hinde 1956, Howard 1948). These benefits act as strong selective forces on most avian species (Andersson 1980, Greenwood and Harvey 1982). Furthermore, their relative importance to the evolution of a species-specific dispersal pattern increases with increased species life expectancy (Andersson 1980). Winter (1986) estimated great gray owl longevity, based on an ecological scaling of body size, at about 10 years. Recaptures of banded individuals indicate wild great gray owls can live up to 13 years (R.W. Nero, unpubl. data).

Suggestions of great gray owl nest-site tenacity between vole peaks came from Fennoscandia when Stefansson (1985, 1986) noted that some great gray owl pairs breed, or attempt to breed, every spring in Sweden despite a poor food supply. Hildén and Solonen (1987) speculated that these "residents" were possibly old experienced individuals capable of surviving periods of food shortages. This idea is not supported by this study. In Manitoba, some great gray owls attempted to nest under these circumstances, but these were unmarked birds and had not previously used these nest-sites. Comparisons with other studies (section 5.1.3.1) demonstrate that when food productivity is regular or predictable the benefits of site-tenacity result in decreased great gray owl dispersal tendencies. Irregular or unpredictable prey population fluctuations appear to result in multi-annual calculated non-removal migration and not nomadism.

Of all radio-marked great gray owls that dispersed from southeastern Manitoba, one adult male returned the following summer to occupy an expanded version of its former breeding home range. Wahlstedt (1976) tagged a breeding female at a nest in Sweden in 1970 and found it breeding only 1.5 km away in 1974. Two nesting females banded in southeastern Manitoba were recaptured at nest-sites within the same original breeding area over a 10- and 7-year period at intervals of 3 to 6 years (R.W. Nero, unpubl. data). It is likely that these females had dispersed in the intervening years, as did the radio-marked great gray owls in this study. One radio-marked adult female dispersed 768 km bearing 13° north after successfully rearing two chicks in 1987 near the Manitoba-Minnesota border. It was found brooding three owlets at a ground nest-site 2 years after dispersing north (1989). That fall it initiated a southward movement and travelled 194 km bearing 192°, almost exactly 180° from its northward dispersal. Unfortunately, its radio-transmitter expired soon after. Two male great gray owls, radio-marked as breeding adults, returned to southeastern Manitoba and renested 3 years after dispersing to summer home ranges 141 and 480 km north. The male that had dispersed the farthest nested at its former nest-site. The other male nested within 400 m of its former nest-site. These observations imply that great gray owls possess some form of homing ability enabling them to return to former breeding territories after dispersing many hundreds of kilometres.

5.3 Conclusions

Most bird species are philopatric and undergo relatively low levels of natal and breeding dispersal (Greenwood and Harvey 1982). Natal dispersal is more extensive than breeding dispersal because dominant adults already established on territories force juveniles to travel farther in search of territories (Murray 1967) and young birds have not yet established a locality-fixation (cf. Williams 1958). Once established as a breeding bird, individuals of most species become more philopatric as they age (Nice 1937, Williams 1958, Greenwood and Harvey 1982). As such, dispersal should be considered an open-ended ontogenic process rather than a fixed-end product of evolution (Williams 1958).

Svärdson (1957) noted that at least 40 Swedish bird species displayed invasion (nomadic) tendencies, and thought that these tendencies were differently evolved in different species according to the average food variations. His view of dispersal strategies as adaptations extended to the full range exhibited by all bird species. He considered there to be a delicate balance of three selective forces, that which results in ordinary migrations, that which leads to invasion and finally that which results in completely sedentary habits. Migration, with its homing and seasonal stability, was thought of as an adaptation to a seasonal food shortage. Under such circumstances, annual variations in food supply are thought to be evolutionarily insignificant. Svärdson (1957) saw invasion phenomena as an inherited adaptation to significant annual differences in food supply. Within-species variation in dispersal tendencies was accounted for as subspecific differences, each subspecies having a different dispersal adaptation.

Collins (1980) analyzed 2,200 North American great gray owl specimen and sight records spanning 1890 to 1976. He suggested that the extent to which great gray owls appeared south of their boreal forest range represented a continuum of nondiscrete events. The appearance of small numbers of great gray owls in a specific location could be accounted for by the increased visibility of local populations due to winter habitat shifts (Nero 1980, Bouchart 1991). An "invasion" denotes a larger-scale movement of great gray owls into a specific area, and an "irruption" describes a large-scale movement over a widespread area, or on a continental scale (Ulfstrand 1963, Mysterud 1970, Nethersole-Thompson 1975). Of the 23 invasions that Collins (1980) identified over the 86-year period, most were small and local, but some were widespread and coordinated across North America.

Svärdson (1957) proposed the "pendulum" theory to explain the irruptive movements of birds in northern Europe: populations move east to west, reversing direction when boundaries to dispersal are encountered. Ulfstrand (1963) revised this by suggesting the dispersal pattern was more circular. Mysterud (1970) also proposed a circular multi-annual dispersal pattern for boreal owls in northern Europe. Collins (1980) felt that a different model or hypothesis was needed to account for the variation in magnitude of great gray owl invasions and extra-limital records. The degree of synchrony among great gray owl prey populations within its breeding range should affect the magnitude of subsequent invasions. If microtine prey population dynamics are chaotic, then widespread synchronous microtine declines and subsequent large-scale great gray owl irruptions should be infrequent and unpredictable, as indeed they are. Widespread great gray owl invasions and irruptions outside their normal breeding range are atypical extreme expressions of non-calculated dispersal behaviour. Perhaps these dramatic events were afforded undue bias as evidence that great gray owl are nomadic.

Svärdson's (1957) explanation seems infinitely more complex than William's (1958) aforementioned view. The dispersal pattern exhibited by an individual great gray owl should be thought of as the interaction of inherited traits, sex, the nature of prey biomass production, age and experience (home range memory repertoire resulting from locality fixation), and topography. This explains the variety of dispersal patterns observed throughout the species' range. This interaction provides individual owls with a flexible dispersal mechanism of greater survival and reproductive value than an inherited fixed action pattern.

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7. APPENDICES

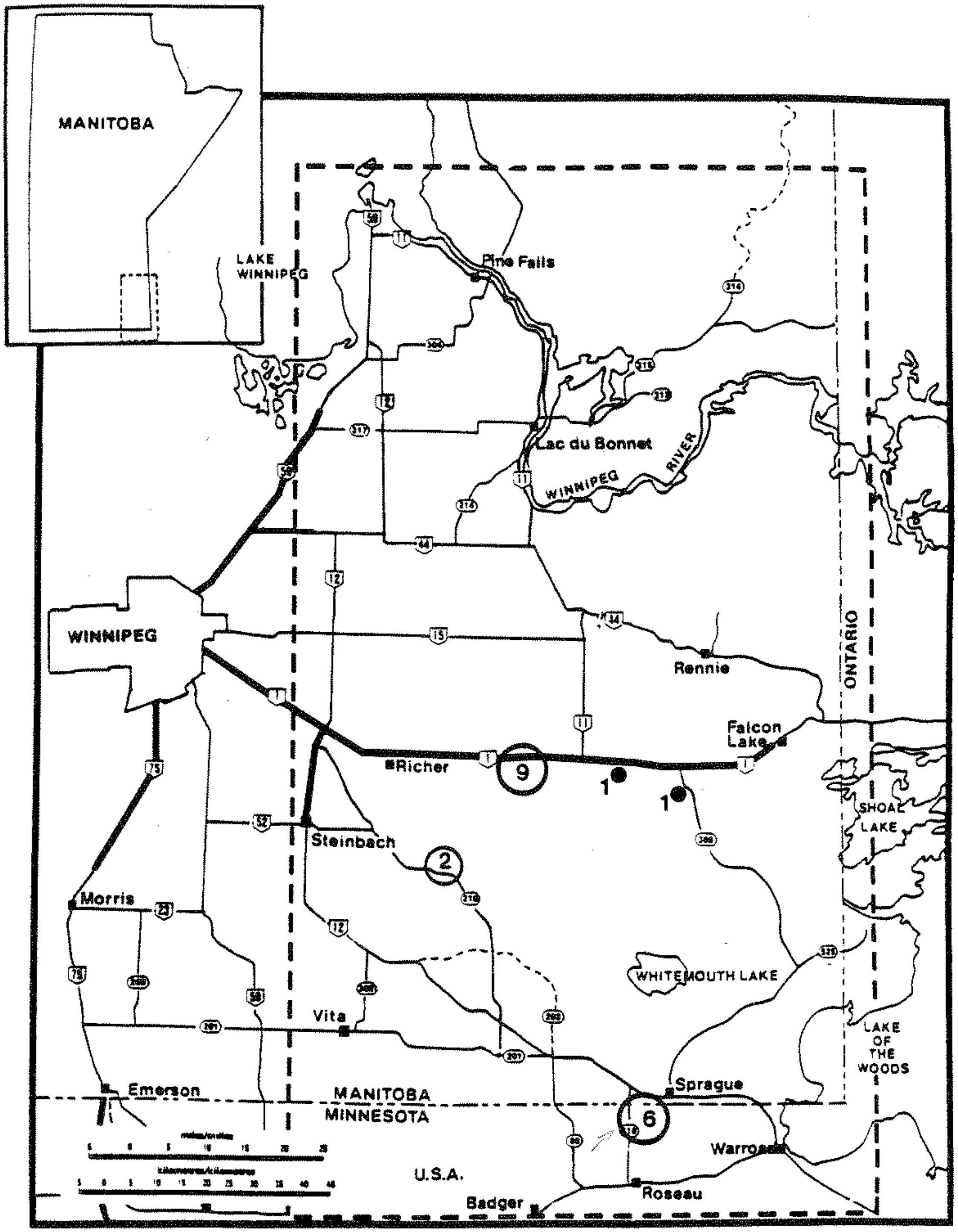
Appendix A. Climate normals for southeastern Manitoba and selected areas (Environment Canada 1982).

Location	Long.	Lat.	A	B	C	D	E	F	G
Sprague	95°38'	49°02'	327	-19	19	117	45.6	57.3	20.42
Whitemouth L.	95°45'	49°17'	351	-19	19	127	42.7	55.3	22.78
Falcon Lake	95°23'	49°41'	338	-20	19	137	39.8	56.9	30.05
Beausejour	96°31'	50°04'	302	-19	19	140	40.7	51.5	20.97
Pinawa	96°03'	50°11'	267	-20	19	140	41.2	56.7	27.34
Great Falls	96°00'	50°28'	249	-19	20	114	35.2	46.5	24.30
Pine Falls	96°13'	50°34'	229	-20	19	121	42.5	53.9	21.15
Bissett	95°40'	51°02'	258	-21	18	171	43.4	58.9	26.32
Red Lake	93°48'	51°04'	375	-21	18	181	42.3	58.9	28.18
Big Trout L.	89°52'	53°50'	219	-25	16	214	38.1	58.1	34.42
Island Lake	94°40'	53°52'	238	-25	17	282	36.1	56.7	36.33
Norway House	97°48'	54°00'	217	-24	18	163	30.4	44.1	31.07
Cross Lake	98°02'	54°35'	219	-25	18	163	30.6	43.4	29.49
Wabowden	98°38'	54°55'	233	-25	17	148	31.5	46.4	32.11
Gillam	94°42'	56°21'	138	-27	15	155	28.2	42.2	33.18
Gillam A	94°42'	56°21'	145	-28	15	239	29.2	48.5	39.79
Churchill	94°04'	58°45'	29	-28	12	196	22.1	40.2	45.02

A	Elevation above sea level(m)
B	January mean daily temperature (°C)
C	July mean daily temperature (°C)
D	Total annual snowfall (cm)
E	Total annual rainfall (cm)
F	Total annual precipitation (cm)
G	Percent total precipitation falling as snow

Appendix B. Annual distribution of occupied nest-sites.

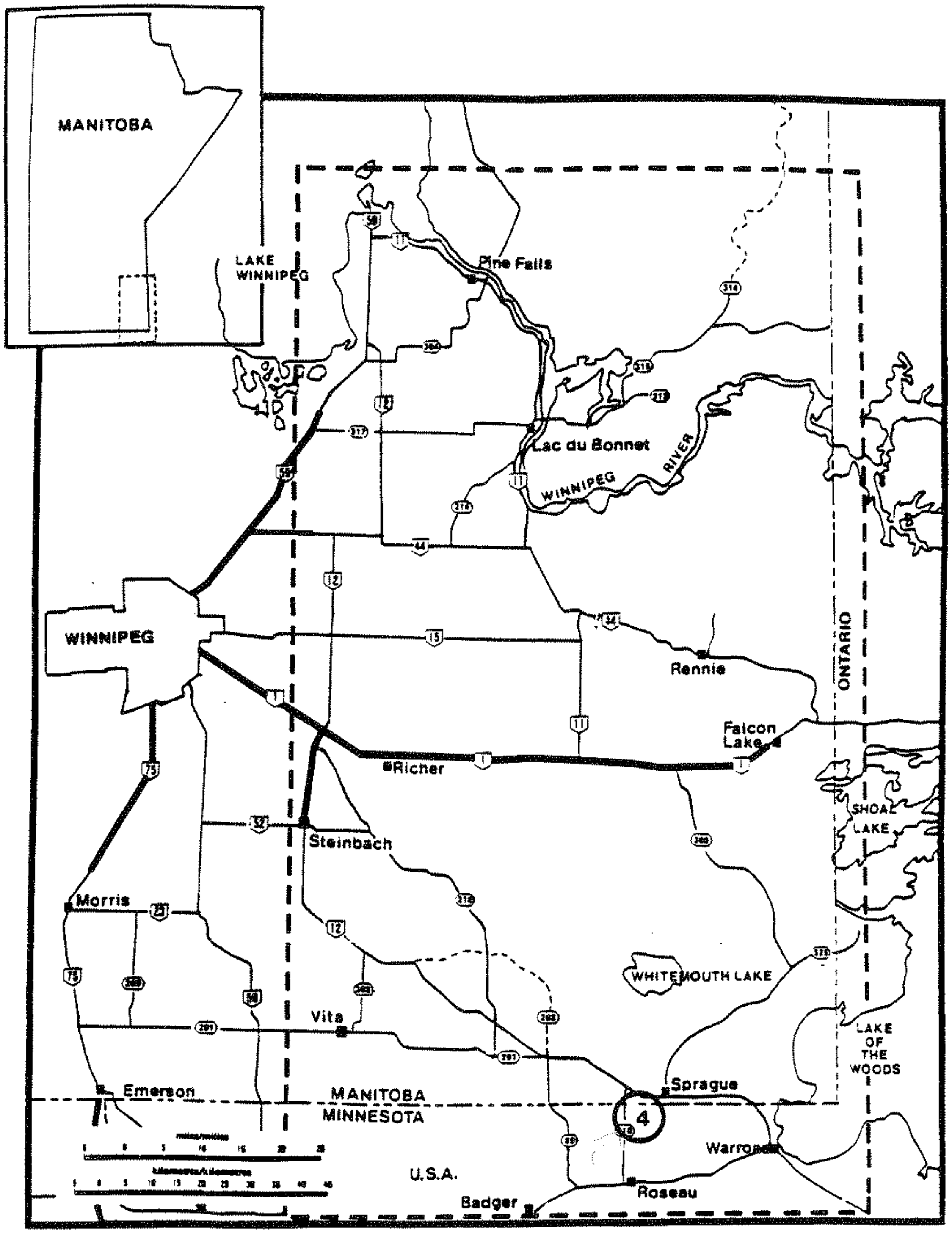
1984



1984

Appendix B. Annual distribution of occupied nest-sites.

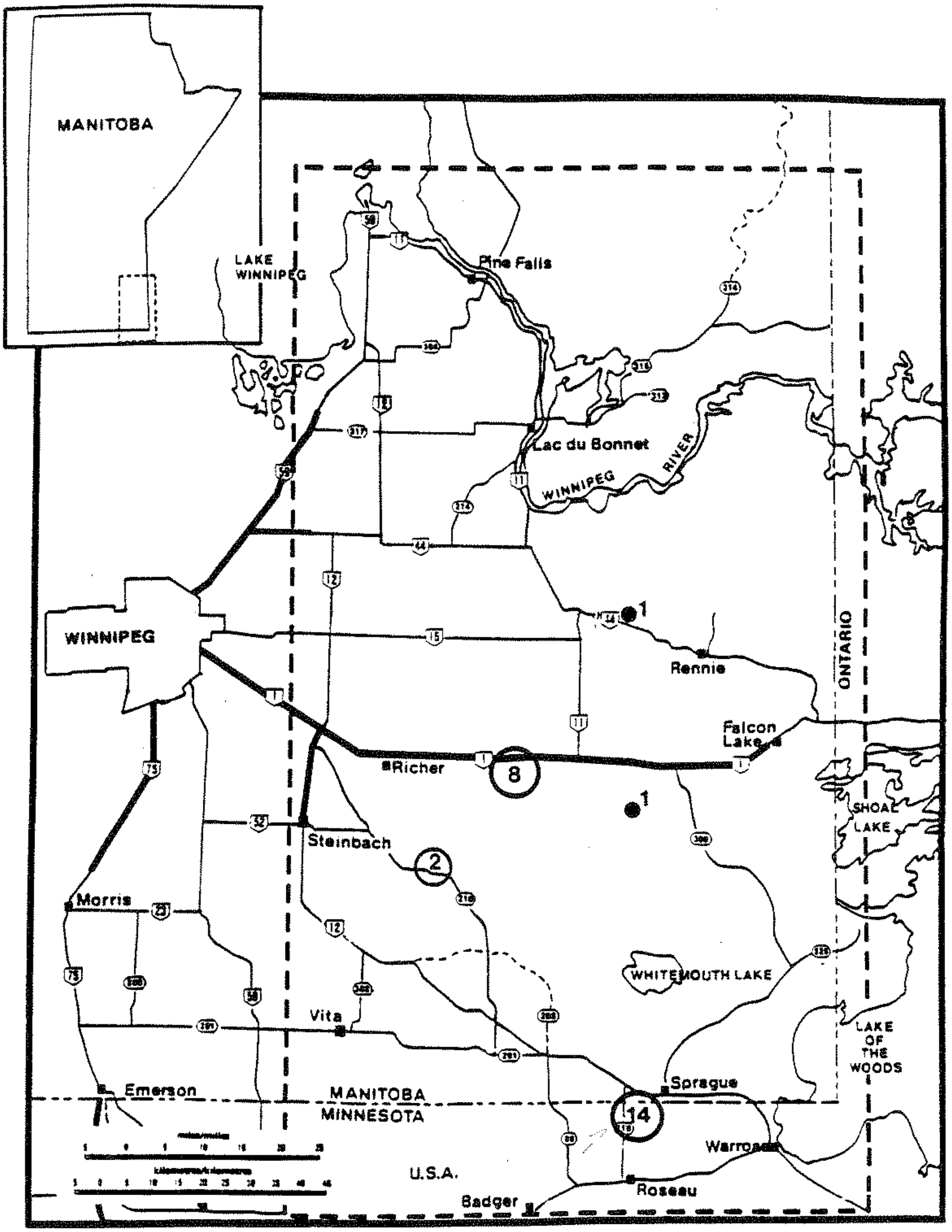
1986[1]



1986

Appendix B. Annual distribution of occupied nest-sites.

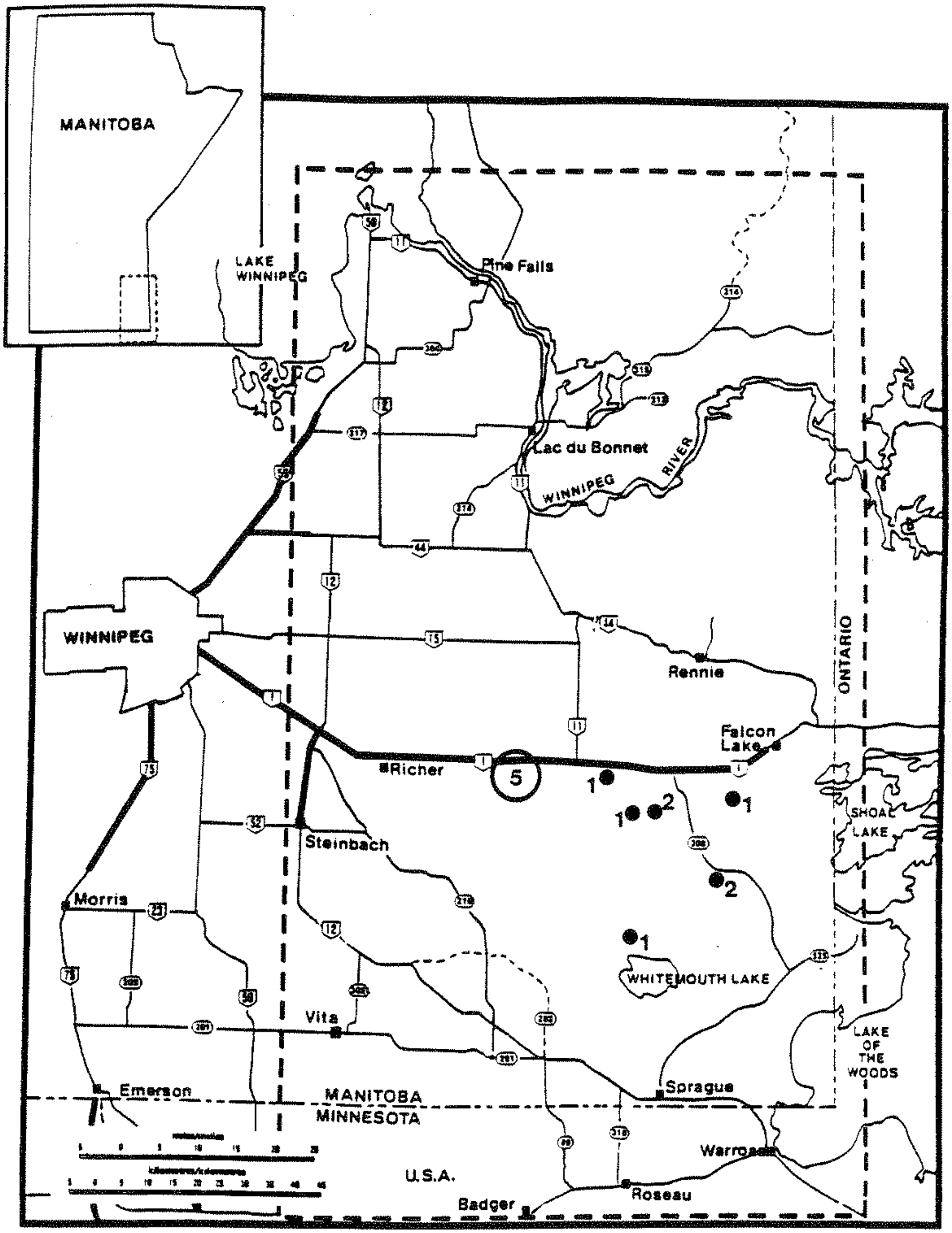
1987



1987

Appendix B. Annual distribution of occupied nest-sites.

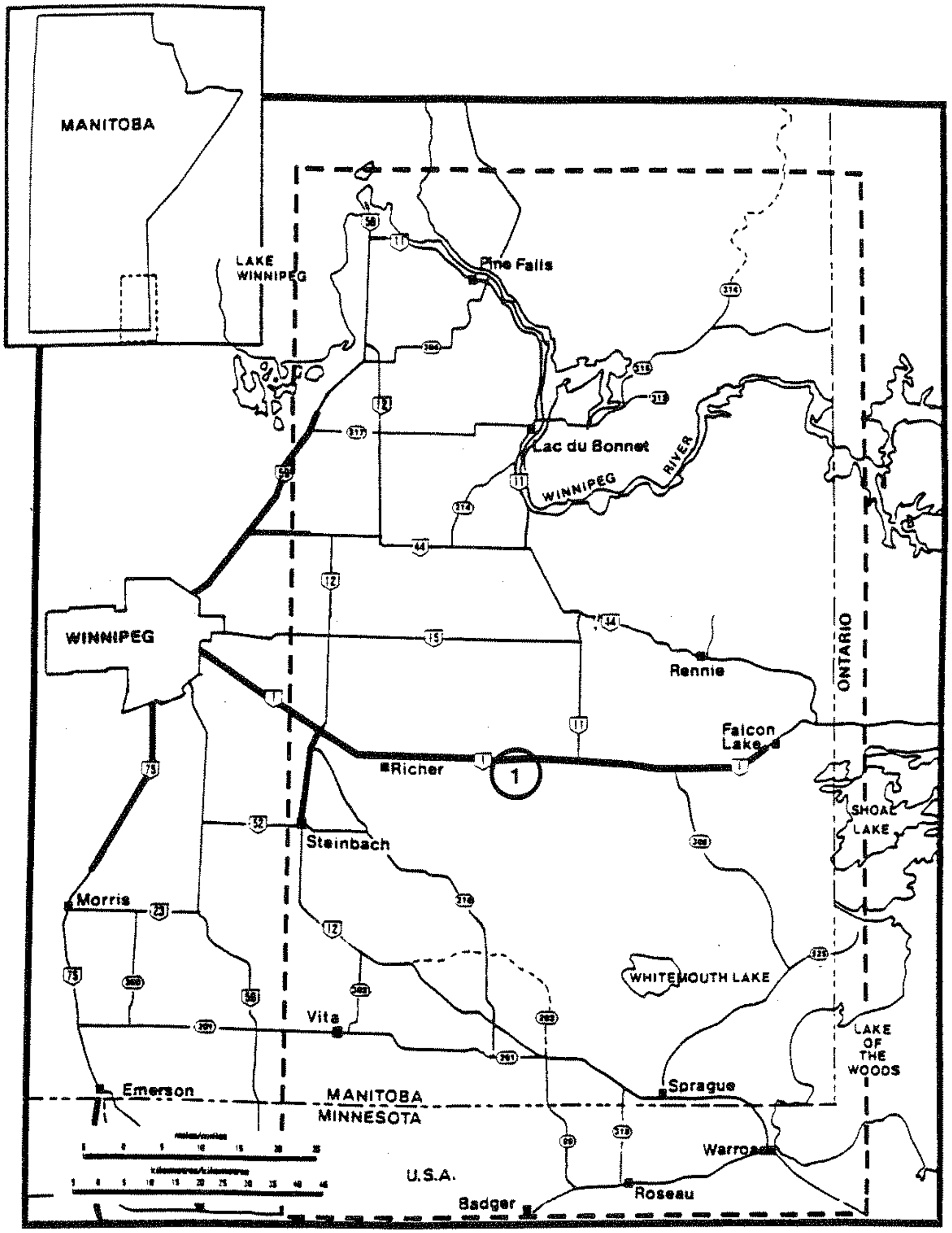
1988



1988

Appendix B. Annual distribution of occupied nest-sites.

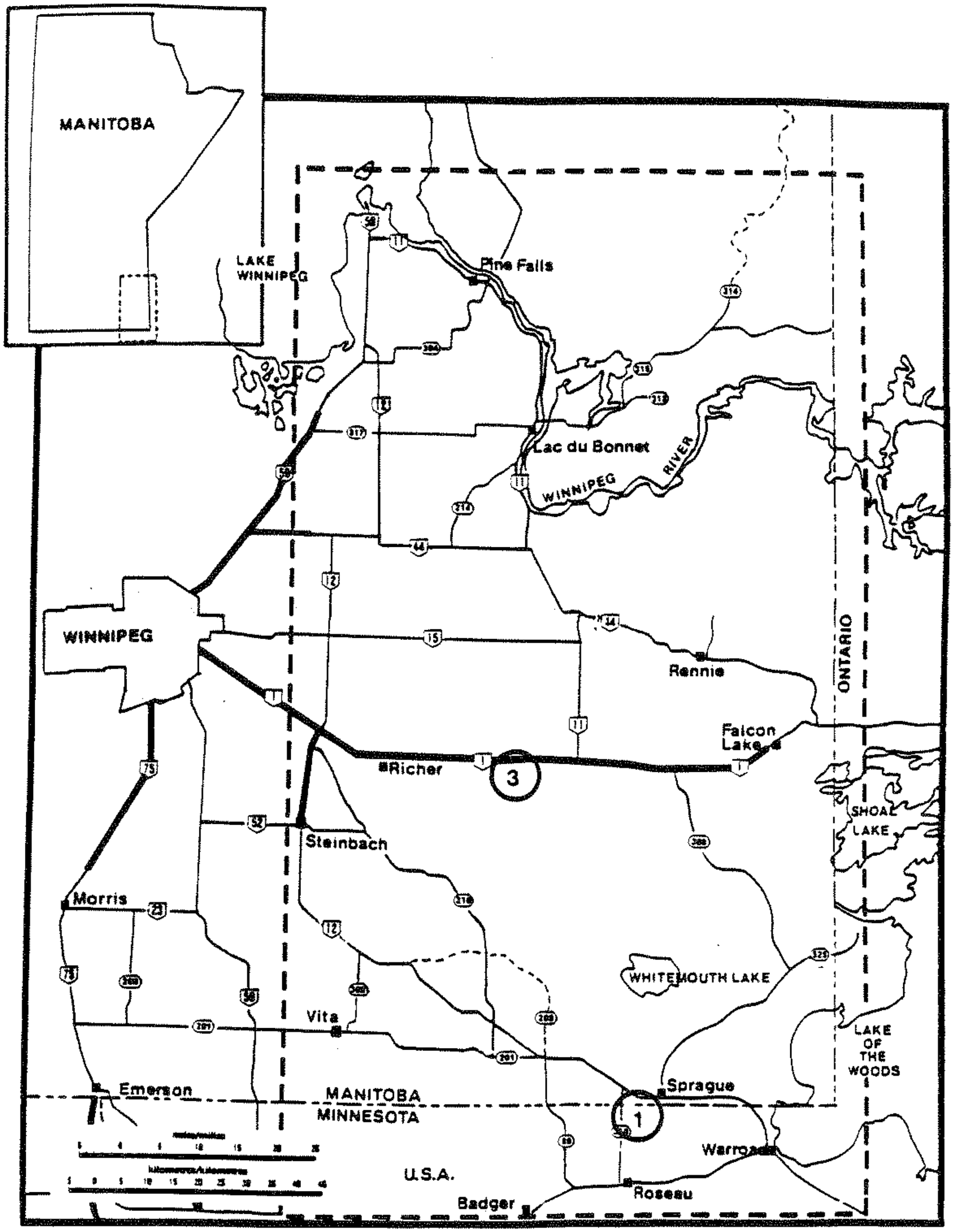
1989



1989

Appendix B. Annual distribution of occupied nest-sites.

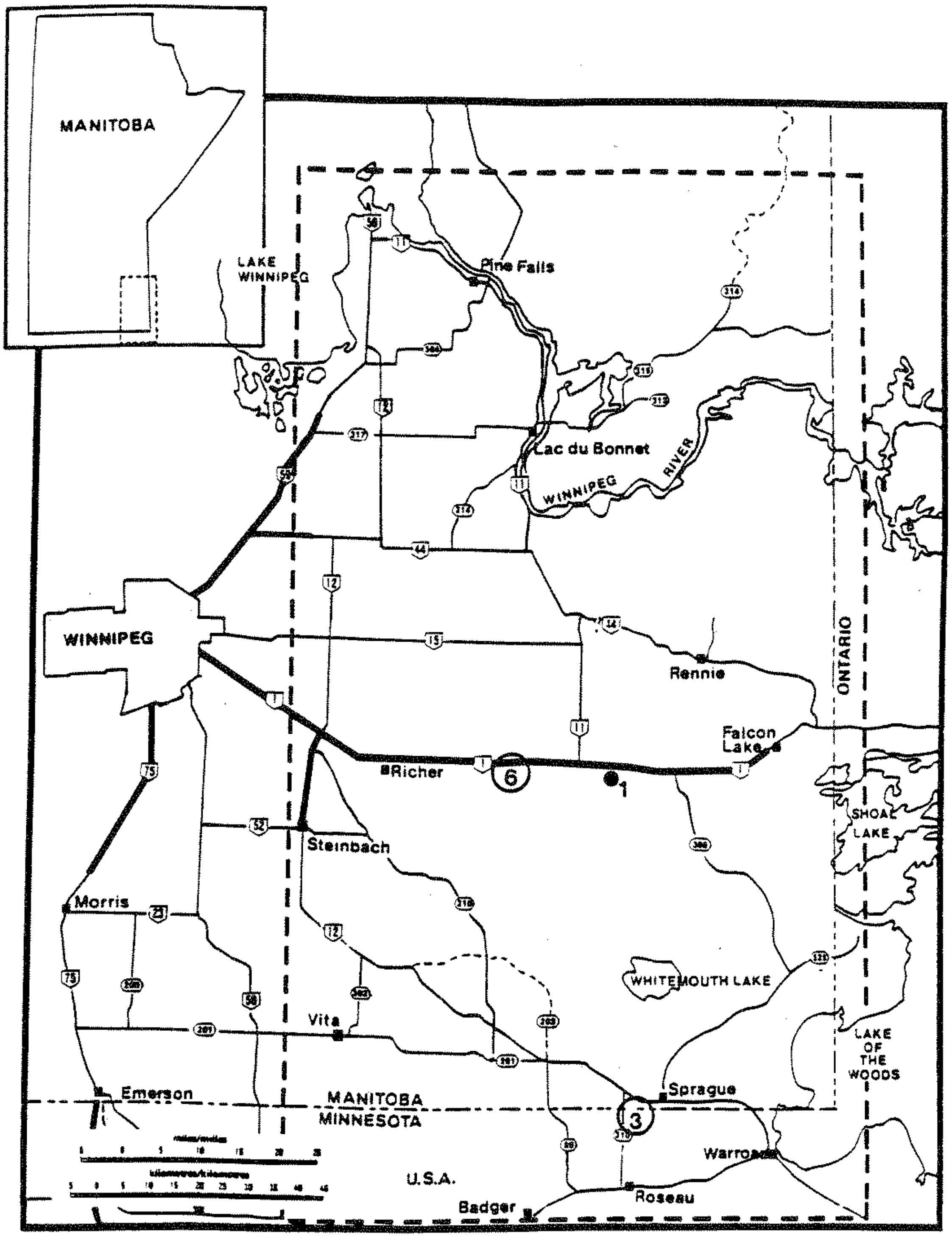
1990



1990

Appendix B. Annual distribution of occupied nest-sites.

1991



1991

Appendix C. Chi-Square analysis of nest-site use versus availability.

Year		Area[1] RB	SS	O	Total
1984	Observed	4	8	7	19
	Expected	2.85	3.23	12.9	
	Chi Square	0.46	7.04	2.71	
1985	Observed	0	0	0	0
	Expected	0	0	0	
	Chi Square	0	0	0	
1986	Observed	4	0	0	4
	Expected	0.6	0.68	2.72	
	Chi Square	19.2	0.68	2.72	
1987	Observed	15	6	5	26
	Expected	3.9	4.42	17.6	
	Chi Square	31.5	0.56	9.09	
1988	Observed	0	7	6	13
	Expected	1.95	2.21	8.84	
	Chi Square	1.95	10.3	0.91	
1989	Observed	0	1	0	1
	Expected	0.15	0.17	0.68	
	Chi Square	0.15	4.05	0.68	
1990	Observed	1	2	1	4
	Expected	0.6	0.68	2.72	
	Chi Square	0.27	2.56	1.09	
1991	Observed	3	6	1	10
	Expected	1.5	1.7	6.8	
	Chi Square	1.5	10.8	4.95	
Proportion of nest-sites available		0.15	0.17	0.68	
Total Observed		27	30	20	77

Total Chi Square = 112.49, df=12, p<0.001

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[1] Roseau Bog (RB), Spruce Siding (SS) and other (O) areas defined in methods.

Appendix D. Pianka's index[1] and percent similarity calculations for great gray owl diet[2].

	RB	SS	O	RB&SS	RB&O	SS&O	RB	SS	O
Prey Species	p	p	p	p*p	p*p	p*p	p^2	p^2	p^2
Condylura cristata	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Microtus pennsylvanicus	0.84	0.79	0.89	0.66	0.74	0.70	0.71	0.62	0.78
Synaptomys borealis	0.07	0.10	0.06	0.01	0.00	0.01	0.00	0.01	0.00
Clethrionomys gapperi	0.04	0.03	0.02	0.00	0.00	0.00	0.00	0.00	0.00
Peromyscus maniculatus	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Phenacomys intermedius	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Tamiasciurus hudsonicus	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Eutamias minimus	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Sorex cinereus	0.01	0.02	0.01	0.00	0.00	0.00	0.00	0.00	0.00
Blarina brevicauda	0.01	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.00
Sorex arcticus	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Microsorex hoyi	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Mustela rixosa	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Mustela erminea	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Lepus americanus	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Accipiter striatus	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Buteo platypterus	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Perisoreus canadensis	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Turdus migratorius	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Dendragapus canadensis	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Anas spp.	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Sparrow-sized birds	0.01	0.02	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Rana sylvatica	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Totals				0.67	0.75	0.71	0.71	0.64	0.79

Combination	Pianka's Index (% diet overlap)	Percent Similarity
RB & SS	99.86	90.4
RB & O	99.96	94.5
SS & O	99.79	89.3

1 See methods and Krebs (1989).

2 Items identified from nest-sites at Roseau Bog (RB) Spruce Siding (SS) and other (O) locations in southeastern Manitoba and adjacent Minnesota (1986-90).

Appendix E. Morisita's index[1] calculations for great gray owl diet[2].

	Number								
Prey Species	RB	SS	O	RB*SS	RB*O	SS*O	RB*(RB-1)	SS*(SS-1)	O*(O-1)
Condylura cristata			1	0	0	0	0	0	0
Microtus pennsylvanicus	620	554	500	343480	310000	277000	383780	306362	249500
Synaptomys borealis	49	70	36	3430	1764	2520	2352	4830	1260
Clethrionomys gapperi	26	23	12	598	312	276	650	506	132
Peromyscus maniculatus	2	2		4	0	0	2	2	0
Phenacomys intermedius			1	0	0	0	0	0	0
Tamiasciurus hudsonicus	2	9		18	0	0	2	72	0
Eutamias minimus		3		0	0	0	0	6	0
Sorex cinereus	5	11	4	55	20	44	20	110	12
Blarina brevicauda	7	3	6	21	42	18	42	6	30
Sorex arcticus	6	2	1	12	6	2	30	2	0
Microsorex hoyi	1	1	2	1	2	2	0	0	2
Mustela rixosa	1	1		1	0	0	0	0	0
Mustela erminea	2			0	0	0	2	0	0
Lepus americanus		3	2	0	0	6	0	6	2
Accipiter striatus		2		0	0	0	0	2	0
Buteo platypterus	1	1		1	0	0	0	0	0
Perisoreus canadensis	2	4		8	0	0	2	12	0
Turdus migratorius	2			0	0	0	2	0	0
Dendragapus canadensis	1			0	0	0	0	0	0
Anas spp.	1			0	0	0	0	0	0
Sparrow-sized birds	9	12		108	0	0	72	132	0
Rana sylvatica	1			0	0	0	0	0	0
Totals	738	701	565	347737	312146	279868	386956	312048	250938
A = Total * Total				517338	416970	396065			
B = Total(Total-1)							543906	490700	318660
C = Total X*(X-1)/Total X(Total X-1)							0.711	0.636	0.787

Combination	Morisita's Index[1]	Pianka's Index[3]	Percent Similarity[3]
RB & SS	0.998	99.86	90.4
RB & O	0.999	99.96	94.5
SS & O	0.993	99.79	89.3

[1] See Methods and Krebs (1989).

[2] Prey items identified from nest-sites at Roseau Bog (RB), Spruce Siding (SS) and other (O) locations in southeastern Manitoba and adjacent Minnesota (1986-90).

[3] Calculations presented in Appendix D.

Appendix F. Summer versus winter diet[1] of great gray owls in Alaska (Osborne 1987).

	Winter	Summer	W*S	W*(W-1)	S*(S-1)	W+S	%
Mammals							
Microtus xanthognathus	196	75	14700	38220	5550	271	65.9
Microtus pennsylvanicus	22	52	1144	462	2652	74	18.0
Microtus oeconomous	4	2	8	12	2	6	1.5
Microtus spp.		4	0	0	12	4	1.0
All *Microtus*	222	133				355	86.4
Clethrionomys rutilus	23	8	184	506	56	31	7.5
Synaptomys borealis	4	3	12	12	6	7	1.7
Other Microtinae	27	11				38	9.2
Sorex spp.	1		0	0	0	1	0.2
Mustela erminea	1		0	0	0	1	0.2
Lepus americanus		1	0	0	0	1	0.2
Other Mammals	2	1				3	0.7
Birds							
Grouse	2	1	2	2	0	3	0.7
Perisoreus canadensis		1	0	0	0	1	0.2
Passerine bird		1	0	0	0	1	0.2
Unidentified feathers	2	8	16	2	56	10	2.4
All Birds	4	11				15	3.6
Totals	255	156		39216	8334	411	
A = Total W*S			16066				
B = Total W * Total S			39780				
C = Total W*(W-1)/Total W(Total W-1)				0.606			
D = Total S*(S-1)/Total S(Total S-1)					0.345		

Morisita's Index = 2(A)/[(C+D)*B] = 0.85
% Similarity Index = 66.2
% Similarity Index of Major Groups = 94.6

[1] Data presented is the number of prey items.

Appendix G. Summer versus winter diet[1] of great gray owls in boreal forest regions of Canada.

Prey Species	Summer	Winter	W*S	S*(S-1)	W*(W-1)	W+S	%
Microtus pennsylvanicus	1674	151	252774	2800602	22650	1825	82.42
Synaptomys borealis	155	7	1085	23870	42	162	7.317
Clethrionomys gapperi	61	15	915	3660	210	76	3.432
Peromyscus maniculatus	4		0	12	0	4	0.180
Phenacomys intermedius	1	2	2	0	2	3	0.135
Condylura cristata	1		0	0	0	1	0.045
Sorex cinereus	20	17	340	380	272	37	1.671
Blarina brevicauda	16	3	48	240	6	19	0.858
Sorex arcticus	9	1	9	72	0	10	0.451
Microsorex hoyi	4		0	12	0	4	0.180
Tamiasciurus hudsonicus	11	2	22	110	2	13	0.587
Eutamias minimus	3		0	6	0	3	0.135
Mustela rixosa	2		0	2	0	2	0.090
Mustela erminea	2	1	2	2	0	3	0.135
Lepus americanus	5	6	30	20	30	11	0.496
(juveniles)			0	0	0	0	0
Sylvilagus floridans		1	0	0	0	1	0.045
Rattus norvegicus		1	0	0	0	1	0.045
Accipiter striatus	2		0	2	0	2	0.090
Buteo platypterus	2		0	2	0	2	0.090
Otus asio		1	0	0	0	1	0.045
Perisoreus canadensis	6		0	30	0	6	0.271
Turdus migratorius	2		0	2	0	2	0.090
Dendragapus canadensis	1		0	0	0	1	0.045
Bonasa umbellus		1	0	0	0	1	0.045
Anas spp.	1		0	0	0	1	0.045
Plectrophenax nivalis		1	0	0	0	1	0.045
Sparrow-sized birds	21		0	420	0	21	0.948
Rana sylvatica	1		0	0	0	1	0.045
Totals	2004	210		2829444	23214	2214	
A = Total W*S			255227				
B = Total W * Total S			420840				
C = Total S*(S-1)/Total S(Total S-1)				0.705			
D = Total W*(W-1)/Total W(Total W-1)					0.529		

Morisita's Index (Krebs 1989) = 2(A)/[(C+D)*B] = 0.98

% Similarity Index (Krebs 1989) = 81.2

% Similarity Index of Major Groups = 87.7

[1] Data presented are the number of prey items.
Data from Smith (1968), Nero (1969), and this study.

Appendix H. Summer versus winter diet of great gray owls in Fennoscandia (Mikkola 1983).

Prey Species	Summer	Winter	S*W	S*(S-1)	W*(W-1)
Microtus agrestis	3425	156	534300	11727200	24180
Microtus arvalis	7	13	91	42	156
Microtus oeconomous	366		0	133590	0
Microtus spp.	6		0	30	0
All *Microtus*	3804	169			
Arvicola terrestris	86	2	172	7310	2
Myopus schisticolor	95		0	8930	0
Clethrionomys glareolus	533	9	4797	283556	72
Clethrionomys rufocanus	152		0	22952	0
Clethrionomys spp.	167		0	27722	0
Other Microtinae	1033	11			
Talpa europaea	1		0	0	0
Sorex minutus	26	11	286	650	110
Sorex araneus	145	9	1305	20880	72
Sorex isodon	2	2	4	2	2
Sorex caecutiens	9		0	72	0
Sorex minutissimus	2		0	2	0
Sorex spp.	38		0	1406	0
Neomys fodiens	10		0	90	0
Ondatra zibethicus	1		0	0	0
Sciurus vulgaris	4	1	4	12	0
Micromys minutus	15	1	15	210	0
Apodemus flavicollis		1	0	0	0
Mus musculus		1	0	0	0
Rattus norvegicus	1		0	0	0
Mustela rixosa	4	1	4	12	0
Other Mammals	258	27			
			0	0	0
Aves	53		0	2756	0
Amphibia (*Rana* spp.)	26		0	650	0
Invertebrates (Coleoptera & Gastropoda)	3		0	6	0
Totals	5177	207		12238080	24594
A = Total W*S			540978		
B = Total W * Total S			1071639		
C = Total W*(W-1)/Total W(Total W-1)					0.577
D = Total S*(S-1)/Total S(Total S-1)				0.457	

Morisita's Index = 2(A)/[(C+D)*B] = 0.98
% Similarity Index = 75.4
% Similarity Index of major groups = 83.8

Appendix I. Small mammal census data.

A. Roseau Bog

Year	Season	RBV*	MV*	S*	Other*	Total	Index[1]
1986	Spring	16	58	5	4	83	9.22%
1986	Fall	188	79	108	8	383	42.56%
1987	Spring	34	18	8	9	69	7.67%
1987	Fall	48	28	5	4	85	9.44%
1988	Spring	19	0	1	1	21	2.33%
1988	Fall	118	1	23	6	148	16.44%
1989	Spring	10	0	8	5	23	2.56%
1989	Fall	151	12	15	5	183	20.33%
1990	Spring	34	2	3	1	40	4.44%
1990	Fall	171	21	32	5	229	25.44%
Total		789	219	208	48	1264	

B. Spruce Siding

Year		RBV	MV	S	Other	Total	Index[1]
1986	Spring	0	0	6	1	7	0.78%
1986	Fall	142	25	49	1	217	24.11%
1987	Spring	8	11	0	0	19	2.11%
1987	Fall	89	23	3	8	123	13.67%
1988	Spring	0	7	13	0	20	2.22%
1988	Fall	39	43	20	0	102	11.33%
1989	Spring	2	1	2	0	5	0.56%
1989	Fall	11	26	8	0	45	5.00%
1990	Spring	0	2	8	0	10	1.11%
1990	Fall	26	36	17	0	79	8.78%
Total		317	174	126	10	627	

C. Combined Data from Both Areas

Year		RBV*	MV*	S*	Other*	Total	Index[1]
1986	Spring	16	58	11	5	90	5.00%
1986	Fall	330	104	157	9	600	33.33%
1987	Spring	42	29	8	9	88	4.89%
1987	Fall	137	51	6	12	206	11.44%
1988	Spring	19	7	14	1	41	2.28%
1988	Fall	157	44	43	6	250	13.89%
1989	Spring	12	1	10	5	28	1.56%
1989	Fall	162	38	23	5	228	12.67%
1990	Spring	34	4	11	1	50	2.78%
1990	Fall	197	57	49	5	308	17.11%
Total		1106	393	332	58	1889	

* RBV = *Clethrionomys gapperi*
MV = *Microtus pennsylvanicus & Synaptomys borealis*
S = *Sorex cinereus, Sorex hoyi, Sorex arcticus & Blarina brevicauda*
Other = *Peromyscus maniculatus & Napaeozapus insignis*

[1] Index = (Total # Caught/1800 trap nights) x 100

Appendix J. Dispersal distance and direction of radio-marked great gray owls*

ID	Distance[1]	Azimuth[2]	A	B	C	Sex
15	416	356	6.213	-0.06	0.997	female
279	360	2	0.034	0.034	0.999	female
103	684	26	0.453	0.438	0.898	female
255	521	41	0.715	0.656	0.754	female
643	494	35	0.610	0.573	0.819	female
602	488	8	0.139	0.139	0.990	female
672	544	4	0.069	0.069	0.997	female
759	548	8	0.139	0.139	0.990	female
480	330	32	0.558	0.529	0.848	female
621	448	10	0.174	0.173	0.984	female
702	58	21	0.366	0.358	0.933	female
702	472	343	5.986	-0.29	0.956	female
712	42	0	0	0	1	female
612	405	347	6.056	-0.22	0.974	female
640	69	28	0.488	0.469	0.882	female
632	67	6	0.104	0.104	0.994	female
295	398	1	0.017	0.017	0.999	male
842	325	34	0.593	0.559	0.829	male
347	141	8	0.139	0.139	0.990	male
44	172	53	0.925	0.798	0.601	male
209	41	263	4.590	-0.99	-0.12	male
435	0					male
848	230	349	6.091	-0.19	0.981	male
581	53	21	0.366	0.358	0.933	male
830	291	10	0.174	0.173	0.984	male
682	448	10	0.174	0.173	0.984	male
970	480	350	6.108	-0.17	0.984	male

* Adults dispersing from breeding home ranges in southeastern Manitoba following prey population crashes.

1 Distance (km) between an owl's successive summer home range.

2 Azimuth from an owl's former summer home range to its subsequent home range.

A Azimuth converted to Radians (Azimuth*PI/180).
B sine of degrees in radians.
C cosine of degrees in radians.

Summary statistics for owl breeding dispersal data.

	Distance	
	Female	Male
Avg.	372	235
Std. Dev.	204	168
Maximum	684	480
Minimum	42	0
n	16	10

Mean Direction Vector Data		
	Female	Male
sample size n	16	10
mean x	0.939	0.817
mean y	0.226	0.086
y/x	0.241	0.106
ATan(y/x)	0.237	0.105
mean angle	14 °	6 °
mean r	0.966	0.822
mean angular dev. (s)	15 °	41 °

Appendix K. Dispersal dates of radio-marked great gray owls*

Month	Degree	Radians	A	B	C	D	A*C	A*D	B*C	B*D
Jul	15	0.26	1	4	0.26	0.97	0.26	0.97	1.04	3.86
Aug	45	0.79		1	0.71	0.71	0.00	0.00	0.71	0.71
Sep	75	1.31	2	1	0.97	0.26	1.93	0.52	0.97	0.26
Oct	105	1.83	2	7	0.97	-0.26	1.93	-0.52	6.76	-1.81
Nov	135	2.36		5	0.71	-0.71	0.00	0.00	3.54	-3.54
Dec	165	2.88		1	0.26	-0.97	0.00	0.00	0.26	-0.97
Jan	195	3.40	5	1	-0.26	-0.97	-1.29	-4.83	-0.26	-0.97
Feb	225	3.93	2		-0.71	-0.71	-1.41	-1.41	0.00	0.00
Mar	255	4.45	2		-0.97	-0.26	-1.93	-0.52	0.00	0.00
Apr	285	4.97	1		-0.97	0.26	-0.97	0.26	0.00	0.00
May	315	5.50			-0.71	0.71	0.00	0.00	0.00	0.00
Jun	345	6.02			-0.26	0.97	0.00	0.00	0.00	0.00
		n =	15	20		Total	-1.48	-5.54	13.01	-2.45
						Total/n	-0.10	-0.37	0.65	-0.12

* Adults dispersing from breeding home ranges in southeastern Manitoba following prey population crashes.

A Male frequency
B Female frequency
C Sine of midpoint of month's arc
D Cosine of midpoint of month's arc

Mean Vector Data

	Female	Male
mean x	-0.122	-0.369
mean y	0.650	-0.099
mean r	0.662	0.382
y/x	-5.309	0.268
ATan(y/x)	-1.385	0.262
mean angle	101 °	195 °
corrected mean r	0.669	0.387
mean angular deviation	47 °	64 °

Appendix L. Holarctic great gray owl diet[1] comparison.

Prey Group	Study & Location												
	A	B	C	D	E	F	G	H	I	J	K	L	M
Soricidae	49	14	1	2	255	1	2	9		6	100	10	2
Talpidae	1		1		1		1	3			1	15	12
Leporidae	5		1			1		5				1	
Sciuridae	14				5			1	3	3	41	5	1
Geomyidae								1	23	252	1309	377	122
Cricetinae	4				1		1	6	1	13	43	25	1
Microtinae	1891	31	482	101	5016	393	26	110	55	151	3014	217	143
Muridae					19								
Mustelidae	4		1		5	1							
Aves	35				53		1	1	1	10	4	3	
Other	1				29	15		3			34	9	12
Total	2004	45	486	103	5384	411	31	139	83	435	4546	662	293

[1] Number of prey items.

A This Study, southeastern Manitoba, Canada & adjacent Minnesota, USA
B Nero (1969), Manitoba, Canada
C Collins (1980), Manitoba, Canada
D Oeming (1955), Alberta, Canada
E Mikkola (1983), Fenno-Scandia
F Osborne (1987), Alaska, USA
G Smith (1968), North America
H Fisher (1893), North America
I Craighead & Craighead (1956), Wyoming, USA
J Franklin (1987), Idaho and Wyoming, USA
K Bull & Henjum (1990), Oregon, USA
L Winter (1986), California, USA
M Reid (1989), California, USA

Appendix L. (cont.) Holarctic great gray owl diet[1] comparison.

Percent total of prey groups identified in great gray owl diet studies in the Holarctic.

Prey Group	Location?						
	MB	AB	AL	FS	WY	OR	CA
Soricidae	2.52	1.94	0.24	4.74	1.16	2.20	1.26
Talpidae	0.08	0.00	0.00	0.02	0.00	0.02	2.83
Leporidae	0.24	0.00	0.24	0.00	0.00	0.00	0.10
Sciuridae	0.55	0.00	0.00	0.09	1.16	0.90	0.63
Geomyidae	0.00	0.00	0.00	0.00	53.09	28.79	52.25
Cricetinae	0.16	0.00	0.00	0.02	2.70	0.95	2.72
Microtinae	94.83	98.06	95.62	93.16	39.77	66.30	37.70
Muridae	0.00	0.00	0.00	0.35	0.00	0.00	0.00
Mustelidae	0.20	0.00	0.24	0.09	0.00	0.00	0.00
Aves	1.38	0.00	0.00	0.98	2.12	0.09	0.31
Other	0.04	0.00	3.65	0.54	0.00	0.75	2.20
Total	100	100	100	100	100	100	100
Sample size	2535	103	411	5384	518	4546	955

Matrix of percent similarity indices for the above data

	MB	AB	AL	FS	WY	OR
MB	1					
AB	96.8	1				
AL	95.6	95.9	1			
FS	96.9	95.1	94.0	1		
WY	43.0	40.9	40.0	42.0	1	
OR	69.4	68.2	67.3	69.3	71.7	1
CA	40.2	39.0	40.2	39.9	94.8	70.2

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[1] MB = southeastern Manitoba
AB = Alberta
AL = Alaska
FS = Fennoscandia
WY = Wyoming and Idaho
OR = Oregon
CA = California

Appendix M. Biophysics calculations to estimate the pressure force required to penetrate hard snow surfaces by snow-plunging great gray owls.

Given: Mass of owl, $M = 1600$ g
Contact area, $A = 50\ \text{cm}^2$
Snow hardness (Pressure required to break through),
$p = 3500\ \text{g/cm}^2$

Height from which owl "drops" $h = 7$m

v = velocity ms^{-1} at time of contact
g = acceleration due to gravity = $10\ \text{ms}^{-2}$

If the owl fell, then potential energy (PE) becomes kinetic energy (KE) because energy is conserved. Therefore PE = KE. Hence,

$$\begin{aligned} Mgh &= (1/2)Mv^2 \\ v &= [2(10\text{ms}^{-2})(7)]^{0.5} \\ &= 12\text{m/s or } 43\ \text{km/hr}\ ! \end{aligned}$$

Since the owl does not "drop", but slows down its descent, we estimate $v = 5$ m/s or 18 km/hr (estimated from photographs in Nero 1980, pg 89). This is the owl's speed when it hits the snow surface. Therefore, its momentum, p, equal:

$$p = Mv = (1.6\ \text{kg})(5\ \text{m/s}) = 8\ \text{kgm/s}$$

If the owls barely manages to break through, its final speed and momentum is zero. Therefore, its change in momentum is

$$p\ \text{final} - p\ \text{initial} = -8\ \text{kgm/s}$$

With a snow crust 1 cm thick ($d= 0.01$ m) and approximating that the owl's deacceleration is constant, the approximate time to go through the crust is $t = d/(v\ \text{average}) = (0.01\ \text{m})/\{(5\ \text{m/s} + 0\ \text{m/s})/2\} = 0.004$ s

The average force the owl exerts on the snow surface or crust is:

$$\begin{aligned} F &= (\text{change in p})/(\text{change in time}) = (8\ \text{kgm/s})/(0.004\text{s}) \\ &= 2{,}000\ \text{kgm/s}^2 \\ &= 2{,}000{,}000\ \text{gm/s}^2 \end{aligned}$$

To measure the "force" in grams, one must divide the force, F, by the acceleration due to gravity, $10\ \text{m/s}^2$.

Therefore, "F average" = 200,000 g

Therefore, the average pressure exerted by the owl when hitting the snow is:

$$P = F/A = 200{,}000\ \text{g}/50\ \text{cm}^2 = 4{,}000\ \text{g/cm}^2$$

Appendix M (cont.)

Estimated pressure exerted by a snow-plunging great gray owl with varying velocity at impact and weight. Assuming constant area of contact of 50 cm². Pressure value units are grams/cm².

Weight (g)	Velocity of Great Gray Owl at Impact (m/s)							
	3	4	5	6	7	8	9	10
700	1050	1400	1750	2100	2450	2800	3150	3500
800	1200	1600	2000	2400	2800	3200	3600	4000
900	1350	1800	2250	2700	3150	3600	4050	4500
1000	1500	2000	2500	3000	3500	4000	4500	5000
1100	1650	2200	2750	3300	3850	4400	4950	5500
1200	1800	2400	3000	3600	4200	4800	5400	6000
1300	1950	2600	3250	3900	4550	5200	5850	6500
1400	2100	2800	3500	4200	4900	5600	6300	7000
1500	2250	3000	3750	4500	5250	6000	6750	7500
1600	2400	3200	4000	4800	5600	6400	7200	8000
1700	2550	3400	4250	5100	5950	6800	7650	8500

Estimated pressure exerted by snow-plunging great gray owl with varying area of contact and weight. Assuming constant velocity of impact of 5 m/s. Pressure value units are grams/cm².

Weight (g)	Area of contact (cm²)				
	10	20	30	40	50
700	8750	4375	2917	2188	1750
800	10000	5000	3333	2500	2000
900	11250	5625	3750	2813	2250
1000	12500	6250	4167	3125	2500
1100	13750	6875	4583	3438	2750
1200	15000	7500	5000	3750	3000
1300	16250	8125	5417	4063	3250
1400	17500	8750	5833	4375	3500
1500	18750	9375	6250	4688	3750
1600	20000	10000	6667	5000	4000
1700	21250	10625	7083	5313	4250

Appendix N. Estimated winter great gray owl sex-ratio using discriminant function analysis.

N.1 Introduction: The Sample

Each winter great gray owls were captured and banded in the study area to monitor population changes (Nero et al. 1984). Great gray owls are more conspicuous during winter months, hunting in relatively open areas and for longer daytime periods (Nero 1980). Road networks throughout the study area were driven in search of owls most often when weather conditions were best suited to finding them: cold, calm and overcast with light snowfall (Nero 1980).

Inaccessible areas of suitable habitat within the study area could have harboured varying numbers of undetected owls. A simultaneous helicopter and road survey revealed that road surveys counted 91% of the total numbers of owls seen (Duncan 1991). Therefore, the numbers of winter-caught owls are likely suitable for year-to-year comparisons within the study area.

Another indication of yearly winter population changes in the study area is the number and locations of reported owl sightings by local residents; these represented over 840 different observers over a 23-year period (Nero et al. 1984, J.R. Duncan and P.A. Duncan, unpubl. data). The number of owls banded each year was significantly correlated with the number reported by observers (J.R. Duncan, unpubl. data).

N.2 Sex Determination with Discriminant Function Analysis

Great gray owls cannot be sexed using qualitative plumage characteristics. While they are among the most size-dimorphic of the owls (McGillivray 1987), males and females overlap in size so as to preclude accurate sexing using univariate external measurements. The benefit of a multivariate approach is that males and females are more distinct when the variables are viewed simultaneously.

Sex discriminant analysis determines two linear equations that best separate two known sex data sets in n-dimensional space, where n = the number of measurements used. Measurements from individuals of known sex, either breeding birds or internally sexed specimens, were used to develop the discriminant functions. Discriminant function analysis has been used frequently to sex morphologically indistinct bird species accurately, especially when individuals are reproductively inactive (Green and Theobald 1989, Johnstone and Niven 1989, Desrochers 1990, Brennan et al. 1991, Clark et al. 1991). Minimal sample size requirements, measurement error, geographic size variation and improper interpretation of results have limited the use of this powerful technique (Mueller 1990, Lougheed et al. 1991).

While measurement error was not evaluated in this study, Bortolotti (1984) found that for bald eagles (*Haliaeetus leucocephalus*), foot pad and feather measurements were the most repeatable, and hence reliable for predictive purposes. Weight was perhaps the least reliable measurement due to unknown stomach contents and large annual weight changes, especially for female great gray owls (J.R. Duncan, unpubl. data). Its inclusion is justified, however, because weight is the best indication of overall body size (Earhart and Johnson 1970). Furthermore, Edwards and Kochert (1986) concluded that the effect of partial or full crops on the accuracy of golden eagle (*Aquila chrysaetos*) sex classification was negligible.

The technique assumes multivariate normal data distributions within the classes as determined by the sample covariance matrices (Manly 1986). SAS (Statistical Analysis System, Box 8000, Cary, NC 27511) procedure DISCRIM was used to develop an objective classification of great gray owl sex using two different data sets. One data set (n=117 owls) included weight, wing chord and tail length for each owl of known sex measured. A second data set (n=37 owls) included the above variables plus foot pad.

The default prior probabilities for a two class discrimination analysis is 0.5 per class, i.e., an equal chance of an unknown being a male or a female. These are called the prior proportions and they can be altered before the analysis. The three-variable analysis was run with the default prior proportions (referred to as Equal in Tables and Figures) and also with two other prior proportions: the proportion of known sex owls used in the analysis (Proportional) and the proportion of known sex winter-killed owls in the study area (Specimen). Given that female and male great gray owls were equally catchable and assuming that females were caught in the same proportion as they were killed, then the analysis using Specimen prior proportions (2:1 female biased ratio) likely resulted in the most accurate sex ratio determination of unknown-sex winter-caught birds. However, the results of all three analyses are presented and compared below. The four-variable analysis was performed with Proportional probabilities only.

The influence of three post-analysis sex probability cut-off levels (the probability that an owl sexed by the discriminant function is the sex indicated) on sex ratio and percentage sexed was also examined.

N.3 Great Gray Owl Measurements

Owls were weighed with a 2 kg Chatillon model-4 spring scale to the nearest 25 g. Wing chord was the distance from the front of the folded wrist to the tip of the longest primary, with the feather unflattened, checking that it was not affected by moult (Pettingill 1970). Similarly, tail length was the distance from the feather-skin junction of the central pair of rectrices to their tips. Foot pad was the distance from the base of the talon of the hallux to that of the middle front toe, with the toes fully extended (Bortolotti 1984).

Measurements from live, nesting owls (only females incubate and develop brood patches), and from internally sexed dead specimens, were summarized separately. Student's t-tests were used to determine if within-sex mean values of these groups differed significantly (Ostle and Mensing 1975).

Mean measurement values, sample sizes, and other descriptive statistics are presented in Table N.1. Shapiro-Wilk W statistics and Rankit plots (Statistix 1991, version 3.5, analytical software, P.O. Box 130204, St. Paul, MN 55113) were examined for each measurement and sample combination, prior to subsequent analysis, to determine if measurement data were normally distributed (Table N.2). When data were not normally distributed, nonparametric statistical tests were used.

There were no significant differences between measurements of breeding and specimen males (Table N.3). Hence, these data were pooled for discriminant function analysis. The mean weight and mean wing chord of breeding females were significantly larger than those of specimen females (Table N.3). Therefore, these data were not pooled in subsequent analyses.

N.3.1 Comparisons with other studies

Statistical comparisons of great gray owl measurements between different studies were restricted to those few which reported measures of variance (Tables N.4, N.5, N.6). Measurement comparisons help characterize differences between subspecies, geographic variation and trends within species, and to determine if sex discrimination models (see section N.4) developed from local populations can be applied to measurements of birds from across the species' range.

N.3.1.1 *Weight*

The weights of great gray owls recorded in this study fall within 100 g of the ranges of those reported by others (Table N.4). Höglund and Lansgen (1968) reported the mean weights of male and female great gray owls from Sweden and Finland for three time periods: August to November, December to March, and April to June. There was a small, non-significant decrease in mean weight from the non-breeding season (either of the first two time periods) to the breeding season (April to June) for both males and females (Table N.4, t-tests, p>0.05). The mean weights of breeding males and breeding females from Manitoba (this study) were significantly larger (Table N.4, t-tests, p<0.005) than those of great gray owls from Sweden and Finland (Höglund and Lansgen 1968) weighed in the period from April to June. The mean weights of specimen great gray owls from Manitoba (this study) were significantly larger (Table N.4, t-tests, p<0.005) than those of great gray owls from Sweden and Finland (Höglund and Lansgren 1968) weighed in the periods from April to June (males and females), August to November (females only) and December to March (males only). This suggests that the North American subspecies *Strix nebulosa* is heavier than the Eurasian subspecies *S.n. lapponica*. Voous (1988) stated that the North American subspecies is 4% larger in body weight and wing length than the Eurasian, but provided no reference to this claim. However, statistically significant differences may not always equate to biologically significant differences. The maximum differences in mean weights reported from different studies are 190 g for males and 298 g for females (Table N4). These could be readily explained by the presence/absence of undigested prey items in the stomach in combination with small sample sizes reported. For example, the remains of up to 12 meadow voles, with an average weight of 45 g, have been identified from one great gray owl pellet! Furthermore, annual weight changes of up to 300 g have been recorded for individual wild male and female great gray owls (J.R. Duncan, unpubl. data).

N.3.1.2 *Wing Chord*

Comparisons of mean wing chord lengths between great gray owls measured from this study and others were not possible because of different methods used to record wing chords (unflattened versus flattened), as well as the lack of reported variance measures (Table N.5). Values are presented in Table N.5 for future comparisons and for dimorphism index calculations (Table N.7). There were no significant differences between the flattened wing chords of the two subspecies (Oeming 1955, Cramp 1985, Table N.5, t-tests, p>0.1).

N.3.1.3 *Tail Length*

Female great gray owls from northern Europe (Cramp 1985) had longer mean tail lengths than breeding and specimen females from Manitoba (Table N.6, t-test, p<0.025). The same relationship was true for males, but only with the specimen sample, and not the breeding sample (Table N.6, t-test, p<0.01 and p>0.05, respectively). A longer tail increases maneuverability (Rüppell 1975), but the biological importance of a maximum mean difference of 9.3 mm is likely minimal. Furthermore, another comparison (Oeming 1955, Cramp 1985) revealed that a significant reverse difference in tail length was found between the two subspecies (Table N.6, t-tests, $p<0.01$).

N.3.2 Reversed sexual size dimorphism

In most avian species the male is larger than the female. However, in the orders Falconiformes (falcons, hawks and eagles), Strigiformes (owls), and in the families Stercorariidae (jaegers) and Fregatidae (Man-o-war birds), the reverse is true (Amadon 1959). Mueller (1986) and Norberg (1987) provided excellent reviews of hypothetical selection pressures resulting in the peculiar "reversed" sexual size dimorphism exhibited by these groups. Norberg (1987) stated that reversed size dimorphism has arisen independently in some species of Charadriidae and Scolopacidae due to selective pressures involving reversed sexual roles in pair formation.

Male measurement values were significantly smaller than female values for specimens, breeding birds, and both samples combined (Table N.3). This was also true for all measurements from other studies (Tables N.4, N.5, N.6, t-tests, $p<0.025$) except for wing chord lengths reported by Cramp (1985) and Oeming (1955). The latter two deviations may be due to small sample size. Significant sexual size differences are not surprising given that great gray owls are among the most size-dimorphic owls (Earhart and Johnson 1970, Mikkola 1981, McGillivray 1987). Dimorphism indices for weight, wing chord and tail length measurements are comparable with values obtained by others (Table N.7).

N.3.3 Morphological differences between subspecies

Both Oeming (1955) and Mikkola (1981) concluded that the two subspecies were very similar in size. In light of similar ecological conditions within the species' range, i.e., diet and climate, the hypothesized recent arrival of the species in North America (Oeming 1955, Voous 1988), and current theory on species' stability (Eldredge and Gould 1972), the lack of subspecies size differences should not be surprising. Plumage differences do occur: the European subspecies is generally paler, more conspicuously streaked on the breast, and has a less prominent white loral crescent and supercilliary line (Oberholser 1922 *in* Voous 1988, Oeming 1955).

N.4 RESULTS

The discriminant functions that were developed are shown in Table N.8. Substituting the appropriate measurements from an individual owl of unknown-sex into a set of male and female equations yields two discriminant scores. The equation that yields the highest discriminant score denotes the sexual classification of the individual great gray owl in question. Therefore, if one subtracts the DS of the female equation from that of the male equation the result will be a positive value for a male and a negative value for a female. The magnitude of the discriminant score difference is related to the probability that the owl is correctly sexed (Fig. N.1).

While logistically circular, one can test the accuracy of discriminant functions using the same measurement sets from known sex birds that were used to develop the functions. All 21 known-sex males and all 16 known-sex females were correctly classified in the four-variable analysis (Fig. N.2). The inclusion of the foot pad measurement greatly improved the discrimination of males from females. Figure N.2 shows the separation of the sample of 109 unknown-sex winter-caught great gray owls. All but two of the 109 unknown-sex owls had a posterior (post-analysis) sex probability greater than 0.9 (Fig. N.3). However, foot pad measurement data were unavailable for most of the sample of winter-caught great gray owls.

The three-variable discriminant functions, using Equal and Proportional prior probabilities (see section N.2), misclassified three of 54 (5.6%) known sex males and five of 63 (7.9%) known sex females (Fig. N.4). Fewer females were misclassified (1.6%) when Specimen prior probabilities were used for the analysis. Consequently, the frequency distribution of posterior sex probabilities (Fig. N.5) of 453 unknown-sex winter-caught owls is not as cleanly separated as with the four variable function (Fig. N.3). The distribution of discriminant score differences for 453 unknown-sex winter-caught great gray owls appears to be bimodal with considerable overlap (Fig. N.4). In order to estimate a sex ratio for this sample of unknown-sex birds, it was necessary to decide on a posterior sex probability cut-off to minimize the inclusion of misclassified owls. Three probability levels; $p \geq 0.9$, $p \geq 0.8$ and $p \geq 0.7$, were chosen. These related to different magnitudes of DS differences (Fig. N.1). Figure N.6 shows that as the probability cut-off level increases from $p \geq 0.7$ to $p \geq 0.9$, fewer unknown-sex owls are included in the sex ratio estimate.

N.4.1 Winter Sex Ratio

With the four-variable discriminant analysis, 41 great gray owls were classified as male and 68 as female (Table N.9). This yielded a significant female biased sex ratio (1.5:1, one-tailed Binomial, $p=0.0062$). The influence of posterior sex probability cut-off levels on the estimated sex ratio of winter-caught great gray owls sexed with the three-variable function can be seen in Figure N.7. As the probability cut-off level increases from $p \geq 0.7$ to $p \geq 0.8$, the ratio increases, as relatively more males are excluded from the estimate. From $p \geq 0.8$ to $p \geq 0.9$ the estimated sex ratio then drops slightly as relatively more females are subsequently excluded (Fig. N.7). The reason for the overall exclusion of relatively more males than females as probability cut-off levels increase is found in Figure N.1. The point of inflection of the probability versus DS differences curve is skewed towards females (Fig. N.1).

The most conservative sex ratio estimated by the three-variable discriminant functions was with Equal prior probabilities and with a posterior sex probability of $p \geq 0.07$ (Fig. N.7). This was significantly female-biased (2.4:1, one-tailed Binomial, $p=0.0004$), as were all other estimates (data in Table N.9).

N.4.2 Annual Sex Ratio Fluctuations

Female to male sex ratios as calculated above represent an average based on varying numbers of great gray owls captured over a 14-year period. In fact, the estimated sex ratio varied dramatically from year to year (Fig. N.8) and was not correlated to the number of owls caught per year (Pearson correlations, two-tailed t-test, $p>0.6$, Table N.10). Significant deviation from a 1:1 sex ratio occurred in six of 14 years (Table N.10, Fig. N.8). However, whenever the ratio deviated significantly from 1:1, it was always female biased.

N.4.3 Age-Sex Interactions

Because this study dealt only with the breeding dispersal of adult radio-marked great gray owls, it was necessary to determine if significant age-sex interactions were present in the winter-caught great gray owl sex-ratio data. If a great gray owl was at least one year old, as determined by moult (Cramp 1985), it was considered an adult. Immatures were those less than one year old. The annual age-sex data are presented in Table N.11 and Figure N.9.

For the data combined, over a 14-year period, the null hypothesis of age-sex independence was rejected (Yates' Corrected Chi-Square 7.06, df=1, $p<0.01$, Table N.11). This may be the result of averaging because only two of 10 years (1984 and 1990) yielded barely significant age-sex interactions (Table N.11). All age-sex classes were significantly correlated with the total number caught per year (Spearman Rank Correlations, $p<0.05$, Table N.11) over the 14-year period. The numbers of adults of either sex were not correlated with the numbers of immatures of either sex (Spearman Rank Correlations, $p>0.05$, Table N.11). However, within each age class, the numbers of males correlated positively with that of females (Spearman Rank Correlations, $p<0.05$, Table N.11).

Because the sex and age of winter-caught owls were, for the most part, independent, it is of value to consider sex ratio of adults and immatures separately. While significantly more immature females than immature males were captured over the 14-year period, this was true for only one of 10 years when immatures were caught (Table N.12). Therefore, it would seem that the sex ratio among winter-caught immatures approached unity. Conversely, the adult sex ratio was significantly female-biased for eight of 14 years (62% of years versus 43% of years when immatures were pooled with adults, Table N.10) and for the combined total period (Table N.13). Furthermore, fluctuations of age-class sex ratios over the 14-year period were not correlated (Spearman Rank Correlations, $p>0.05$, Tables N.12, N.13).

TABLE N.1. Descriptive statistics for measurement data from known sex great gray owls.

	Male - Breeding			
	Weight	Wing Chord	Tail Length	Foot Pad
n	21	23	23	9
Mean	890.5	404.5	289.5	63.3
S.D.	53.31	13.33	9.89	1.41
S.E.	11.63	2.78	2.06	0.47
CV	5.99	3.30	3.42	2.23
Min.	825	380	270	60
Median	875	405	291	64
Max.	1050	430	305	65

	Male - Specimen			
	Weight	Wing Chord	Tail Length	Foot Pad
n	35	35	33	12
Mean	880.6	401.5	285.7	64.0
S.D.	156.9	10.22	9.68	1.65
S.E.	26.52	1.727	1.69	0.48
CV	17.82	2.55	3.39	2.58
Min.	500	370	270	61
Median	900	400	285	64.5
Max.	1175	425	315	66

	Female - Breeding			
	Weight	Wing Chord	Tail Length	Foot Pad
n	63	70	70	16
Mean	1267	424.7	298	70.8
S.D.	148.7	10.54	10.1	1.6
S.E.	18.73	1.26	1.21	0.4
CV	11.73	2.48	3.39	2.26
Min.	1025	397	270	67
Median	1250	423	298	71
Max.	1700	455	320	73

	Female - Specimen			
	Weight	Wing Chord	Tail Length	Foot Pad
n	69	70	67	22
Mean	1172	419.6	298.2	71.6
S.D.	208.7	12.58	10.73	1.77
S.E.	25.12	1.5	1.31	0.38
CV	17.81	3	3.6	2.47
Min.	600	390	273	68
Median	1200	420	300	72
Max.	1650	450	320	75

TABLE N.2. Shapiro-Wilk W statistic values and sample sizes (n) for measurement data[1] from known sex great gray owls.

Source/Sex	Measurement			
Breeding	Weight	Wing Chord	Tail Length	Foot Pad
Female	0.93* (63)	0.97 (70)	0.98 (70)	0.87* (16)
Male	0.86* (21)	0.97 (23)	0.94 (23)	0.76* (9)
Specimens				
Female	0.98 (69)	0.98 (70)	0.97 (67)	0.94 (22)
Male	0.97 (35)	0.94 (35)	0.95 (33)	0.92 (12)
Combined				
Female	0.97 (132)	0.99 (140)	0.98 (137)	0.93 (38)
Male	0.96 (56)	0.98 (58)	0.98 (56)	0.93 (21)

1 See methods for measurement description.

* Data distribution not normal, $P<0.05$, after significance tables in Shapiro & Wilk (1965), for $n<50$, and in Shapiro & Francia (1972), for $n>50$.

TABLE N.3. Statistical analysis of sexual and sample measurement differences from known sex great gray owls.

Comparison[1]	Weight	Wing Chord	Tail Length	Foot Pad
Breeding versus specimen: males[2]	U test P=0.69	t=0.97 P=0.34	t=1.43 P=0.16	U test P=0.29
Breeding versus specimen: females[2]	U test P=0.02	t=2.58 P=0.01	t=0.12 P=.91	U test P=0.19
Male versus female: specimens[3]	t=7.96 P<0.01	t=7.38 P<0.01	t=5.65 P<0.01	t=12.17 P<0.01
Male versus female: breeders[3]	U test P<0.01	t=7.45 P<0.01	t=3.52 P<0.01	U test P<0.01
Male versus female: combined samples[3]	t=14.09 P<0.01	t=10.6 P<0.01	t=6.68 P<0.01	t=16.66 P<0.01

1. Mann-Whitney U test (Daniel 1978) used when data distribution of at least one sample was not normal. Otherwise, the two sample t-test (Ostle & Mensing 1975) was used.

2. Two-tailed test.

3. One-tailed test.

TABLE N.4. Comparison of great gray owl weights (g) from North American and Eurasian studies.

	Male				Female			
Source	Range	Mean	n	s.d.	Range	Mean	n	s.d.
A: North America*								
This Study:								
Breeding Birds	825-1050	890.5	21	53.3	1025-1700	1267	63	148.7
Specimens	500-1175	880.6	35	156.9	600-1650	1172	69	208.7
Oeming 1955		1026	1		1057-1337	1181.8	3	142.5
Craighead & Craighead 1969						1084	7	
Earhart & Johnson 1970	790-1030	935.3	7		1144-1454	1298	6	
Bull & Henjum 1990	763-1080	894	18		1030-1310	1149	30	
B: Eurasia*								
Höglund & Lansgren 1968:								
August-November	500-1050	846	13	138	700-1450	1125	16	183
December-March	568-1100	789	17	175	680-1900	1159	21	306
April-June	490-1095	778	16	183	700-1250	1005	11	217
Demente'ev et al. 1951	700-810	745	4	47.1	995-1200	1097.5	2	145
v. Hartman et al. 1967 in Mikkola 1983	650-1100	871	31		995-1900	1242	24	
Mikkola 1981	660-1100	884	30		977-1900	1186	44	

* North America: *Strix nebulosa nebulosa*
Eurasia: *Strix nebulosa lapponica*

TABLE N.5. Comparison of great gray owl wing chord (mm) from North American and Eurasian studies.

	Male				Female			
Source	Range	Mean	n	s.d.	Range	Mean	n	s.d.
A: North America*								
This Study[1]:								
Breeding Birds	380-430	404.5	23	13.3	397-455	424.7	70	10.5
Specimens	370-425	401.5	35	10.2	390-450	419.6	70	12.6
Oeming[2] 1955	441-432	436.5	2	6.4	437-465	446.4	5	11.7
Earhart & Johnson[1] 1970	387-429	404.4	7	17.2	408-438	423.1	14	9.8
Godfrey[1] 1986	396-438	416.3	10		417-462	433.4	10	
Ridgway[2] 1914 in Johnsgard 1988	410-447	433	5		430-465	446	7	
Bull & Henjum[2] 1990	410-455	433	18		430-485	463	30	
B: Eurasia[2]*								
Oeming[2] 1955	430-450	440	6	8.9	440-460	451.8	6	7.5
Mikkola 1981	432-477	449	17		443-483	463	24	
Cramp 1985	430-466	446	8	11.5	441-467	452	13	8.3
Dement'ev et al. 1951	405-436	432.5	21		438-480	464.8	57	

* North America: *Strix nebulosa nebulosa*
Eurasia: *Strix nebulosa lapponica*

1 Studies reporting unflattened wing chord

2 Studies reporting flattened wing chord

TABLE N.6. Comparison of great gray owl tail length (mm) from North American and Eurasian studies.

	Male				Female			
Source	Range	Mean	n	s.d.	Range	Mean	n	s.d.
A: North America*								
This Study:								
Breeding Birds	270-305	289.5	23	9.9	270-320	298	70	10.1
Specimens	270-315	285.7	33	9.7	273-320	298.2	67	10.7
Oeming 1955	304-320	312	2	11.3	330-340	333	5	4.5
Godfrey 1986	296-305	299.1	10					
Ridgway 1914 in Johnsgard 1988	330-323	313.6	5		310-347	323.3	7	
Bull & Henjum 1990	230-310	295	18		215-330	311	30	
B: Eurasia*								
Oeming 1955	310-320	316	5	5.5	320-340	328	5	8.4
Mikkola 1981	276-319	298	17		279-322	308	26	
Cramp 1985	285-303	295	8	6.3	287-323	305	13	9.8

* North America: *Strix nebulosa nebulosa*
Eurasia: *Strix nebulosa lapponica*

TABLE N.7. Comparison of great gray owl dimorphism indices[1] from North America and Eurasian studies.

Source	Measurement			
	Weight	Wing Chord	Tail Length	Foot Pad
A: North America*				
This Study:				
Breeding Birds	11.74	4.87	2.89	11.2
Specimens	9.52	4.41	4.28	11.2
Oeming 1955		2.24	6.51	
Earhart & Johnson 1970	10.92	4.52		
Godfrey 1986		4.02		
Ridgway 1914 in Johnsgard 1988		2.96	3.05	
Bull & Henjum 1990	8.34	6.7	5.28	
B: Eurasia*				
Dement'ev et al. 1951	12.89	7.2		
Oeming 1955		2.65	3.73	
v. Hartman et al. 1967	11.81			
Höglund & Lansgren 1968:				
August-November	9.49			
December-March	12.80			
April-June	8.53			
Mikkola 1981	9.79	3.07	3.3	
Cramp 1985			3.33	

1 Dimorphism Index = $\frac{100 \times (\text{size average female} - \text{size average male})}{1/2 \times (\text{size average female} + \text{size average male})}$

* North America: *Strix nebulosa nebulosa*
* Eurasia: *Strix nebulosa lapponica*

TABLE N.8. Great gray owl sex discriminant functions generated with SAS Procedure Discrim.

A. Three variable discriminant functions:
Weight (Wt), wing chord (WC) and tail length (TL)

Proportional[1] Prior Probability: 0.54 female & 0.46 male

Male	2.459*(WC) + 1.431*(TL) - 0.003*(Wt) - 699.366
Female	2.571*(WC) + 1.463*(TL) + 0.014*(Wt) - 774.014

Equal[2] Prior Probability: 0.5 female & 0.5 male

Male	2.459*(WC) + 1.431*(TL) - 0.003*(Wt) - 698.593
Female	2.571*(WC) + 1.463*(TL) + 0.014*(Wt) - 773.395

Specimen[3] Prior Probability: 0.67 female & 0.33 male

Male	2.459*(WC) + 1.431*(TL) - 0.003*(Wt) - 699.701
Female	2.571*(WC) + 1.463*(TL) + 0.014*(Wt) - 773.796

B. Four variable discriminant function:
Weight (Wt), wing chord (WC), tail length (TL) and foot pad (FP)

Proportional Prior[1] Probability: 0.43 female & 0.58 male

Male	1.357*(WC) + 1.825*(TL) - 0.021*(Wt) + 19.898*(FP) - 1156.058
Female	1.405*(WC) + 1.672*(TL) - 0.001*(Wt) + 22.736*(FP) - 1344.808

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[1] Prior sex probability same as known sex bird data set

[2] Prior sex probability equal

[3] Prior sex probability same as winter killed specimens

TABLE N.9. The total number of winter-caught great gray owls sexed, the number that were males, and the female to male (F:M) ratio using SAS procedure DISCRIM.

A. Three variable discriminant functions: weight, wing chord and tail length. (n=453 winter caught owls)

Probability Cut-off level		Prior Probability		
		Equal	Proportional	Specimen
p>0.9	# Sexed	348	350	352
	# Males	85	83	73
	F:M Ratio	3.1	3.2	3.8
p>0.8	# Sexed	367	369	368
	# Males	85	84	74
	F:M Ratio	3.3	3.4	4.0
p>0.7	# Sexed	415	412	399
	# Males	122	118	97
	F:M Ratio	2.4	2.5	3.1
p>0.0*	# Sexed	453	453	453
	# Males	147	144	127
	F:M Ratio	2.1	2.2	2.6

B. Four variable discriminant functions: weight, wing chord, tail length and foot pad.

p>0.7	# Sexed		107	
	# Males		40	
	F:M Ratio		1.5	
p>0.0*	# Sexed		109	
	# Males		41	
	F:M Ratio		1.6	

* No posterior sex probability cut-off. This likely included misclassified owls.

TABLE N.10. Annual fluctuations of female to male sex ratios for winter caught great gray owls estimated by SAS procedure DISCRIM[1].

		Prior Probability		
Year	# Caught	Equal	Proportional	Specimen
1977*	31	4.4	5.5	12.5
1978	88	1.3	1.3	1.6*
1979*	50	3.0	3.1	4.4
1980	24	1.6	1.6	1.8
1981	2	-	-	-
1982*	26	4.2	5.3	7.0
1983*	70	6.6	6.6	10.5
1984*	38	3.1	3.1	5.0
1985	8	0.8	0.8	0.8
1986	4	3.0	3.0	-
1987	6	0.5	0.5	0.5
1988	16	1.3	1.3	1.3
1989	6	5.0	5.0	5.0
1990*	84	2.2	2.3	2.7
n	14	13	13	12
W^2	0.8831	0.9366	0.9522	0.8805

1 With cut-off probability p>0.7

2 Shapiro-Wilk W statistic: all samples normally distributed (p>0.05, Shapiro & Wilk 1965).

* sex-ratio significantly different from 1:1 (one-tailed Binomial test). Only one estimated sex ratio was significant in 1978.

TABLE N.11. Annual number of immature and adult winter-caught great gray owls that were males and females estimated by SAS procedure DISCRIM[1].

	Immatures		Adults			
Winter	Males	Females	Males	Females	Total	Probability[2] of Sex & Age Independence
1977	1	5	3	18	27	p=0.1000
1978	13	10	21	35	79	p=0.1932
1979	1	5	10	29	45	p=0.1000
1980	9	9	0	5	23	p=0.0595
1981	0	0	0	0	0	
1982	0	0	4	21	25	
1983	0	0	9	57	66	
1984	3	21	5	4	33	p=0.0345
1985	3	0	1	3	7	p=0.1143
1986	0	0	1	3	4	
1987	1	1	3	1	6	p=0.6000
1988	0	1	6	7	14	p=0.5714
1989	1	0	0	5	6	p=0.1667
1990	4	1	19	53	77	p=0.0426
Total	36	53	82	241	412	p=0.0080
Expected	25.5	63.5	92.5	230.5		
X^2	4.32	1.74	1.19	0.48		
W[3]	0.693	0.683	0.815	0.822	0.882	

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[1] with proportional prior sex probability and cut-off posterior sex probability p>0.7

[2] Lower Tail Fisher Exact Probability Test used when n<25
Yates Corrected Chi Square used when n>25

[3] Shapiro-Wilk W statistic: all samples not normally distributed (p<0.05, n=14, Shapiro & Wilk 1965) except Total (W=0.882)

TABLE N.12. Annual number of immature winter-caught great gray owls that were males and females estimated by SAS procedure DISCRIM*.

Winter	Immatures Males	 Females	Total	One-tailed Binomial Test
1977	1	5	6	0.109
1978	13	10	23	0.339
1979	1	5	6	0.109
1980	9	9	18	0.593
1981	0	0	0	-
1982	0	0	0	-
1983	0	0	0	-
1984	3	21	24	0.000
1985	3	0	3	0.125
1986	0	0	0	-
1987	1	1	2	0.750
1988	0	1	1	1.000
1989	1	0	1	1.000
1990	4	1	5	0.188
Total	36	53	89	0.045

* With proportional prior sex probability and cut-off posterior sex probability p>0.7

TABLE N.13. Annual number of adult winter-caught great gray owls that were males and females estimated by SAS procedure DISCRIM*.

Winter	Adults		Total	One-tailed Binomial Test
	Males	Females		
1977	3	18	21	0.001
1978	21	35	56	0.041
1979	10	29	39	0.002
1980	0	5	5	0.031
1981	0	0	0	-
1982	4	21	25	
1983	9	57	66	
1984	5	4	9	0.500
1985	1	3	4	0.310
1986	1	3	4	0.310
1987	3	1	4	0.310
1988	6	7	13	0.500
1989	0	5	5	0.031
1990	19	53	72	0.000
Total	82	241	323	0.000

* With proportional prior sex probability and cut-off posterior sex probability p>0.7

Figure N.1. Great gray owl sex probability versus discriminant score difference generated with SAS Procedure DISCRIM using three measurements and equal prior proportions (n = 453 unknown sex great gray owls).

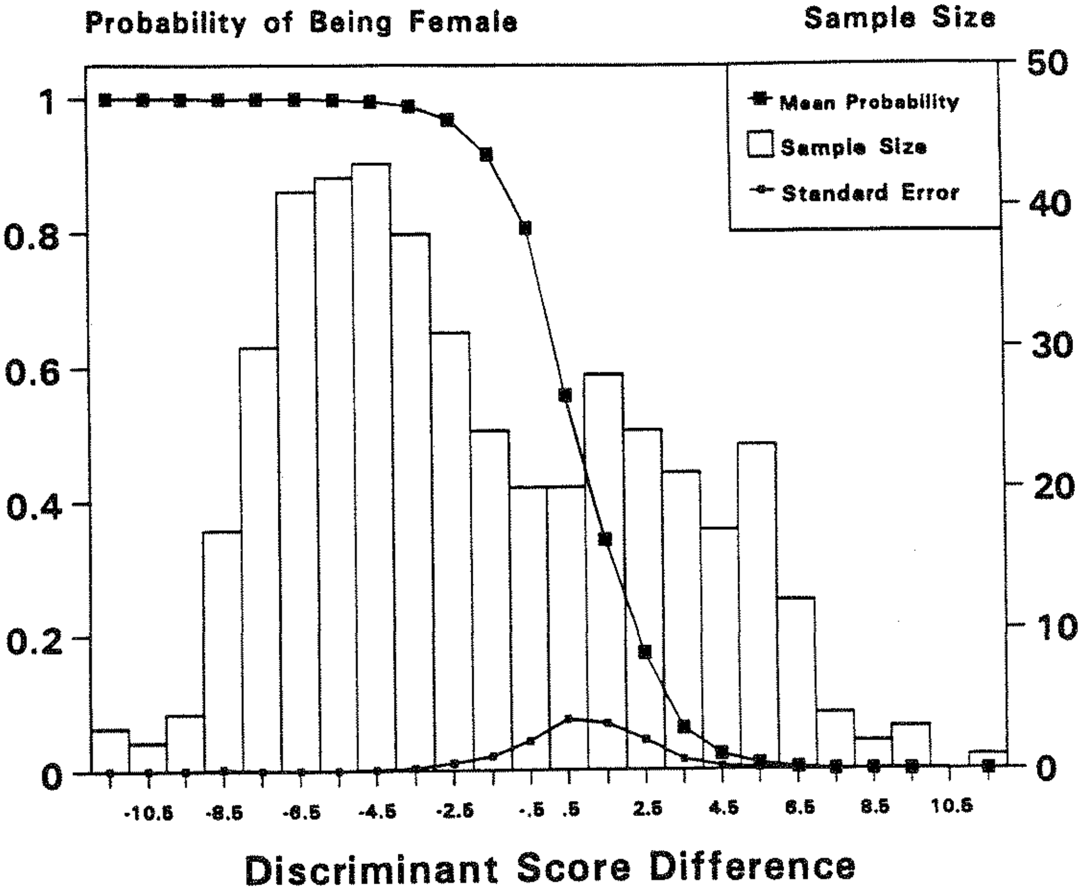

Figure N.2. Great gray owl sex discriminant score differences generated with SAS Procedure DISCRIM using four measurements and proportional prior proportions.

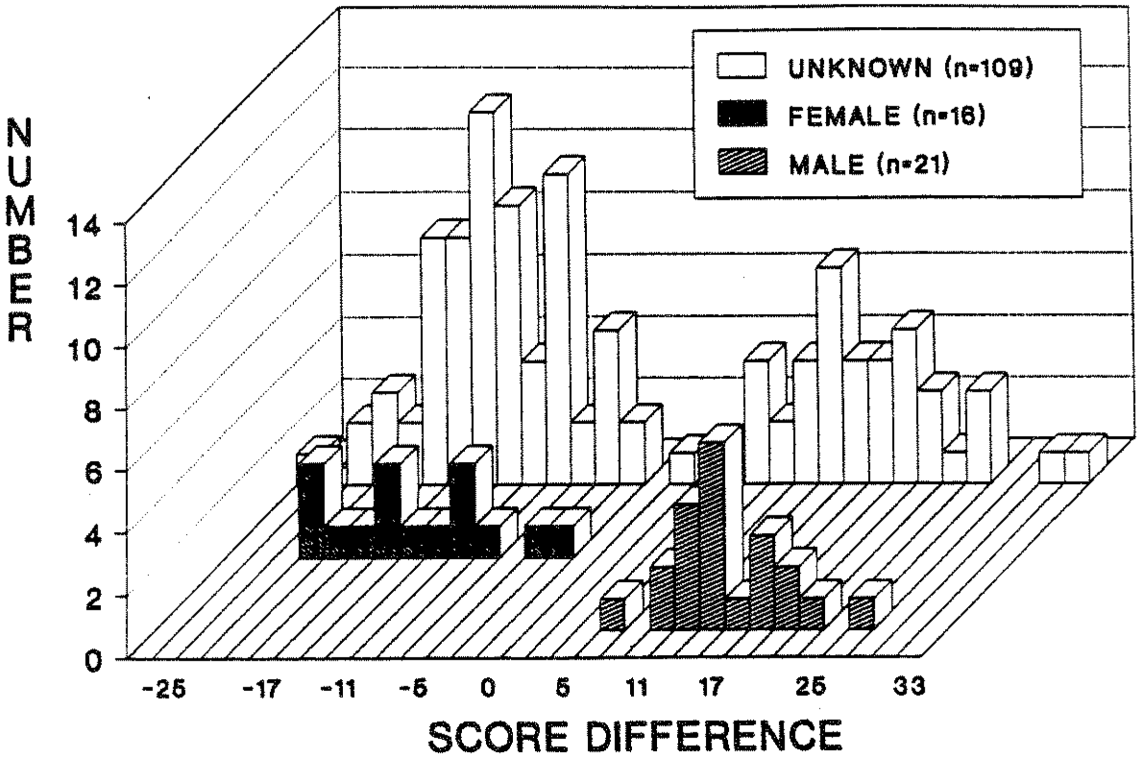

Figure N.3. Owl probability frequency generated with SAS Procedure DISCRIM for 109 unknown-sex great gray owls using four measurements and proportional prior proportions.

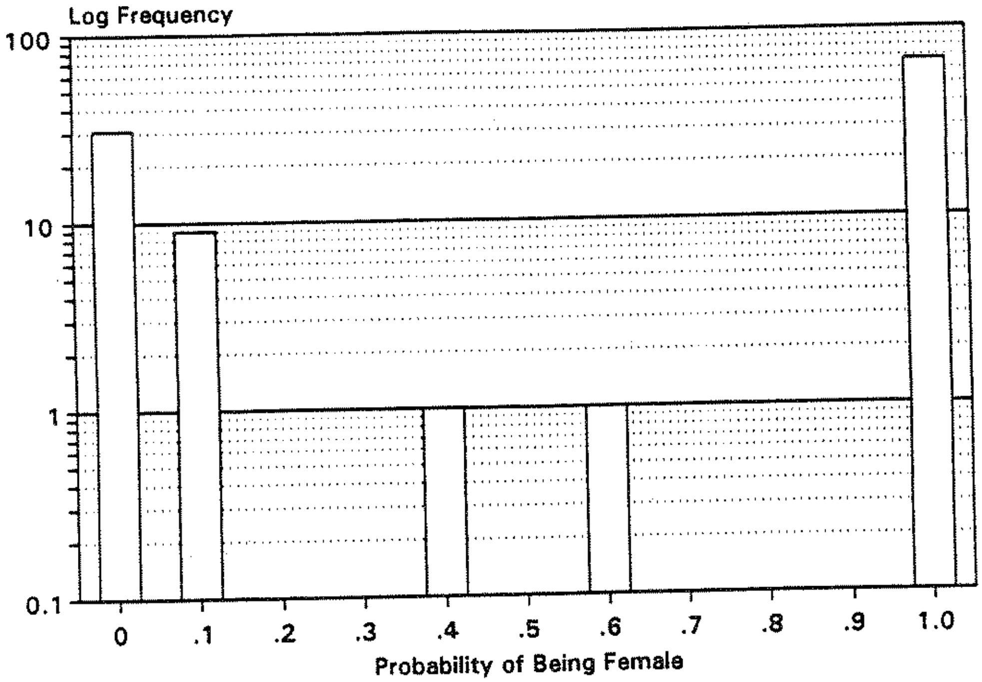

Figure N.4. Great gray owl sex discriminant score differences generated with SAS Procedure DISCRIM using three measurements and proportional prior proportions.

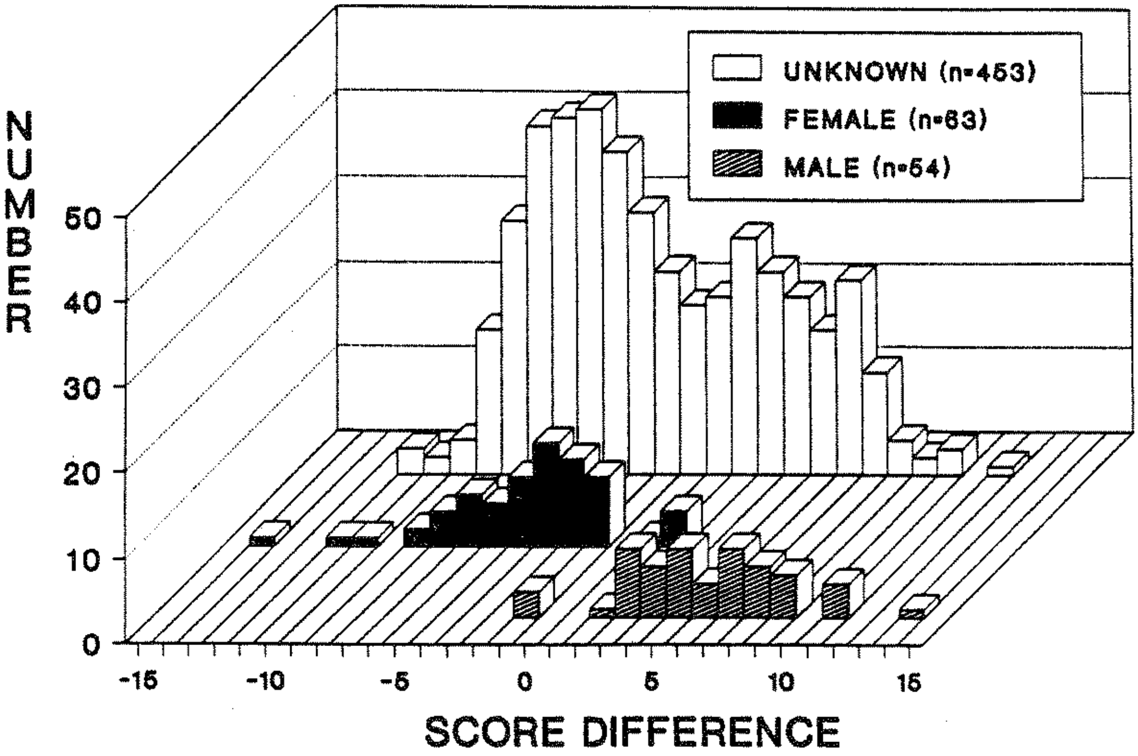

Figure N.5. Great gray owl sex probability frequency generated with SAS Procedure DISCRIM for 453 unknown-sex great gray owls using three measurements.

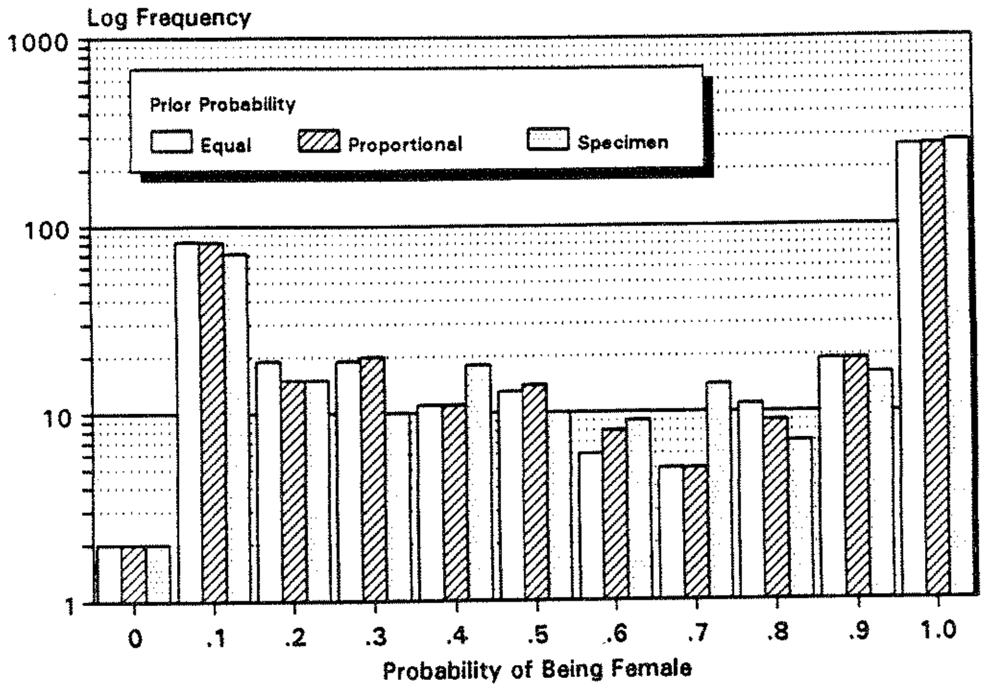

Figure N.6. Effect of prior sex probability on percentage of great gray owls sexed.

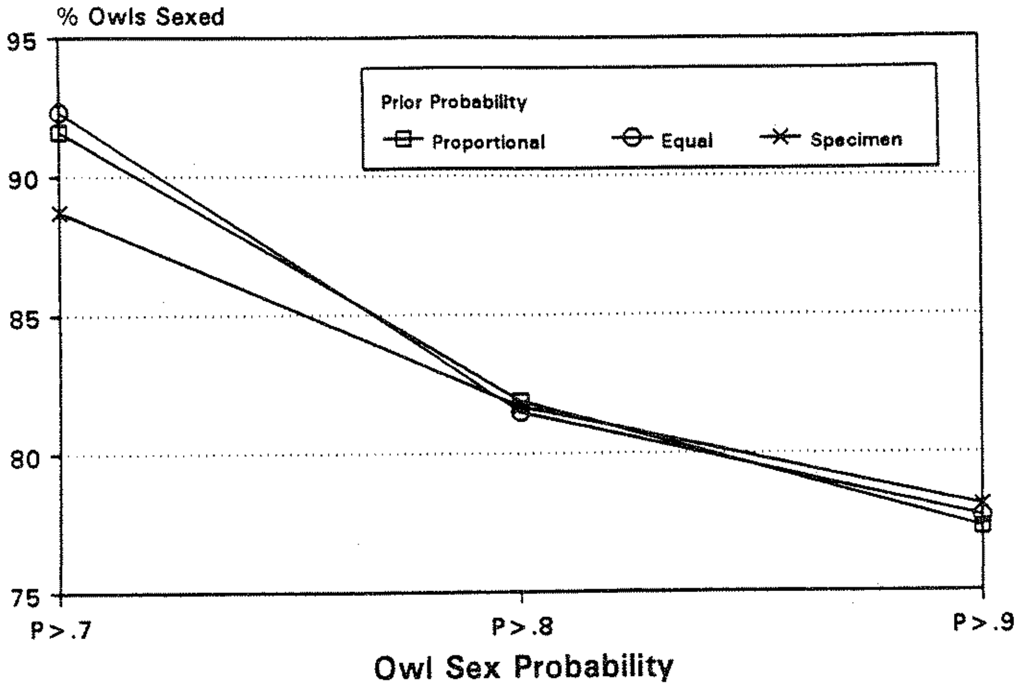

Figure N.7 Effect of prior probability on estimated winter great gray owl sex ratio.

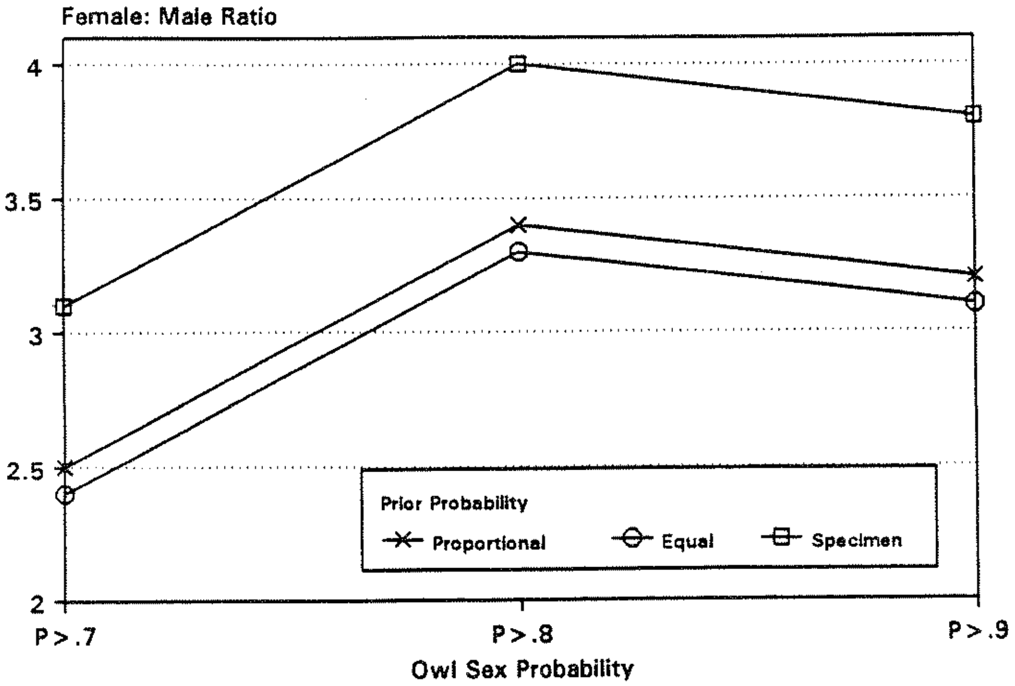

Figure N.8 Annual fluctuations of winter female:male great gray owl sex ratio (1977-90).