

**HABITAT USE, MOVEMENT PATTERNS, AND BODY CONDITION OF MALE AND
FEMALE SNOWY OWLS (*BUBO SCANDIACUS*) IN WINTER**

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By

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ABSTRACT

Birds that winter in northern latitudes face challenges associated with cold climates, including reduced food abundance and availability. Additionally, metabolic requirements are greater in colder weather and more food is required to meet these demands. Consequently, competition for resources in winter may be greater than in the breeding season. Competitive ability and dominance within species is often related to sex, if there is sexual size dimorphism, as in raptors. I studied various aspects of the winter ecology of male and female Snowy Owls wintering in Saskatchewan. Females are the larger sex and dominant, and I tested hypotheses that female dominance would translate into priority access to resources through sex differences in winter habitat use and home range size and movement patterns. Further, I tested whether differential access to resources manifested as a difference in winter body condition and survival between the sexes.

Using information obtained from Global Positioning System - Global System for Mobile Communications (GPS-GSM) satellite transmitters, driven transects, and habitat ground-truthing, I found that females occupied home ranges in areas with lower proportions of canola than males, but males avoided canola fields within their home range. Male home range sizes tended to be smaller than those of females. Females in higher body condition (weight adjusted for body size) had significantly smaller home ranges than individuals in lower body condition. These findings are consistent with the prediction that dominant individuals place home ranges in higher quality habitat and so require smaller areas to meet their food requirements.

I extended this finding and demonstrated that there are population level physical consequences to female dominance in winter. Using records from an 18 year-long dataset of Snowy Owl winter trapping and wildlife rehabilitation centers, I found that males have lower

body condition than females in winter, carrying lower amounts of fat and muscle energy reserves, and experiencing higher mortality.

My research demonstrates the importance of the winter period as a stressful time for owls that stay in northern latitudes year-round. It also raises as yet unanswered questions as potential topics for future research. It would be interesting to extend my findings to determine whether winter body condition has carryover effects to the subsequent breeding season, by investigating the relationship between condition and mating status, breeding territory quality, reproductive output, and survival. Also, as my research focused on differences between males and females, similar work could be done to compare the dominance relationship between age classes and its implications.

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CHAPTER 1: GENERAL INTRODUCTION

1.1 Introduction

Many species of birds migrate to warmer climates after breeding to avoid harsh winter weather but those species which overwinter in cold climates must face the energetic challenges posed by cold temperatures and reduced food supply. As temperatures decrease, birds must increase their metabolic rate to maintain their body temperature and require more food to do so (West 1965; Gessaman 1972). However, in winter, food is often less abundant (Heisler et al. 2014) and less available (Kostrzewa and Kostrzewa 1991, Riegert and Fuchs 2011). Because of a greater demand for resources, which are available in decreased supply, competition may also be stronger during winter than summer (DuBowy 1988). Thus, for species resident in northern latitudes year round, winter may be a critical period affecting individual fitness through carryover effects in other aspects of the annual cycle, as demonstrated in some migrating bird species (Marra and Holmes 2001; Robles et al. 2007; Duriez et al. 2012). As birds are not breeding in winter and rarely in family groups, competition between the sex and age classes may be may widespread and competitive ability or dominance is often linked to the ability to access resources and ultimately survival (Marra 2000; Ardia and Bildstein 2001; Buij et al. 2012). In particular, where there is intraspecific competition for winter resources, one sex may dominate the other, and older birds usually dominate younger ones.

Competition for limited resources often manifests as competition for habitats associated with these resources. Habitats which contain or offer greater access to food may be preferred by wintering individuals (Sherry and Holmes 1996) and hence if the best quality habitats are limited, individuals may assort themselves into habitats of different quality based on competitive ability (an "ideal despotic distribution", Fretwell and Lukas 1970). Furthermore, the distribution

and abundance of limiting resources in space and time may affect its economic defendability. Food is often profitable to defend if it is somewhat spatially clumped or if it is uniformly distributed and occurs in moderate to high richness (Brown 1964). However, if food is too scarce, required territory size increases past a threshold where the costs of defence exceed the benefits of sole ownership, and individuals may roam widely on the landscape (Krebs and Davies 1993; Restani et al. 2001). At the other extreme, if resources are highly clumped and very rich, territory defense against many competitors becomes uneconomical which may lead to grouping and the tolerance of nearby conspecifics (Krebs and Davies 1993) with hierarchical social structures (Le Boeuf 1974). In this case, strong competitors may acquire more resources than poorer competitors through social dominance of weaker competitors (Banks et al. 1979; Baker et al. 1981).

In general, theory suggests that dominant individuals in a population should be more likely to defend feeding territories in high quality habitat (Brown 1964; Gill and Wolf 1975) than poorer competitors which may be relegated to habitats with sparser prey. If prey density in the poorer habitat is still economically defendable, territories there will need to be larger to meet the same energetic needs of individuals and hence an inverse relationship between territory size and habitat quality is predicted (Boxall and Lein 1982a). If prey is too scarce, poorer competitors likely adopt alternative strategies for accessing sufficient resources such as partial migration or nomadism, in response to resources that are variable in space and time either because of resource distribution or competition (Allen and Saunders 2002). The wide-ranging winter movements of Gyrfalcons (*Falco rusticolus*) which include extended periods at sea may be evidence of nomadism during an annual period of decreased food availability (Burnham and Newton 2011).

Poorer competitors may also switch to alternative food sources to reduce intraspecific competition with dominant individuals (Votier et al. 2007; Buij et al. 2012).

Raptors exhibit reversed sexual size dimorphism, where females are larger and heavier than males (reviewed in Kruger 2005). Hence, female raptors are often socially dominant over males and may exclude males from high quality winter habitat through aggression (e.g. American Kestrels – *Falco sparverius*, Ardia and Bildstein 1997; Northern Harriers – *Circus cyaneus*, Littlefield and Johnson 2005; Barred Owls – *Strix varia*, Spotted Owls – *Strix occidentalis*, Hamer et al. 2007). Some studies have shown that wintering raptors may compensate for reduced access to food by using larger feeding territories (Boxall and Lein 1982a), using alternative prey (Toland 1986; Riegert and Fuchs 2011), or by adopting nomadic winter behaviour (Restani et al. 2001; Burnham and Newton 2011). Failing to compensate for reduced food access could result in physical and fitness costs to poor competitors, but the extent of overwinter mortality in raptors is not well understood. Such questions are becoming more possible to answer with the advancement and development of new telemetry and monitoring technologies.

1.2 Study Species and System

My thesis research focuses on Snowy Owls (*Bubo scandiacus*), a large raptor with reversed sexual size dimorphism, as females are on average 33% heavier than males (Chang and Wiebe 2016). Little is known about the migration movements of the species as a whole, but during winter, part of the Arctic breeding population migrates south to the prairies, while part remain on the breeding grounds (Potapov and Sale 2012; Holt et al. 2015). Inter- and intra-sexual aggression within Snowy Owls has been reported in the winter (Evans 1980; Appendix 1),

suggesting that the sexes may compete strongly for limited food resources in winter. Their winter diet is comprised of mainly of small mammals (upwards of 90%) but also includes alternative bird and mammal prey (Detienne et al. 2008). Furthermore, Snowy Owls winter in large numbers annually on the Canadian prairies, where temperatures may be sustained below -20°C and may be as low as -40°C , making this an ideal system in which to study aspects of winter competition in a raptor species. I was generally interested in how owls use habitat during winter and the resultant consequences to winter body condition and survival. Much of my research relies on data collection from Global Positioning System - Global System for Mobile Communications (GPS-GSM) satellite transmitters, a relatively new technology which gives frequent, scheduled, and precise locations, allowing for more detailed studies of movement and space use over time than previously. However, like some previous studies, I also incorporated direct sighting and survey data in the field, which may be less accurate and more difficult to obtain.

1.3 Objectives and chapter synopses

The main objective of my thesis research is to understand how male and female Snowy Owls relate to each other in winter, in terms of competition, and whether this is associated with differences between the sexes in use of habitat or movements on the landscape. I also wanted to relate this winter ecology to longer term effects on body condition and survival of the sexes. To accomplish this, I drove a 60 km transect route twice weekly in the winter to count, locate, and identify Snowy Owls on a landscape of known habitat cover. I also trapped and equipped 17 Snowy Owls with GPS-GSM satellite transmitters to monitor their locations and movements during the winter. To understand how competition influences winter condition and survival in the sexes, I used existing datasets from wildlife rehabilitation centers and owl banders. Below, I

outline the hypotheses and predictions in each of my three data chapters which focus on answering these questions.

In chapter 2, I tested whether the sexes differ in the type of habitats used and in the habitat composition of their home ranges. I first quantified small mammal prey abundance, as a measure of habitat quality, in common habitats used by Snowy Owls. If females are the dominant sex, I predicted that they would be more strongly associated with high quality habitat (with high prey density) than males. I also tested whether the habitat used by Snowy Owls was affected by proximity to a congeneric competitor, the Great Horned Owl (*Bubo virginianus*).

In chapter 3, I tested whether males and females differ in the use of space and movement patterns over winter. I did this by using locations collected by GPS-GSM satellite transmitters to estimate home range size and distances moved by Snowy Owls during winter. If females are the dominant sex, I predicted that they would have priority access to areas of high prey density and therefore would have smaller home ranges than males. I also predicted that females would travel less than males during the winter, because males might be more nomadic than females.

In chapter 4, I tested whether males and females differ in body condition during winter and whether condition is linked to survival, presumably the longer term effects of sex-biased access to food resources. I did this by comparing multiple body condition measures of trapped owls between the sexes. I also compared wild population sex ratios to sex ratios of sick or weak owls being admitted to rehabilitation centers. If females are the dominant sex, I predicted that they would be in better winter physical condition than males, and consequently, that the sex ratio of owls admitted to rehabilitation centers would be male-biased compared to the wild population.

1.4 Thesis format

This thesis has been organized in manuscript format for publication. As a result, there may be some repetition of information throughout the text.

Chapter 2 and Chapter 3 are in preparation for publication in peer-reviewed journals. Chapter 4 has been published in full in *The Auk: Ornithological Advances*, under the joint authorship of Karen L. Wiebe (University of Saskatchewan).

CHAPTER 2: HABITAT USE OF WINTERING MALE AND FEMALE SNOWY OWLS ON THE CANADIAN PRAIRIES IN RELATION TO PREY ABUNDANCE AND A COMPETITOR, THE GREAT HORNED OWL

2.1 Abstract

Birds overwintering at high latitudes may find it challenging to meet their energy budgets when thermoregulatory costs are high and food availability is low. Snowy Owls (*Bubo scandiacus*), like most raptors, exhibit reversed sexual size dimorphism, so if high quality (food-rich) habitats are limited, I predicted that the larger and dominant females may use better quality wintering habitat than males. In Saskatchewan where many Snowy Owls overwinter annually, I measured prey (small mammal) abundance in fields with four types of cover, and related this estimate of habitat quality to its use by the sexes. Small mammal abundance varied annually but not among three types of crop cover; however, prey was less abundant in pastures than in croplands in one of three years. Bi-weekly surveys of owls conducted during two winters along a 60 km transect revealed a weak selection for legume fields, especially for males. The home ranges of 9 females fitted with Global Positioning System - Global System for Mobile Communications (GPS-GSM) transmitters contained proportionally less canola stubble than 8 males with transmitters. Within home ranges, males avoided canola stubble, and tended to use legume fields more than expected, whereas females used habitats in proportion to availability. I suggest that owls may avoid canola stubble because the rigid stalks impair hunting compared to the easier accessibility offered by stubble-free legume fields. Fewer Snowy Owls than expected at random were seen at locations along the transect within 800 m of Great Horned Owls (*Bubo virginianus*) and their associated habitats suggesting that Snowy Owls also avoided these potential competitors on the landscape.

Keywords: Bubo scandiacus, competition, habitat use, prey availability, satellite transmitters, Snowy Owl, winter

2.2 Introduction

Much research on birds has focused on the use of habitat during the breeding season but there is increasing recognition that behaviour and performance during the winter months are important parts of the annual life cycle which can have carry-over effects on lifetime fitness (Marra and Holmes 2001, Duriez et al. 2012). For those birds which overwinter at high latitudes, winter may represent a time of energy stress as a result of increased metabolic demands for thermoregulation in cold temperatures (Gessaman 1972). In addition, it may be challenging to maintain a positive energy balance if the availability of food is reduced because of snow cover (Kostrzewa and Kostrzewa 1991, Riegert and Fuchs 2011) or lower prey population densities (Heisler et al. 2014). If resources are limited in winter and distributed unevenly on the landscape, one would predict that the more competitive individuals in the population would use habitat types which afford high resource availability, whereas poorer competitors would use poorer quality habitats (Sherry and Holmes 1996, Marra 2000) or adopt different overwintering strategies such as nomadism or partial migration (Allen and Saunders 2002, Littlefield and Johnson 2005, Burnham and Newton 2011).

When individuals live alone on winter home ranges, sex differences in competitive ability may translate into the dominant sex claiming habitat that is of greater quality than that used by the subordinate sex. This can be seen across a wide range of animals including small mammals (e.g. red squirrels, *Sciurus vulgaris* – Wauters and Dhondt 1992), large mammals (e.g. mule

deer, *Odocoileus hemionus* – Bowyer 1984), marine mammals (e.g. grey seals, *Halichoerus grypus* – Breed et al. 2006), and birds. For example, American Redstarts (*Setophaga ruticilla*) wintering in Jamaica segregated by sex, such that dominant males were more commonly found in the more food-rich mangrove forests and females were common in scrub habitat (Marra 2000). Many birds of prey exhibit reversed sexual size dimorphism which underlies female dominance over males (reviewed in Kruger 2005). Therefore, in some raptors it has been reported that the smaller, subdominant males tend to use poorer quality habitat (i.e. with lower prey abundance) than the larger females (Ardia and Bildstein 1997, Littlefield and Johnson 2005, Buij et al. 2012). Alternatively, the sexes may use different habitats to specialize on preferred prey which differ in type and size, (Massemin et al. 2000, Buij et al. 2012), reducing competition between the sexes: the "niche specialization hypothesis" (Storer 1966).

Competition for winter habitat may operate not only among age and sex classes within a species but also between species. In raptors, for example, an increase in the Peregrine Falcon (*Falco peregrinus*) population was correlated with changes in Merlin (*Falco columbarius*) hunting behaviour, timing, and fine-scale habitat use, presumably in response to interspecific competition (Buchanan 2012). Similarly, in an area of sympatry, Barred Owls (*Strix varia*) are thought to exclude Spotted Owls (*Strix occidentalis*) from winter and breeding habitat because the former species is more aggressive (Hamer et al. 2007) and may kill the latter (Leskiw and Gutierrez 1998).

Snowy Owls (*Bubo scandiacus*) wintering south of their breeding range predominantly use flat open prairie land (Kerlinger et al. 1985, Kerlinger and Lein 1988a). Habitat use by wintering Snowy Owls has been studied previously using opportunistic observations (Boxall and Lein 1982a), but there have been no studies using known locations unbiased by detectability and

so selection for certain types of landscape cover by Snowy Owls in human-modified landscapes and spacing patterns are unknown.

I studied the habitat use of Snowy Owls wintering on the prairies in Saskatchewan during two field seasons. These owls breed in the Arctic tundra and a component of the population migrates south every year to winter on the North American prairies (Kerlinger et al. 1985, Potapov and Sale 2012), whereas others remain in the Arctic year-round (Therrien et al. 2011). Female Snowy Owls in the wintering prairie population are 33% heavier than males (Chang and Wiebe 2016) and others have noted that the larger females displace, or are aggressive to males in winter (Evans 1980, Boxall and Lein 1982a) which means females are likely dominant (Kerlinger and Lein 1988b). Hence, I tested three hypotheses with respect to habitat use by the owls. First, if habitat types differ in quality but habitat is not limiting, I expected owls of both sexes to use the habitats with most small mammal prey more than expected. Alternatively, if the amount of good quality habitat is limited, I predicted that the dominant females would use the most productive habitat more than the males. Finally, my study area also presents a system in which to study interspecific competition from resident Great Horned Owls (*Bubo virginianus*). Thus, I expected that Snowy Owls may avoid habitats close to, or associated with, Great Horned Owls.

2.3 Methods

2.3.1 Study Site and Study Species

I studied Snowy Owls during the winters of 2014-15 and 2015-16 in south-central Saskatchewan roughly as far north as Shellbrook, SK (53.2167°N), and as far south as Swift Current (50.2881°N). Less than 20% of the original short- and mixed-grass native prairie remains

(Samson and Knopf 1994), including dominant species such as needle-and-thread grass (*Stipa comata*), western wheatgrass (*Agropyron smithii*), and thickspike wheatgrass (*A. dasystachyum*). Today, agricultural lands predominate and include pasture (rangeland), as well as cropland growing mainly canola, pulses, and cereals. Agricultural land is gridded in square miles leading to mosaic-like blocks of habitat usually between 1.28-5.12 km² (0.5-2 miles²). Winters are cold in south-central Saskatchewan, with frequent sustained temperatures below –20°C and some days as low as –40°C. Snow cover is variable but may persist from late October to early April.

Snowy Owls arrive annually on the Canadian prairies in late October to early November and most migrate north again by early April. Here, the owls may prey on land birds such as Grey Partridge (*Perdix perdix*) and Rock Pigeons (*Columba livia*) but most (e.g. 76-91% of individual items, 28-62% of biomass) of the diet is composed of small rodents (Boxall and Lein 1982b). Snowy Owls sitting on the ground may launch attacks on prey, but often hunting is done from perches such as fence posts or telephone poles where those occur on the landscape (Boxall and Lein 1982b).

2.3.2 Surveying small mammal prey

I sampled small mammals in the four most abundant habitat types: canola fields, grain fields, legume fields, and pastures. The chosen fields were in areas where I caught and observed Snowy Owls (Figure 2.1a). In twelve different (independent) fields of each of the four habitat types, 10 stations, each 30 m apart with 2 snap-traps (Museum Special, Woodstream Corp.), were set out along transect lines, one along the field edge and one in the field interior (see Figure 2.1b for arrangement of the stations). I baited the traps with peanut butter and checked them each morning after three consecutive nights (Stickel 1946, Mengak and Guynn 1987). I trapped small

mammals before snowfall and just before Snowy Owl arrival during three fall (mid-October) periods (2014-2016) and after snowmelt and departure of most owls in spring (mid-April), 2015 and 2016. With 3 nights per trap, 20 traps per field, 12 fields per habitat, I had 720 potential trap-nights per habitat per season. However, the number of trap-nights was adjusted downwards whenever both paired traps at a station were sprung or filled with small mammals by subtracting 1 trap-night at each such station and assuming traps were sprung on average midway between checks.

2.3.3 Habitat use by owls

I recorded habitat use by owls using two methods, one of which was to survey individuals from the roadside along a 60 km long transect route along gravel roads from approximately Harris to Elrose, Saskatchewan (latitude at midpoint: 51.3873°N). In each of the two winters, before snowfall and before owls arrived in fall, I ground-truthed and mapped the habitat cover within 1600 m on both sides of transect. After owls arrived in late October/ early November, I conducted surveys twice weekly by driving at a constant speed of 40 km/h and recording every owl seen from the vehicle. Owls along the transect were sexed by sight using multiple cues such as size, amount of plumage barring and whether or not the dark tail bands were unbroken across the retrices. Such shapes and patterns of plumage bars were effective at sexing 100% of juvenile Snowy Owls (Seidensticker et al. 2011). I also recorded its location using GPS and the type of habitat where it was sitting or perched. I tried to conduct most surveys in sunny conditions with good visibility and was able to detect owls up to 1600 m away from the vehicle; detectability of owls within 800 m was probably near 100% in the open landscape. Although I likely resighted some individuals over the season, I considered owl observations as independent based on the

typical large-scale nomadic movements of owls over the winter, as indicated by individuals tracked by Global Positioning System - Global System for Mobile Communications (GPS-GSM) transmitters. Also, during the season I saw many different individual owls on the transect (recognized by distinctly different plumage) that appeared and then disappeared in subsequent surveys suggesting that there was continual movement of owls and new individuals appearing during the season.

I also assessed habitat use by 17 Snowy Owls (8 males, 9 females) which were fitted with transmitters. The birds were trapped by two licensed banders between December and February, in both winters, using a variety of traps including bal-chatris, drop-nets, and remotely-triggered bow-nets. Upon capture, owls were sexed by plumage, weight, and size (Josephson 1980, Boxall and Lein 1982a, Seidensticker et al. 2011), and fitted with a 25g backpack style GPS-GSM transmitter (Ecotone Telemetry, model Saker H). The lightest owl I equipped with a transmitter was 1646g, so the weight of the transmitter never exceeded 2% of the body weight of an owl. I deployed transmitters on three owls during the first winter and on 15 owls in the second. The home range of one owl which returned in the second year was included as an independent observation because it used a different area of the province and because weather, small mammal numbers, and the distribution of land cover types differed between years.

Transmitters recorded locations (accurate to 20 m) every 6 hours. I considered an owl to be using a home range if its movements were clustered and non-directional during a period lasting at least 10 days (e.g. Figure 2.2). With 4 locations per owl per day, after 10 days, we had 40 locations, meeting the suggested minimum 30 independent points for home range estimations (Seaman et al. 1999). Some owls used more than one home range during the winter, travelling directionally before establishing a new home range location. After snowmelt, I accessed as many

home ranges as possible to ground-truth and map habitat cover-types used by the owls. Minimum convex polygons (MCP) of each home range were calculated in ArcGIS 10; I calculated 95% MCPs because this is a widespread measure and is easy to compare between studies (e.g. De Solla et al. 1999, Rutz 2006, Burnham and Newton 2011, Sokolov et al. 2014) and also 50% MCPs for setting boundaries to measure habitat composition and area in the cores of the home ranges.

2.3.4 Interspecific and intraspecific competition

In the first field season, I kept track of every Great Horned Owl I saw while conducting the roadside surveys, and also thoroughly searched every farm yard and tree stand within 1600 m of the transect to map Great Horned Owl occupancy. A yard or tree clump was considered occupied if a Great Horned Owl was seen there even if I found no nest. To test the hypothesis that Snowy Owls avoided farmyards or locations with Great-Horned Owls, on ArcGIS 10, I created 1600 m (1 mile) and 800 m (0.5 mile) buffers around Great Horned Owl locations and around unoccupied yards or tree clumps and compared the density of Snowy Owl sightings in these buffer areas to those at 40 random transect locations determined by a random number generator.

2.3.5 Statistical Analyses

After log-transforming the small mammal data to improve normality, I ran a two-way ANOVA with year and habitat type and the interaction to see whether prey differed among habitats and whether these differences were consistent across time. Very few small mammals were caught in spring leading to many zeros in the data, so I only analysed the fall abundance. To test whether prey abundance differed between the field edge and interior, I compared the number of mammals

trapped on the edge and interior transect lines within each field using a paired Wilcoxon test. To quantify habitat selection on the transect route, I used chi-square tests to compare the number of owls counted in given habitats relative to an expected count in that habitat (Manly et al. 1993, McLoughlin et al. 2002, Moe et al. 2007), based on the proportion of different habitat types available within the 3.2 x 60 km belt transect. I pooled owl sightings within each year, but kept years separate because crop cover changed between years.

For each owl with a transmitter, I compared the proportions of habitat types on home ranges held by males versus females with t-tests. Within home ranges, I looked at habitat selection by calculating habitat use ratios (the proportion of locations in a given habitat divided by the proportion of the habitat available within its 95% and 50% MCPs). A ratio significantly greater than 1 indicates positive selection, while a ratio significantly less than 1 indicates avoidance, and equal to 1 indicates a habitat was used in proportion to its availability. I present standardized habitat selection ratios, such that the sum of all habitat ratios sums to 1. Therefore, since I classified ground cover into 4 different habitat types, a selection ratio significantly greater or less than 0.25 indicates positive or negative selection, respectively. This measure represents the probability of a habitat being selected if all habitats could somehow be made equally available (Rettie and Messier 2000, Osko et al. 2004). For individuals with more than one wintering area, I calculated available habitat by weighting each of the wintering areas by the amount of time the owl spent there. Of the owls equipped with transmitters, I compared habitat use by sex using ANOVA. Data from owls with transmitters were pooled between years.

I compared the numbers of Snowy Owls within 1600 m and 800m buffers around random locations on the transect, with numbers within buffers around Great Horned Owl locations, and unoccupied yards/tree stands using a one-way ANOVA. Data were analyzed using SPSS 22.0

with significance set at $\alpha = 0.05$. Using transect surveys with ≥ 15 observations, I classified Snowy Owl distribution as clumped, random, or dispersed, using the average nearest neighbor analysis on ArcGIS 10, to look at intraspecific spacing at different times throughout the winter.

2.4 Results

2.4.1 Small mammal abundance

Deer mice (*Peromyscus maniculatus*) constituted the majority of small mammals trapped over both years (775 of 829, 93.5%). The second most common mammal trapped were voles (*Microtus pennsylvanicus* and *Clethrionomys gapperi* – 47 of 829, 5.6%), which were mostly trapped in pastures (39 of 47, 83.0%). In comparison, 12.2% (101 of 829) of deer mice were trapped in pastures.

I caught significantly more small mammals during the first field season than subsequently (year effect: $F_{2, 122} = 8.7$, $P < 0.001$; Figures 2.3, 2.4). Small mammal numbers decreased by 86% over the winter in the first year and 87% over the second winter. There was a significant interaction between year and habitat type ($F_{6, 122} = 2.6$, $P = 0.02$) and so I analyzed the effect of habitat type independently by year. Densities of small mammals in fall did not differ among habitat types in 2014 ($F_{3, 43} = 1.1$, $P = 0.34$) and 2016 ($F_{3, 36} = 0.5$, $P = 0.67$) but in 2015, there was a significant habitat effect ($F_{3, 43} = 10.9$, $P < 0.001$) and a Tukey's B test indicated significantly fewer small mammals in pastures compared to all other habitats. Wilcoxon paired tests on the fall abundances showed that within crop fields, more small mammals were trapped near field edges than closer to field centers (canola, $n = 58$ fields, $P = 0.03$, grain, $n = 58$, $P = 0.002$; legumes, $n = 54$, $P = 0.006$) but there were no edge effects in the pastures ($n = 58$, $P = 0.31$).

2.4.2 Habitat use

Although crop rotation occurred between years on individual fields, overall available habitat along the transect route was similar between the two years (year 1: 12% canola, 53% grain, 32% legumes, and 4% pastures; year 2: 11% canola, 52% grain, 33% legumes, 5% pasture). The use of habitat cover type by owls observed on the transect did not differ between the sexes in the first year ($n = 193$ males and 203 females, $\chi^2_3 = 5.4$, $P = 0.15$; Table 2.1), but in the second year, males ($n = 63/129$, 49%) were seen proportionally more often on legume fields than females ($n = 22/65$, 34%), and females ($n = 11/65$, 17%) were seen proportionally more than males ($n = 5/129$, 4%) on canola fields ($\chi^2_3 = 11.2$, $P = 0.01$; Table 2.1). With sexes pooled, the pattern of habitat selection changed between years, as legumes were selected for and pastures were selected against in the first year ($n = 409$, $\chi^2_3 = 13.0$, $P = 0.005$), but there were no significant positive or negative selections of habitat types in the second year ($n = 195$, $\chi^2_3 = 5.9$, $P = 0.12$).

For the owls with transmitters, the average composition of 95% MCP home ranges was 31.3% canola, 41.6% grain, 20.6% legumes and 6.5% pasture for males whereas the corresponding percent for females was 15.8%, 39.3%, 30.6% and 14.2%. If habitat availability on the transect is representative of the wider Saskatchewan prairie, female home ranges had lower than expected amounts of grain and higher than expected amounts of pasture. Conversely, males had higher than expected amounts of canola, and lower than expected amounts of legumes. Females used home ranges which contained a lower proportion of canola than males ($t_{16} = 2.2$, $P = 0.04$) but the proportion of other habitat types did not differ (all P s > 0.05). For 50% MCP home ranges, the average compositions were: 25.5% canola, 46.1% grain, 23.2% legumes, and 5.2% pasture for males and 15.8% canola, 32.8% grain, 32.5% legumes, and 19.0% pasture for

females. Within these core areas of home range, proportional habitat composition did not differ between the sexes for any habitat. Within their 95% MCP home ranges, there were trends that males selectively used legume fields (selection value = 0.42) more than females (selection value = 0.25; $F_{1, 16} = 3.6$, $P = 0.08$; Table 2.2), whereas females tended to use available pasture (selection value = 0.35) more than males (selection value = 0.15; $F_{1, 12} = 4.1$, $P = 0.07$; Table 2.2). Similarly in areas of core use, at the 50% MCP level, there was a trend that males used their available legume fields (selection value = 0.42) more than females (selection value = 0.25; $F_{1, 16} = 3.7$, $P = 0.07$) but there were no other significant differences.

Within the sexes, at the 95% MCP level, males with transmitters used canola significantly less than expected based on availability ($t_8 = 2.7$, $P = 0.03$). Grain was not used significantly more or less than available ($t_8 = 1.9$, $P = 0.43$), and there were trends that lentils were used more than available ($t_8 = 2.2$, $P = 0.05$), and pastures were used less than available ($t_8 = 2.1$, $P = 0.08$). Females used all four habitats in proportions which did not differ from their availability (all P s > 0.05). At the 50% MCP core use level, both males and females used all four habitats in proportions not significantly different to availability (all P s > 0.05).

2.4.3 Interspecific and intraspecific competition

The density of Snowy Owl sightings within 0.8 km radius buffers differed among the locations of Great Horned Owls on the transect, unoccupied yards/tree clumps, and random locations ($F_{2, 58} = 4.2$, $P = 0.02$; Figure 2.5b). Post-hoc pairwise comparisons (Dunnett T3 – for unequal variances) showed significantly more Snowy Owls within the randomly-located half mile buffers compared to empty yards/ tree clumps (mean difference = 3.4 ± 1.1 , $P = 0.01$), and a trend that random locations had more Snowy Owls within 800 m than did Great Horned Owl-occupied

yards (mean difference = 3.8 ± 1.5 , $P = 0.06$). However, within buffers of 1600 m radius there were no differences in density of Snowy Owls between the three types of locations ($F_{2, 58} = 0.7$, $P = 0.50$; Figure 2.5a).

I observed 15 or more Snowy Owls on 13 survey dates in 2014-15 (11 Nov, 7 Jan, 14 Jan, 17 Jan, 21 Jan, 5 Feb, 11 Feb, 21 Feb, 25 Feb, 28 Feb, 7 Mar, 19, Mar, and 25 Mar). Early in the season, on surveys 1, 2, and 4, owls were distributed randomly along the transect ($P_s > 0.10$). On surveys, 3, 5, and 6, there was a trend that owls were distributed evenly along the transect ($z_s > 0$, $P_s < 0.10$). On surveys 7-11, owls were distributed evenly along the transect ($z_s > 0$, $P_s < 0.05$). On surveys 12 and 13, owls exhibited a clumped distribution along the transect ($z_s < 0$, $P_s < 0.05$).

2.5 Discussion

2.5.1 Small mammal abundance

The annual variation in numbers of small mammals on the Saskatchewan prairie during winter was more dramatic than the differences among habitats, but the pattern depended on year. In particular, in one of three years, pastures had fewer small mammals than cultivated agricultural fields of any crop type. My results corroborate a study which found that rodent track counts on snow, as a measure of winter activity, was higher in stubble fields (i.e., cultivated cropland) compared to hay fields which more resemble pastures in physical characteristics (Boxall and Lein 1982a). This suggests that food for deer mice in the form of spilled seeds is probably greater in cropland and that food abundance or habitat quality for deer mice does not differ according to the type of crop. Annual crop rotation may also reduce long-term differences in numbers of mice between fields if rodent dispersal between habitat types is slow. Small mammal

numbers also decreased seasonally by about 86% over the 6 months I sampled them which is similar to the 77% overwinter decline of deer mice on the Alberta prairies reported by Klausz (1997). Although small mammal prey (mainly lemmings: *Lemmus* spp. and *Dicrostonyx* spp.) of Snowy Owls breeding in the Arctic shows regular and pronounced cycles (Elton 1924, Framstad et al. 1993), there is little evidence for such regular mammal cycles at lower latitudes (Hansson and Henttonen 1985).

I did not analyze weather in detail, but other studies have suggested that temperature and moisture levels may affect the annual population sizes of small mammals at more southern locales. For example, meadow voles (*Microtus pennsylvanicus*), the species I found most often in pastures, have irruptive population growth during winters with long periods of persistent snow cover (Heisler et al. 2014). Anecdotally, the crash in the numbers of deer mice from the first to second fall trapping period may be linked to a summer drought in 2015 (e.g. total May-Aug rainfall 143.5 mm in Saskatoon compared to 211.7 mm as a 1981-2010 long-term average; Government of Canada 2016). If deer mice and voles respond differently to weather conditions, it could explain why the relative prey abundance on pasture habitat (which was characterized by mostly voles) varied annually in relation to cropland habitat, characterized by mainly deer mice. When snow cover is deep and persistent over winter voles may increase leading to pastures having the greatest abundance of small mammals in spring. However, in non-irruptive vole years, cultivated fields likely contain more fall and winter prey than pastures, as I found.

Few other studies on the prairies have compared the abundance of small mammals among habitat types or within the winter diet of owls on the prairies. By analyzing the regurgitated pellets of Burrowing Owls (*Athene cunicularia*) and Great Horned Owls which contain prey remains, deer mice were the predominant small mammal in the diet during summer, especially

on cropland with clay soils (Heisler et al. 2013). A study comparing diets of Great Horned Owls breeding in rangeland to those breeding in agricultural areas found that they were dietary generalists, preying primarily on locally abundant rodent species in both habitats (Marti and Kochert 1996). In winter, Great Horned Owls tended to shift away from medium sized mammals towards small mammals but no habitat associations were reported (reviewed in Errington et al. 1940). Although small mammal abundance did not differ much among cropland types, I did find a strong landscape edge effect with more prey along field edges/ roadside ditches compared to the field interior. Similar edge effects on rodents have been reported in other studies within prairie landscapes. Deer mouse abundance was higher within 5 m of farm woodlot edges than 100 m toward the interior, in summer (Bayne and Hobson 1998). In winter, roadside ditch and fence row habitats contained more small mammals than agricultural stubble fields, hayfields, and fallow fields (Boxall and Lein 1982a).

2.5.2 Habitat use and selection

Perhaps because there was little difference in prey abundance between habitat types, I found weak or inconsistent patterns of habitat selection between years and sexes, and across spatial scales. In one of two years males, but not females observed on the transect selected for legume fields and in another year, a selection for legume fields was only revealed within the larger sample when sexes were pooled. Among the birds marked with transmitters, females established home ranges with proportionally less canola than did males which resulted in their home ranges containing more legume and pasture habitats. Within MCP home-ranges, there were weak patterns of selection for legume fields by males within both 50% and 95% polygons and a weak trend of greater pasture use by females but only within the 95% MCP. Presuming females

are dominant, what emerges is selection against canola and for legumes at the landscape scale. Then, within the constraints of a home range, there is a greater proportional use of existing legume habitat by males compared with more generalist use of habitats by females.

Although small mammal abundance did not differ between types of cultivated fields, availability to Snowy Owls may still differ. Namely, physical characteristics of stubble may affect hunting efficiency and hence availability to owls. For example, canola stubble was tall (approximately 30-60 cm) and rigid, grain stubble was of similar height but softer and easily bent whereas legume fields lacked protruding stubble but rather had a loose, soft, and short layer of chaff and shredded vegetation. Thus, canola stubble may cause a physical barrier to hunting such that it is more profitable to hunt in open legume fields although prey abundance in the habitats may not differ. This may explain why females, the dominant sex, had lower proportions of canola fields in their 95% MCP home ranges.

On the other hand, once home ranges were established, males depended more on legume fields than females whereas females, by virtue of their larger size, may have been able to exploit taller stubble than males and may also include larger prey such as muskrats (*Ondatra zibethicus*) or Sharp-tailed Grouse (*Tympanuchus phasianellus*) which are not associated with croplands but rather with pastures or marshes. Snowy Owls are known to be dietary generalists in winter, exploiting locally abundant prey (Detienne et al. 2008), and females indeed have a wider dietary range than males in Alberta, being the only sex to take white-tailed jackrabbits (*Lepus townsendii*), weasels (*Mustela* spp.), and Grey Partridge (*Perdix perdix*), and relying less heavily on deer mice, the primary prey (Boxall and Lein 1982b). As the physical characteristics of pastures do not change annually as planted fields do, they may be more predictable in terms of

prey availability, and offer more profitable (large) prey especially when deep snow cover obscures cues of stubble characteristics.

2.5.3 Effects of inter and intra-specific competition on spatial distribution

Aside from prey abundance and availability of primary and alternative prey, competition with resident raptors, namely Great Horned Owls, may affect patterns of Snowy Owl habitat use. I found that Snowy Owls avoided Great Horned Owls and treed yards representing potential Great Horned Owl roosting areas at a distance of 800 m but not at 1600 m. Generally, as Great Horned Owls are resident year-round in our study area, an avoidance of Great Horned Owls by Snowy Owls may reduce competition for food, and/or reduce risks of physical confrontation especially because the two species overlap in body size and weight and Snowy Owls may risk injury in fights with Great Horned Owls. Small rodents comprise most prey items for Great Horned Owls wintering in shortgrass prairies in northern Colorado (Zimmerman et al. 1996), like Snowy Owls in the Canadian prairies (Boxall and Lein 1982b, Detienne et al. 2008). Though wintering Great Horned Owls in Colorado prey more heavily on lagomorphs than do wintering Snowy Owls, many common lagomorphs in Colorado (e.g. desert cottontail – *Sylvilagus audubonii*, black-tailed jackrabbits – *Lepus californicus*) are not present in the Canadian prairies, and so northern Great Horned Owls sympatric with Snowy Owls here likely overlap even more strongly in their foraging niche. Another study of two sympatric owl species that overlapped strongly in diet (Barred Owls and Spotted Owls – Hamer et al. 2001) revealed a strong segregation by habitat, with little overlap in territories between the species (Hamer et al. 2007).

Snowy Owls were distributed randomly on the landscape early in the winter, shortly after their arrival in November, possibly because they were still assessing habitat quality. Later in the

season, as progressively more owls settled on winter home ranges, Snowy Owl distribution gradually became more uniform, consistent with territorial spacing. After mid-March, when temperatures rise and snow cover becomes patchy, territories may quickly break down leading to the clumped distribution of owls around still-frozen lakes that I observed late in the season. This may be in preparation for migration, when many raptors are known to congregate (Nijman 2001, Black and Borowske 2009, DeCandido and Nualsri 2009).

In sum, I did not find a strong influence of habitat cover type on small mammal abundance and consequently there was not a strong selection by Snowy Owls for certain agricultural habitats within the prairies. However, the greater abundance of rodents on field edges compared to the interiors suggests that refugia located in habitats undisturbed by farm equipment in intensively cropped landscapes are valuable to conserve as they provide good food resources for wintering owls. Females established home ranges containing less canola stubble than males and I propose that canola may be less preferred because its physical structure makes it hard to hunt in. Thus, the expression of female dominance at the large landscape scale may be to force males into areas with more canola, and males may try to compensate within their home ranges by avoiding canola and focusing on legume fields.

Questions remain concerning habitat use by Snowy Owls with conservation implications. Though small mammal abundance did not vary with crop type in my study, further studies comparing Snowy Owl hunting success in fields of different physical characteristics (within and between crop types: e.g. stubble thickness, height, and flexibility) may inform overwinter land management practices for raptorial species. In addition, more information on the diversity of prey in pastures is needed to see if this habitat is linked to the broader diet of females and perhaps accounts for their higher overwinter survival than males (Chang and Wiebe 2016). If so,

the relative conservation value of pasture habitat may be greater than suggested by its small mammal density.

2.6 Acknowledgments

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Ethics Statement: Owls were trapped under permit numbers 10736 and 10737. And small mammal surveys were done under Animal Care permit 20140085.

Table 2.1. Number of male and female Snowy Owls seen during roadside surveys conducted along a 60 km transect in south-central Saskatchewan during the winters of 2014/15 and 2015/16 in four habitat types. Different letters within a year and habitat type indicate a significant difference ($\alpha < 0.05$, χ^2 test) between the proportions of males versus females in each habitat category.

Year	Sex	Canola	Grain	Legumes	Pasture
2014-15	Male	17 A	101 A	73 A	2 A
	Female	27 A	84 A	90 A	2 A
2015-16	Male	5 A	58 A	63 A	3 A
	Female	11 B	30 A	22 B	2 A

Table 2.2. Mean (\pm SE) habitat selection coefficients for 4 habitat types within home ranges used by male and female Snowy Owls in the Canadian prairies in winter 2014-15 and 2015-16.

Coefficients are proportional habitat use versus proportional habitat available within 95% MCP ranges. For individuals, habitat selection coefficients summed to 1, to represent the probability that a habitat would be selected if all types were equally available (Manly et al. 1993).

Coefficients were compared between the sexes using ANOVA.

Habitat	Male	Female	F	df	P
Canola	0.17 \pm 0.03	0.22 \pm 0.05	0.79	1, 16	0.39
Grain	0.30 \pm 0.06	0.26 \pm 0.03	0.41	1, 16	0.53
Legumes	0.42 \pm 0.07	0.25 \pm 0.05	3.56	1, 16	0.08
Pasture	0.15 \pm 0.05	0.35 \pm 0.09	4.09	1, 12	0.07

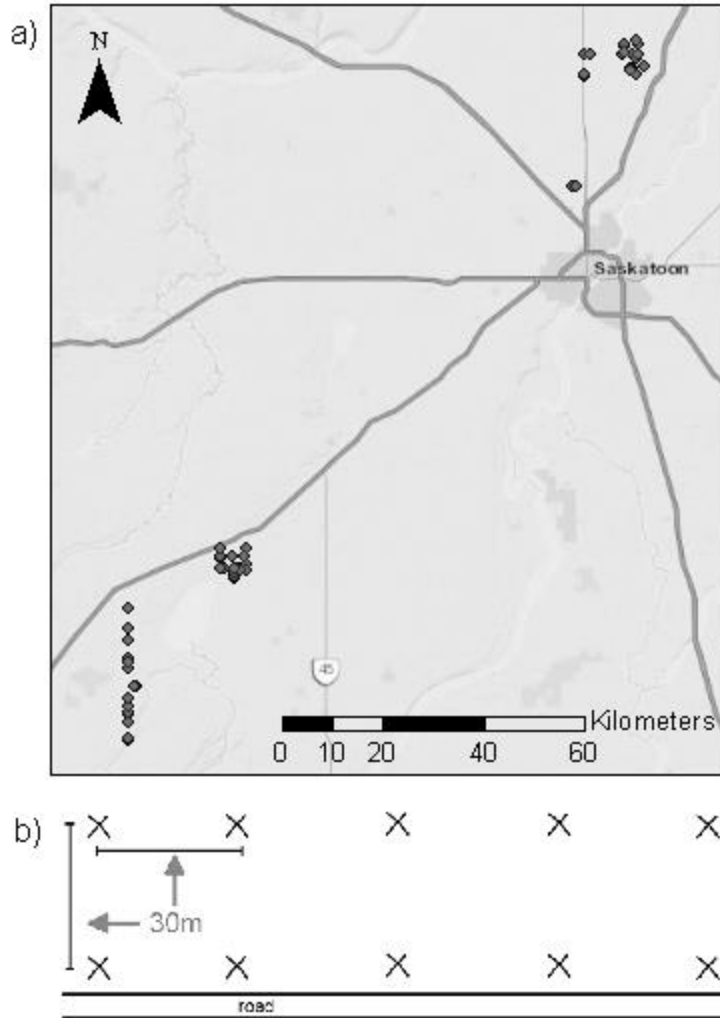


Figure 2.1. (a) Small mammal trapping locations in Saskatchewan. Each dot represents a field where 20 snap-traps were placed, two at each of 10 stations. (b) Layout of traps within each field. Each x represents a set of two traps. Traps were left out over three consecutive nights and checked each morning.

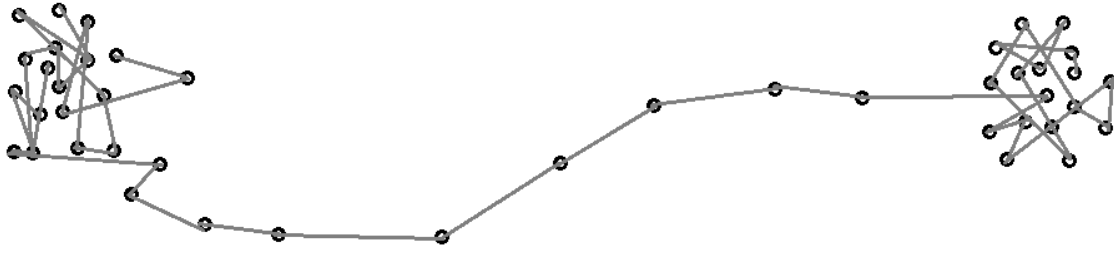


Figure 2.2. Hypothetical example of locations of an individual owl constituting two home ranges, with each cluster of points spanning 10 or more days. Within each home range, directions of movements are not consistent, and locations are clustered. Between home ranges, there is a separation of directional movement, and locations of the separate home ranges do not overlap.

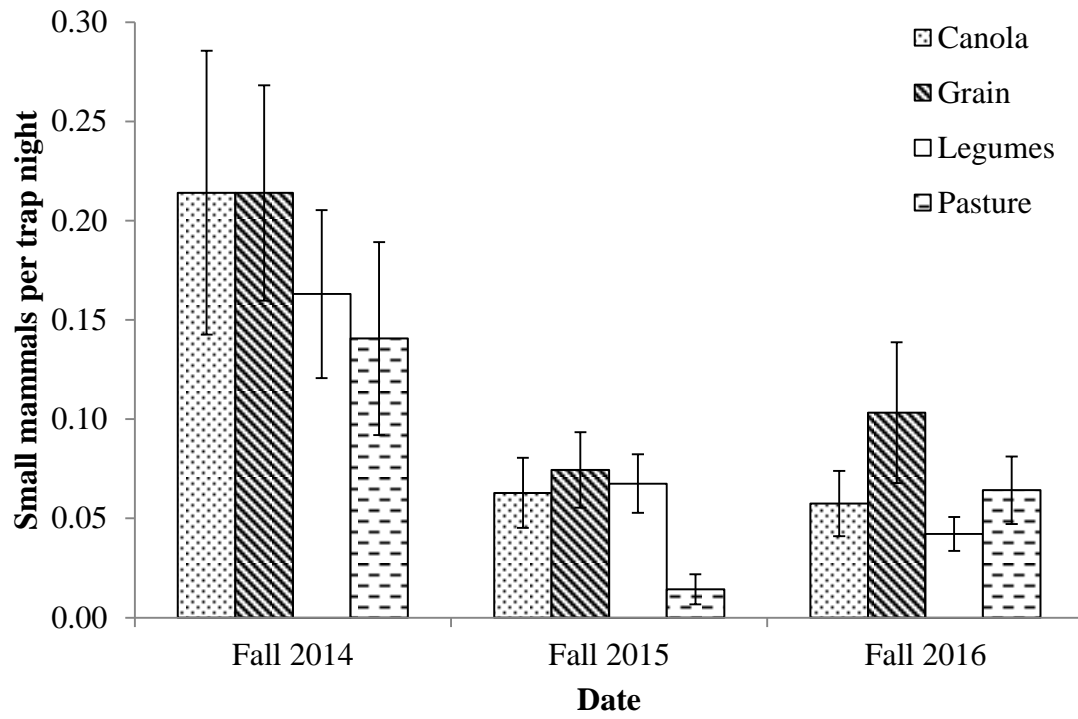


Figure 2.3. Mean annual fall numbers of small mammals trapped in four types of habitats in central Saskatchewan. Sample size was 12 fields (in areas where Snowy Owls were trapped) of each type annually and standard error bars are shown.

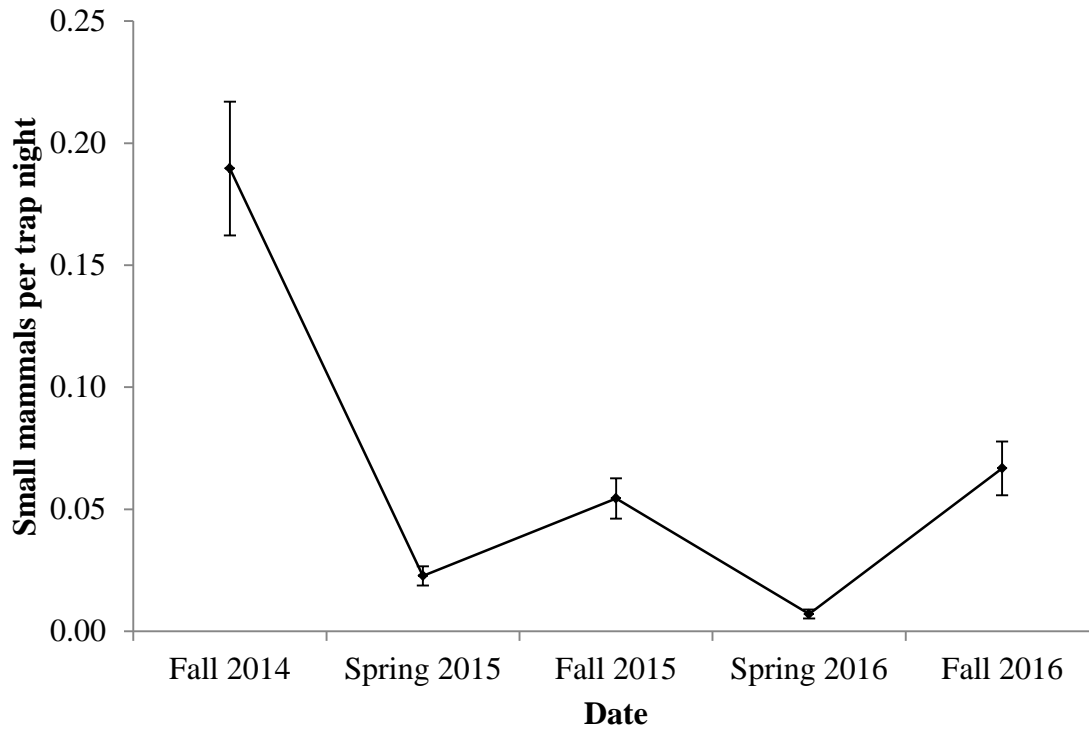


Figure 2.4. Average number of small mammals caught per trap night, showing seasonal trends over three years in central Saskatchewan. The four sampled habitat types are pooled and standard error bars are shown.

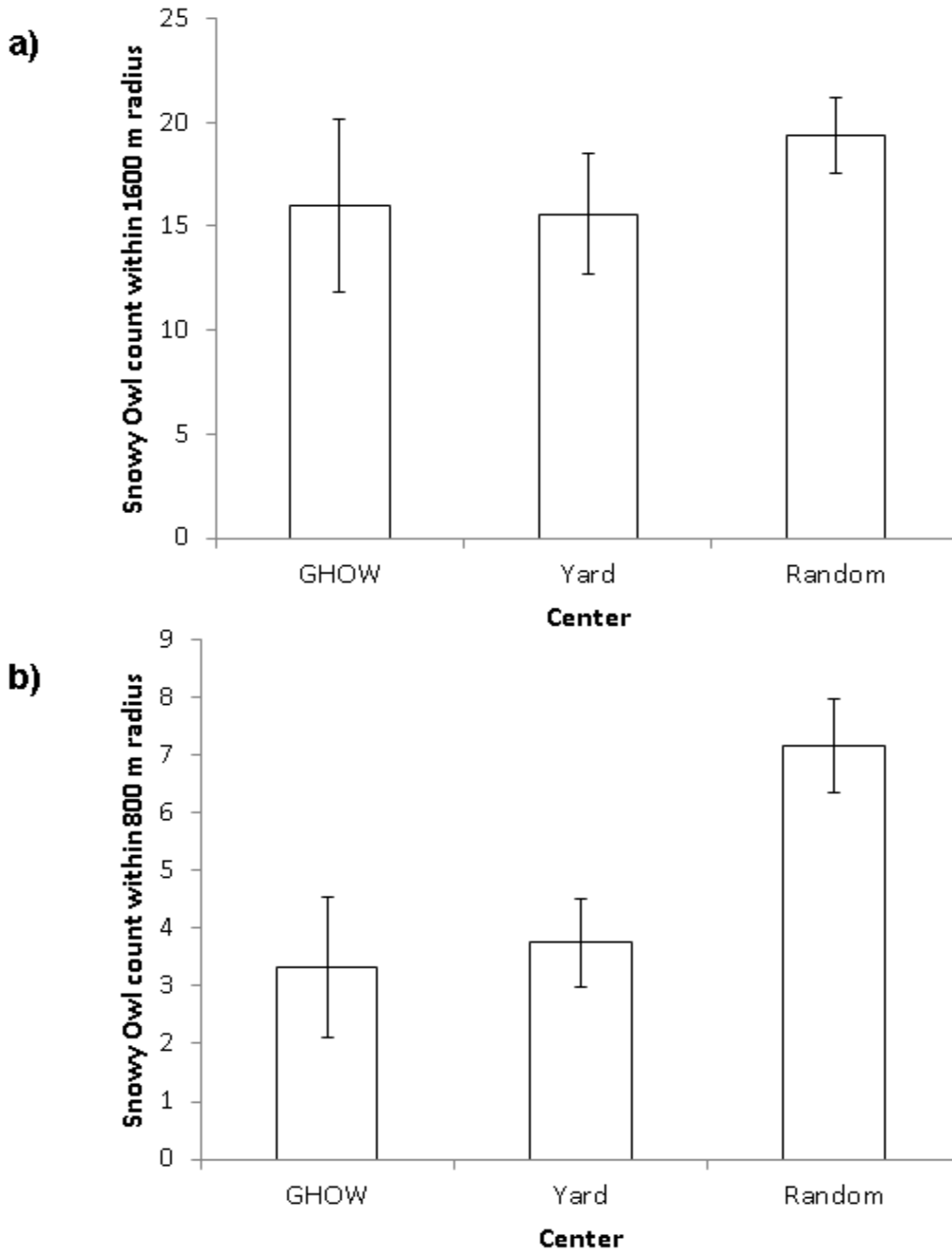


Figure 2.5. Average number of Snowy Owl observations within 1600 m (a) and 800 m (b) radii around Great Horned Owls ($n = 9$), unoccupied farm yards/ tree stands ($n = 12$), and random locations ($n = 40$) sampled along roadside transect in south-central Saskatchewan during winter 2014/2105. Error bars indicate standard error.

CHAPTER 3: COMPARISONS OF HOME RANGE SIZE AND MOVEMENT PATTERNS OF WINTERING MALE AND FEMALE SNOWY OWLS

3.1 Abstract

Birds that winter at northern latitudes are faced with increased food requirements to meet greater metabolic demands. However, competition is often stronger in winter, as food may be less abundant and less available. In birds that exhibit sexual size dimorphism, competitive dominance may be related to sex, resulting in predictable differences in space use between the sexes. I used spatial information obtained from Global Positioning System - Global System for Mobile Communications (GPS-GSM) satellite transmitters to test whether male and female Snowy Owls wintering in Saskatchewan differed in home range size, distances moved, and proportion of time spent on a home range versus travelling. Dominance relationships have been previously demonstrated in Snowy Owls to relate with space use within the sexes. I predicted that females use smaller home ranges, travel shorter distances, and spend proportionally more time on a home range than males, during the winter. There were no significant differences between the sexes in any of these measures, although given that home ranges were on average twice as large for males as females, underlying biological differences may emerge given greater statistical power.

Alternatively, Snowy Owls may not defend territories, but may rather overlap with, or tolerate, conspecifics, reducing variation in home range size and movement patterns between the sexes.

Another possibility is that the degree of sexual size dimorphism in Snowy Owls is sufficiently large to reduce competition through divergent prey niches. However, as both sexes prey predominantly on small mammals, this is unlikely. Given that current data suggest a similar

relationship between the sexes, future work should attempt to resolve this question using a larger sample.

Keywords: *Bubo scandiacus*, competition, home range size, space use, movements, satellite transmitters, Snowy Owl, winter

3.2 Introduction

The non-breeding season is increasingly being recognized as an important period in a bird's annual cycle, with its own challenges that affect an individual's lifetime fitness. Birds overwintering at northern latitudes, for example, have increased metabolic demands for thermoregulation (Gessaman 1972) which may be more difficult to meet if snow cover reduces food availability (Kostrzewa and Kostrzewa 1991, Riegert and Fuchs 2011) or food abundance (Heisler et al. 2014). If food resources are limiting in winter, competition for access to those resources and perhaps high quality wintering habitat may be intense.

Brown's (1964) model of economic defendability suggests that the size of a territory used for obtaining food resources will be a trade-off between the amount of food in a defended area and the costs involved in defense. Studies of many terrestrial vertebrates have confirmed this pattern of an inverse relationship between home range size and food density. For example, in mammals, home range size of bobcats (*Felis rufus*) was inversely correlated with stem cover density and estimated snowshoe hare (*Lepus americanus*) density (Litvaitis et al. 1986). In birds, a similar relationship was found in Spotted Owl (*Strix occidentalis caurina*) home range size and wood rat (*Neotoma* spp.) density (Zabel et al. 1995). The same relationship was also found between prey abundance and winter territory size in Sanderlings (*Calidris alba*), because areas of

higher prey abundance were related to increased intruder frequency and costs of defense (Myers et al. 1979). Therefore, within populations, dominant individuals are expected to choose territories in areas of high food abundance whereas poorer competitors, being unable to meet their metabolic requirements in a small, food-rich area like dominant competitors, may resort to using larger areas in poorer quality habitat, or adopt alternative overwintering strategies such as nomadism or partial migration (ideal despotic distribution: Fretwell and Lukas 1970).

Social dominance has been shown to give priority of access to resources such as food (Banks et al. 1979, Baker et al. 1981), mates (Cockburn et al. 2008; Magana et al. 2011) and good quality habitat (Bruinzeel et al. 2006). If home range size is inversely related to food abundance, one would predict that dominant individuals take smaller home ranges in higher quality habitat, leaving the poor competitors relegated to poor quality habitat or perhaps to adopt different strategies for foraging. For example, in American Redstarts (*Setophaga ruticilla*), wintering habitat segregation exists, with a male (the dominant sex) bias in the preferred mangrove forest habitat, and a female bias in the lower quality scrub habitat (Marra 2000). Further, in territorial intrusion trials, levels of aggression and body size of both males and females were greater in the mangrove habitat, suggesting that habitat segregation is indeed a result of dominance and not niche separation (Marra 2000). Alternatively, if food is relatively scarce or variable in time or space, nomadism may occur because not enough prey can be gleaned from a fixed home range (Restani et al. 2001). Nomadism is more likely to be used as a strategy by large bird species because they have greater energy requirements which may require tracking of unpredictable high-energy resources (Allen and Saunders 2002). The wide-ranging winter movements of Gyrfalcons (*Falco rusticolus*) which include extended periods at sea may

be evidence of nomadism during an annual period of decreased food availability (Burnham and Newton 2011).

Social dominance or competitive ability is often linked to body size or other physical attributes, which in turn, are often linked to sex. If one sex has greater competitive ability, it may dominate in competition for resources, to the exclusion of the less competitive sex. In some species of raptors, females, the larger and dominant sex, reside in higher quality (i.e. higher prey density) habitat in winter to the exclusion of males (Ardia and Bildstein 1997, 2001, Littlefield and Johnson 2005, Buij et al. 2012).

I studied the movements and use of space by wintering male and female Snowy Owls in the Canadian prairies. In contrast to most other bird species, birds of prey exhibit reversed sexual size dimorphism, where females are the larger and heavier sex, and thereby dominant (reviewed in Kruger 2005). Snowy Owls (*Bubo scandiacus*) typify raptors in this regard, with females weighing on average 33% more than males (Chang and Wiebe 2016). Females are believed to be the competitively dominant sex in Snowy Owls given their higher body condition and survival (Chang and Wiebe 2016), dominance in direct interactions (Boxall and Lein 1982a), and displacement of males (Evans 1980). Also, Snowy Owls inhabit northern areas and harsh climates year round (Potapov and Sale 2012), and therefore present a unique opportunity to study sexual competition in space use and movement strategies during winter, when resources are probably challenging to obtain, and intersexual competition is greater than in summer.

Boxall and Lein (1982a) found that within female Snowy Owls, adults, which are dominant, had smaller winter territories than juveniles, because home range size was regulated to provide individuals with a constant supply of food. Here, the goal was to compare home range size between the sexes rather than age classes and I predicted that the dominant female owls

would have smaller home ranges than males. Females were predicted to be dominant by virtue of their larger size and heavier weight conferring dominance, not because of their sex per se.

Therefore, within sex, I predicted that relatively heavier owls would be dominant and have smaller home ranges. Further, whereas previous studies of space use in wintering Snowy Owls relied solely on observations, I employ Global Positioning System - Global System for Mobile Communications (GPS-GSM) satellite transmitters to generate locations unbiased by detectability and road access. I also predicted that females would travel shorter distances, and spend less time travelling during the winter than males.

3.3 Methods

3.3.1 Study site and study species

I studied Snowy Owls during the winters of 2014-15 and 2015-16 in south-central Saskatchewan roughly as far north as Hepburn, SK (52.5221°N), and as far south as Elrose, SK (51.2005°N). Snowy Owls arrive annually on the Canadian prairies in late October to early November and most migrate north again by early April. Today, agricultural lands predominate and include pasture (rangeland), as well as cropland growing mainly canola, pulses, and cereals. Agricultural land is gridded in square miles leading to mosaic-like blocks of habitat usually between 1.28-5.12 km² (0.5-2 miles²). Winters are cold in south-central Saskatchewan, with frequent sustained temperatures below -20 °C and some days as low as -40°C. Snow cover is variable but may persist from late October to early April.

3.3.2 Data collection

I searched for Snowy Owls in rural areas known to consistently have high densities in previous winters. Owls were caught between December and February in both field seasons using a variety of traps including bal-chatris, drop-nets, and remotely-triggered bow-nets. Upon capture, owls were banded and weighed on a digital scale and several measures of body size were taken: unflattened wing chord length, culmen length, tail length, and footpad length. Weight, plumage barring, and molt were used to age and sex individuals. A body condition index was calculated for each owl by taking the residual of a regression of weight over flattened wing chord length (Chang and Wiebe 2016). Body condition index was calculated separately for the sexes because there was no overlap in weight between male and female owls. Juvenile (hatch year) owls can be distinguished by mottling on the greater coverts and primaries and even wear of the remiges whereas older owls possess different generations of remiges with differential fading of the dark bands (Josephson 1980, Boxall and Lein 1982b).

GPS-GSM transmitters (Ecotone Telemetry, model Saker H, 25 g) were attached, backpack style to 17 individuals (8 males, 9 females) using teflon ribbon. The lightest owl I equipped with a transmitter was 1646 g, so the weight of the transmitter never exceeded 2% of the body weight of the owl. I deployed transmitters on three owls during the first winter and on 14 owls in the second. The two winters of data collected from one male owl trapped in the first year which returned in the second year were counted as independent observations because the owl used a different area of the province and because weather and small mammal prey numbers differed between years. All male owls (8 of 8) and all but one female (8 of 9) were adults.

Transmitters recorded locations (accurate to 20 m) every 6 hours. I considered an owl to be using a home range if its movements were clustered and non-directional during a period lasting at least 10 days. Travelling was defined when movement was consistently directional.

Using ArcGIS 10, home range size was calculated using the minimum convex polygon (MCP) method at two levels: 95% (overall home range) and 50% (area of core use). For all owls, only locations up to 15 March were used, because later in spring, many owls moved long distances when snow began to melt, likely related to spring migration.

3.3.3 Statistical analyses

Between capture and 15 March, some owls stayed on a single home range, whereas others travelled intermittently and used multiple, sequential home ranges. Therefore, analyses to compare home range size between the sexes were done on: 1) first home ranges and also 2) the average of the multiple home ranges for owls that travelled. Home range sizes (average home range and first home range) and time spent moving vs remaining on a home range, over the entire winter, were compared between the sexes using t-tests. Similarly, distances travelled over the landscape during winter (total and after first territory) were compared between the sexes using t-tests. For all t-tests, power calculations were done. Data were analyzed using SPSS 22.0 with significance set at $\alpha = 0.05$.

3.4 Results

The average size of the first 95% MCP home range was 97.6 km² for males and 45.3 km² for females, but this difference was not significant ($t_{16} = 1.2$, $P = 0.24$, $1-\beta = 0.21$) and neither did the size of first 50% MCP ranges differ between the sexes ($t_{16} = 0.7$, $P = 0.49$, $1-\beta = 0.10$; Figure 3.1). Nor was there a difference between the sexes in the amount of time spent on the first home range (males: 41 days, females 42 days, $t_{16} = 0.11$, $P = 0.92$). Of the 18 owls, 6 (3 females, 3 males) had more than one home range (5 had two ranges and 1 had three). For those owls with

multiple home ranges the size of the first range was not significantly different from the size of their next range (paired t-tests, 95% MCP: $t_6 = 1.66$, $P = 0.15$, 50% MCP: $t_6 = 0.85$, $P = 0.43$). Including all home ranges used during the entire winter, the average 95% MCP home range size was 107.2 km^2 for males and 47.3 km^2 for females, but this difference was not significant ($t_{16} = 1.4$, $P = 0.17$, $1-\beta = 0.28$) similar to the pattern for the 50% level ($t_{16} = 1.4$, $P = 0.19$, $1-\beta = 0.26$; Figure 3.1).

Some owls were fairly stationary on a home range all winter, whereas others were relatively more nomadic, using multiple home ranges or wandering on the landscape after leaving the first home range. The directions of movements from home ranges depended on date. When owls moved from home ranges in December or January, all went south (4/4). In February, half of the movements from home ranges were northward (3/6) and the others moved southward. In March, up to 15 March, almost all movements from home ranges were northward (13/14) and only 1 owl moved southward. There was also variation in the movement patterns of owls that moved from home ranges during winter; some owls moved gradually and consistently from one home range to another whereas others moved rapidly separated by short periods of reduced movement (e.g. one owl moved a total of 116 km over 60 hours, in 3 spurts of 28 to 46 km, over 6 to 12 hours, stopping for 6 to 18 hours in between, while another owl moved 42 km over 66 hours at a consistent rate; Figure 3.2). The sexes did not differ in the average distance moved after leaving the first home range to the second home range, or to 15 March whichever came first (males: $138 \text{ km} \pm 34 \text{ SE}$, females: $145 \text{ km} \pm 56 \text{ SE}$; $t_{15} = 0.1$, $P = 0.91$, $1-\beta = 0.05$). When owls left their first home range, the duration of this first move until settling on a second home range or until 15 March, whichever came first, did not differ between the sexes (males: $10.8 \text{ days} \pm 4.0 \text{ SE}$, females: $10.0 \text{ days} \pm 3.7 \text{ SE}$; $t_{14} = 0.1$, $P = 0.89$, $1-\beta = 0.05$). There was also no difference

between the sexes in total distance travelled between home ranges over the whole winter (males: 220 km \pm 49 SE, females: 199 km \pm 56 SE; $t_{15} = 0.3$, $P = 0.78$; $1-\beta = 0.06$). Over the whole winter, there was no difference between the sexes in the proportion of time spent on a home range (males: 76% \pm 6 SE, females 83% \pm 6 SE; $t_{15} = 0.7$, $P = 0.47$, $1-\beta = 0.11$).

Within the sexes, for females there was a significant negative correlation between body condition and home range size at the 95% MCP level (first: $r = -0.71$, $P = 0.048$, and average: $r = -0.75$, $P = 0.03$). No significant relationship was found in males. Neither sex had significant correlations between body condition and home range size at the 50% MCP level (first and average).

3.5 Discussion

Although I found no significant differences between the sizes of first home range size or average home range size between the sexes at both the 95% and 50% MCP levels, the size of males' ranges averaged about twice as large as that of females, consistent with the prediction. When comparing large scale winter movements, there were also no differences between the sexes in first distance moved from a home range or overall distance moved over winter. Finally, when comparing time budgets, males and females again did not differ in their proportions of time spent on a home range versus travelling. However, because of small samples, the power of statistical tests was relatively low, (range: 0.05 to 0.28) so there may yet be biological differences that I failed to detect. My finding that body condition was negatively correlated with home range size in females seems to suggest that dominance may indeed affect home range size. Given that breeding pairs form in the arctic on the breeding grounds (Holt et al. 2015), differences in home range size are likely not due to mate searching behaviour by one sex.

Several reasons could explain why the relative size of home ranges between the sexes was quite variable. First, although female Snowy Owls are likely dominant over males in winter, using different habitats (Chang and Wiebe, chapter 2) and having higher body condition and survival (Chang and Wiebe 2016), Snowy Owls may not consistently defend exclusive feeding territories. If the boundaries of ranges are not monitored and defended, there may be some overlap of males and females on the landscape which may reduce the variation in habitat quality between the sexes. Alternatively, owls may tolerate the presence of other individuals on the home range but competition may occur in the form of direct interference competition over specific resources. In this case, dominant females may coexist in areas with males, and conflicts, which females would be more likely to win, would occur over individual prey items. Such intraspecific kleptoparasitism is commonly seen in gregarious birds such as gulls (e.g. Galvan 2003). Specifically, Lesser Black-backed Gulls (*Larus fuscus*) selected victims of equal or younger age, and success in kleptoparasitism increased with age of the aggressor and decreased with age of the victim (Galvan 2003), suggesting an important role of dominance. In raptors, Bald Eagles (*Haliaeetus leucocephalus*) are known to steal food from conspecifics (Jorde and Lingle 1988). Sex-skewed interspecific kleptoparasitism of Common Kestrels (*Falco tinnunculus*) exists such that males defend their prey less vigorously and are more likely to be kleptoparasitized than females (Kitowski 2005). And for intraspecific kleptoparasitism of Lesser Kestrels (*Falco naumanni*), females were almost exclusively the aggressors, while kleptoparasitism was directed mostly at males (Negro et al. 1992).

In our study system, I opportunistically observed two interactions between male and female Snowy Owls, and both times the female was the aggressor towards the male, once with a food item involved. Experimentally, when presented with conspecific taxidermy mounts, I found

that a greater proportion of females than males acted agonistically (approach/attack), whereas a greater proportion of males than females flew away (Appendix 1). The behaviour directed towards taxidermy mounts also varied based on the sex of the mount, with more owls approaching/attacking male mounts, and more owls flying away from female mounts (Appendix 1).

Another possibility is that because of sexual size dimorphism, the dietary niche differs sufficiently between male and female Snowy Owls such that, although individuals defend territories, optimal territory sizes would be based on different distributions of prey species and foraging techniques. In that case, movement patterns and the relationship of home range sizes to energetics and habitat quality could be variable and difficult to compare. According to the female supplemental feeding hypothesis for sexual size dimorphism in raptors (Reynolds 1972), males and females are different sizes so they can exploit different foraging niches and hence be more able to provide for growing chicks by hunting a broader prey base. An added effect of this niche separation is that the sexes experience reduced competition for food (Reynolds 1972, Andersson and Norberg 1981, Massemin et al. 2000). For example, in three harriers: Marsh Harrier (*Circus aeruginosus*), Pallid Harrier (*C. macrourus*), and Montagu's Harriers (*C. pygargus*), males and females preferred different winter foraging habitats associated with smaller and larger prey, respectively (Buij et al. 2012). In a study of three sexually dimorphic forest hawks, Sharp-shinned Hawks, Cooper's Hawks (*Accipiter cooperii*), and Northern Goshawks (*A. gentilis*), mean prey mass was greater for females than males for all species, and this difference increased with the degree of sexual size dimorphism (Storer 1966). Similarly, female Snowy Owls include a wider diversity of larger prey in their diets than males, such as Richardson's ground squirrels (*Spermophilus richarsonii*), white-tailed jackrabbits (*Lepus townsendii*), weasels (*Mustela* spp.),

and Grey Partridge (*Perdix perdix*), than males (Boxall and Lein 1982b). Nevertheless, their prey niche still overlaps greatly as both sexes predominantly feed on small mammals in winter on the Canadian prairies (males: 85%, females 79%, Boxall and Lein 1982b). Furthermore, if anything, the ability to exploit larger and more diverse prey suggests females could meet their energy requirements within a smaller area compared to males.

There did not seem to be consistent differences between the sexes of Snowy Owls in the amount of time they spend on home ranges versus travelling on the landscape or in the time or the distance they moved. In other bird species such as Brown Skuas (*Catharacta antarctica lonnbergi*), dominant breeders defended feeding territories whereas non-dominant breeders and non-breeders, which were unable to do so, moved more on the landscape to exploit temporarily available and less concentrated food resources (Hahn and Bauer 2008). Dominant male Little Bustards (*Tetrax tetrax*), a disperse-lekking species, defended small, concentrated home ranges in high quality habitat whereas more subordinate males used larger home ranges and travelled between multiple leks (Ponjoan et al. 2012). A similar relationship between behavioural dominance and decreasing home range size within the sexes has been found also in Wild Turkeys (*Meleagris gallopavo silvestris*, Badyaev et al. 1996). Compared to Common Ravens (*Corvus corax*) in temperate regions, which hold winter territories, those in the Arctic are more nomadic because of reduced food availability (Restani et al. 2001).

In Snowy Owls, dominance relationships between the age classes relate to differences in winter home range size, as adult females use smaller winter areas than juvenile females (Boxall and Lein 1982a). Because the sample size of transmitter-marked owls in this study was relatively small, I failed to find that home ranges of female owls were significantly larger than males although current data point in that direction. Increasing the sample size would help resolve this

question and future work should also address the degree to which any differences in prey base may affect the movements and energetics of male versus female Snowy Owls.

Annually, a large number of Snowy Owls winter on the North American prairies (Potapov and Sale 2012), yet gaps exist in our knowledge of habitat requirements, and how these affect space use and movements. Such information is important to predict how owls may respond to anthropogenic changes in habitats which affect foraging success and to better understand how the population is using and adapting to the rapidly changing prairie landscape.

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Ethics Statement: Owls were trapped under permit numbers 10736 and 10737. And small mammal surveys were done under Animal Care permit 20140085.

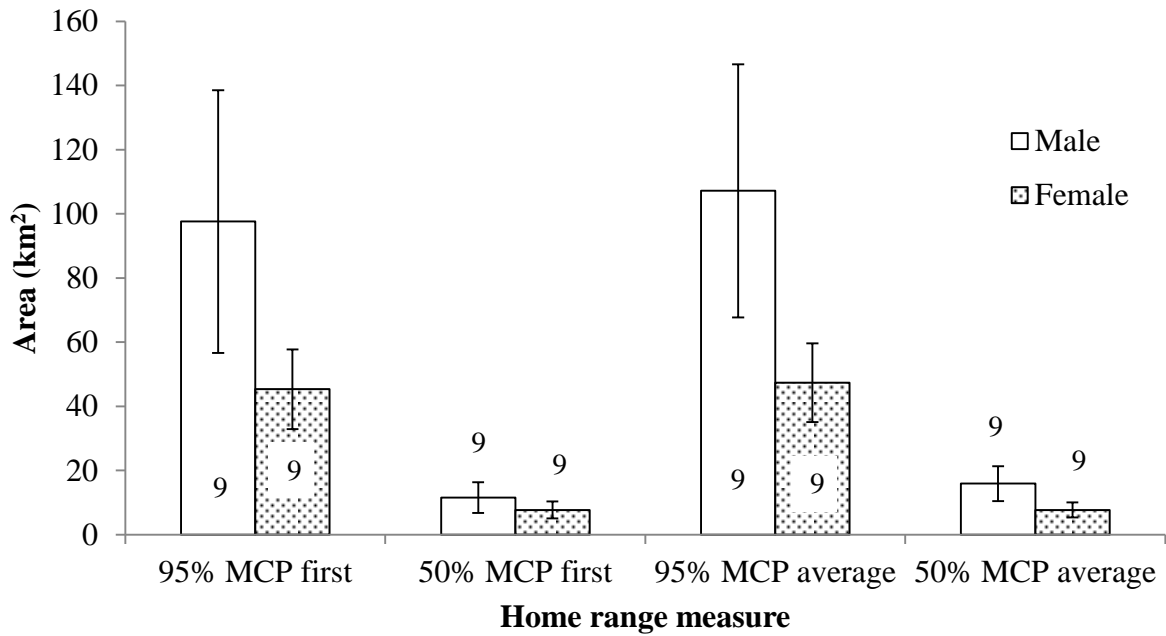


Figure 3.1. Mean areas of winter home ranges of male and female Snowy Owls in Saskatchewan.

Error bars indicate standard error. Numbers indicate sample size.

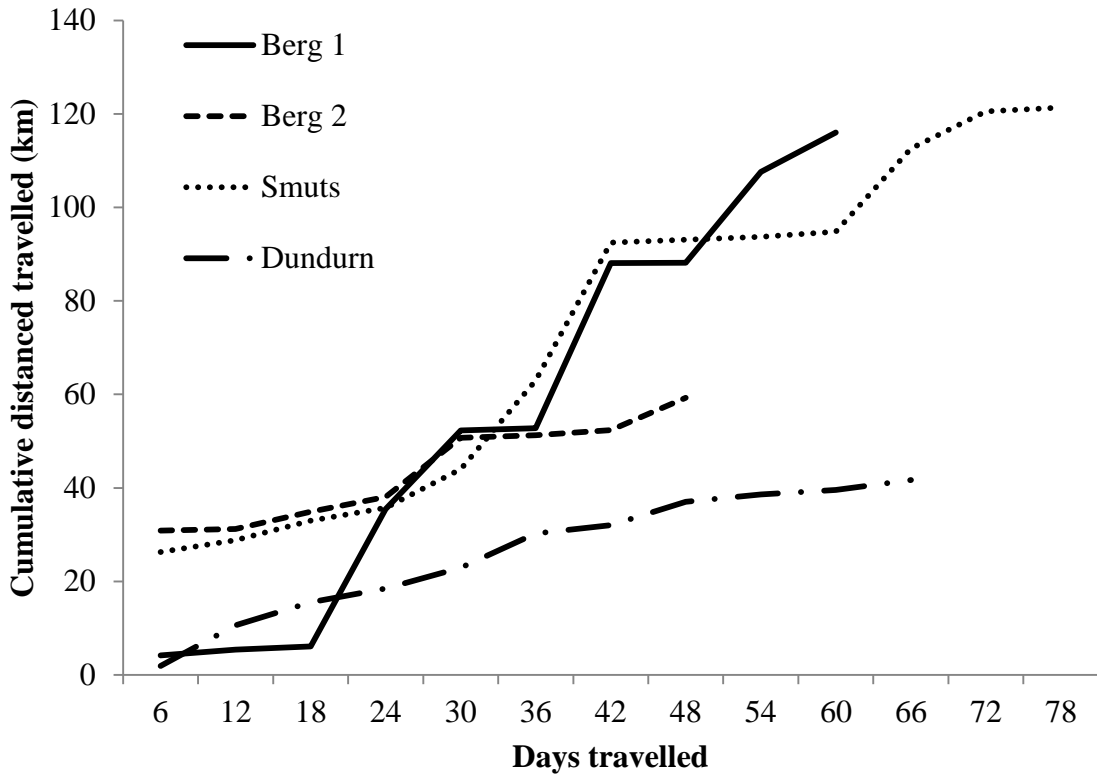


Figure 3.2. Cumulative distanced moved between winter home ranges over time for four male Snowy Owls. Each line represents a different individual.

CHAPTER 4: BODY CONDITION IN SNOWY OWLS WINTERING ON THE PRAIRIES IS GREATER IN FEMALES AND OLDER INDIVIDUALS AND MAY CONTRIBUTE TO SEX-BIASED MORTALITY

4.1 Abstract

Birds that winter in cold northern climates face harsh conditions including reduced food availability and increased energy demands. In raptors, the ability to forage and maintain body condition may be related to age (hunting experience) or the ability to defend good quality territories (dominance). I examined the effect of age and sex on body condition and various sources of mortality in wintering Snowy Owls (*Bubo scandiacus*) on the Canadian prairies. Because of reversed sexual size dimorphism, I predicted that female owls, the dominant sex, would be in better condition than males, and that adults would be in better condition than juveniles. Consistent with these predictions, data from 537 live owls trapped over 18 winter field seasons showed that adults were heavier than juveniles for a given body size and carried more fat reserves. I found that 56% of male owls lacked furcular and wing pit fat whereas only 31% of females lacked such fat and females but not males tended to put on fat during the winter months. A comparison of the sex ratio of starving owls turned in to rehabilitation centers (63% male) and the sex ratio of living owls observed in the wild (45% male) showed a male-bias in starving and diseased owls. Although most of the wild-trapped birds were above the starvation threshold, proximate mechanisms by which sex-biased competitive dominance manifests in differences in body condition and survival warrant further study.

Keywords: Snowy Owl, intraspecific competition, winter, body condition, survival, fat reserves, energy reserves.

4.2 Introduction

Most research on birds has been conducted during their breeding seasons yet there is increasing recognition that behaviour and performance during the winter months are important parts of the annual life history which can have carry-over effects on lifetime fitness (Marra and Holmes 2001, Duriez et al. 2012). In winter, some species of birds move over large spatial areas in conspecific (Warkentin and Morton 2000, Fernandez-Juricic 2002) or mixed-species flocks (King and Rappole 2000) and access food according to dominance (Ketterson 1979, Enoksson 1988, Marra 2000). Other species, however, establish territories on wintering grounds which are often defended from conspecifics of both sexes (Koronkiewicz et al. 2006). This can lead to habitat segregation between sex or age classes with the dominant individuals monopolizing the habitats with the most abundant food. For example, dominant male American Redstarts (*Setophaga ruticilla*) wintering in central America claim the most productive mangrove habitats whereas many females and juveniles are relegated to drier scrub (Marra 2000). Significantly, this habitat use affects body condition of the sex and age classes (Marra and Holmes 2001) and affects migration and breeding performance the subsequent summer (Norris et al. 2004).

Food limitation is likely a significant source of mortality for wintering raptors compared to the breeding season (Riegert and Fuchs 2011) as a result of snow cover which can reduce prey capture rates or harsh weather which reduces prey population sizes (Heisler et al. 2014). Reduced food availability may thus occur exactly when thermoregulatory costs are high and represent a period of high energetic stress during winter. For example, most recovered radio-tagged Golden

Eagles (*Aquila chrysaetos*) wintering from southern Alberta to north-central Mexico died from starvation (McIntyre 2012). Of wintering Great Grey Owls (*Strix nebulosa*) killed in vehicular collisions in Minnesota, emaciated individuals were more likely to have empty stomachs, suggesting a link between hunting success and body condition, and ultimately, survival (Graves et al. 2012). A few raptors, for example European Kestrels (*Falco tinnunculus*, Village 1982), Little Owls (*Athene noctua*, Finck 1990) and Barred Owls (*Strix varia*) and Spotted Owls (*Strix occidentalis*, Hamer et al. 2007) are known to defend larger winter than summer territories, presumably in an attempt to maintain prey capture rates and energy balances in harsher foraging conditions.

A study of overwintering body condition and survival is especially interesting in birds of prey because they show reversed sexual size dimorphism with females larger than males (review in Kruger 2005). Information is scant in winter but in some species, females are dominant over males, excluding them from high quality territories through competition and aggression (e.g. American Kestrels, Ardia and Bildstein 1997, Northern Harriers *Circus cyaneus*, Littlefield and Johnson 2005, Barred Owls and Spotted Owls, Hamer et al. 2007). Adult raptors often outcompete yearlings for high quality habitats (Kjellen 1994) and survival of young raptors in their first winter is often lower than in adults (Anders and Marshall 2005, Roth et al. 2005) and is often strongly dependent on prey abundance (Rohner and Hunter 1996, Todd et al. 2003, Mannan et al. 2004, Wiens et al. 2006). Adult female Red-Tailed Hawks (*Buteo jamaicensis*) wintering in Nebraska increased in body mass over the season, whereas adult males and juvenile females showed no change, suggesting resource competition favoring adult females (Schoenebeck et al. 2014).

I studied the body condition and relative mortality of the sexes of wintering Snowy Owls (*Bubo scandiacus*) on the Canadian prairies. These large raptors breed in the Arctic tundra and a component of the population migrates to winter on the North American prairies (Kerlinger et al. 1985, Potapov and Sale 2012) whereas others remain in the Arctic year-round (Therrien et al. 2011). Some have suggested that Snowy Owls are forced south in winter because of a lack of prey in the Arctic and so such owls are starving (Gross 1947, Lack 1954). Kerlinger and Lein (1988b) argued against this based on fat stores they found in some wintering Snowy Owls, but because of small samples of live birds, their statistical analysis was limited to pooled data of living owls and owls turned in dead. Here, I use a larger sample of live-trapped birds in the wild to investigate patterns of body condition between sexes and age classes.

I did not document social interactions between the sexes but Evans (1980) noted that the larger female Snowy Owls displaced juvenile males in winter and Boxall and Lein (1982a) saw females being aggressive towards males and concluded females were dominant (Kerlinger and Lein 1988b). Hence, I tested the hypothesis that dominance gives females access to the most food-rich areas and predicted that they would have higher body condition and overwinter survival than males. I also tested the hypothesis that juveniles are poorer hunters than older birds, predicting that adults would have higher body condition and survival than juveniles. This pattern of body condition between sex and age classes has been found throughout the year in Northern Goshawks (*Accipiter gentilis*) which also exhibit reversed sexual size dimorphism (Sunde 2002). Furthermore, I expected that body condition of owls may decline during winter, but that the rate of this decline would be higher in males and juveniles. I used a different sample of living, but emaciated, owls turned into veterinary facilities for rehabilitation to see how the body mass of starving owls compared to the average body mass in the wild, wintering population. Finally, I

tested whether the sexes were differentially affected by harsh winter conditions by comparing the sex ratio of injured and sick owls brought to veterinarians and bird rehabilitation centers to the sex ratio in the wild wintering population.

4.3 Methods

4.3.1 Study Site and Study Species

I studied wild, wintering Snowy Owls captured in south-central Saskatchewan roughly as far north as Shellbrook, SK (53.2167°N), and as far south as Swift Current (50.2881°N). Today, agricultural lands predominate and include pasture (rangeland), as well as cropland growing mainly canola, pulses, and cereals. Winters are cold in south-central Saskatchewan, with frequent sustained temperatures below -20 °C and some days as low as -40 °C. Snow cover is variable but may persist from late October to early April.

Snowy Owls arrive annually on the Canadian prairies in late October to early November and most migrate north again by early April. Here, the owls may prey on land birds such as Grey Partridge (*Perdix perdix*) and Rock Pigeons (*Columba livia*) but most of the diet seems to be small rodents (Boxall and Lein 1982b). Female owls are roughly 29% larger than males based on body mass (Holt et al. 2015).

4.3.2 Field data

Living, wild Snowy Owls were trapped in the field by two licensed banders between October and April, from 1997/98 to 2014/15 using a variety of traps including bal-chattris, drop-nets, and remotely-triggered bow-nets. Upon capture, owls were banded and weighed on a digital scale and several measures of body size were taken: unflattened wing chord length, culmen length, tail

length, and footpad length. Weight, plumage barring and molt were used to age and sex individuals. Juvenile (hatch year) owls can be distinguished by mottling on the greater coverts and primaries and even wear of the remiges whereas older owls possess different generations of remiges with differential fading of the dark bands (Josephson 1980, Boxall and Lein 1982b). For simplicity, I only categorized age of owls as juvenile (HY/SY) and adult (AHY/ASY). The thickness of breast muscle reflects the amount of protein stores on a bird and is used to indicate nutritional status (DeLong 2006, Bedrosian and St. Pierre 2007). The owl banders scored this by feeling the keel projection and I ranked it on a scale of 1 to 4. One bander recorded the amount of subcutaneous fat in the furculum and wing pit and this was scored on a scale of 0 to 7 (e.g. Rogers and Heath-Coss 2003).

Because the sex ratio of wild-trapped owls may be influenced by the willingness of each sex to attack bait, I used systematic counts of owls seen in the wild to obtain an unbiased estimate of wintering sex ratio on the prairies. To locate Snowy Owls, I drove along a 60 km transect once or twice weekly, from November to April, during the 2013-14 and 2014-15 winters. Owls were spotted from the vehicle, up to 1.6 km away, and detection is probably nearly 100% within 0.8 km within the bare and flat landscape. Owls along the transect were sexed by sight using multiple cues such as size, amount of plumage barring and whether or not the dark tail bands were unbroken across the retrices. Such shapes and patterns of plumage bars were effective at sexing 100% of juvenile Snowy Owls (Seidensticker et al. 2011).

4.3.3 Data on sick and injured owls

I created a separate dataset of sick and injured Snowy Owls admitted for treatment at veterinary schools and bird rehabilitation facilities on the prairies in Canada to determine: 1) the

lowest threshold body mass indicative of emaciated owls and 2) the sex ratio of owls suffering various sources of stress or mortality. I obtained case records from Saskatoon (1992-2015), Calgary (1992-1999) and Winnipeg (2015). Owls which subsequently died or were euthanized in care were sexed by veterinarians when necropsied and other owls which were released were sexed by physical measurements and plumage. Where possible, I obtained photographs of the tails and outstretched wings of the birds to confirm the sex myself. I excluded any cases where the sex was not recorded or was unclear and only used weights of owls which were still alive at the time of admittance so the weights were not biased by desiccation or scrounging by predators.

I categorized causes of admittance as "trauma" which included being hit by a vehicle and any other impact which caused broken bones or external wounds. Other causes were listed as "emaciation" or "disease". The proximate versus ultimate cause of death is not always easy to determine but I excluded any owls with trauma when calculating body mass for owls diagnosed as emaciated or diseased in order to calculate a body condition indicative solely of nutritional stress. For comparison, I also calculated the body condition of those birds which suffered trauma to see whether such birds were also emaciated.

4.3.4 Statistical Analyses

To compare body reserves between sex and age classes I used three variables: a body condition index, fat scores and keel scores. These analyses were done only on the wild-trapped owls and did not include veterinary birds. I used residuals of a regression of mass on structural body size (wing chord) as a condition index (e.g. Sarasola et al. 2004) calculated separately for each sex because of the sexual size dimorphism. There was no difference between wing chord as measured by the two banders (t -tests: males, $t_{217} = 0.23$, $P = 0.82$; females, $t_{302} = 0.55$, $P = 0.58$),

so I pooled captures. To test for differences in condition between age classes, I ran ANCOVAs for each sex with date of capture as a covariate.

Fat and keel scores were analyzed in several ways. Because many birds lacked furcular and wing pit fat entirely, I used a binary logistic regression to look at presence versus absence of any fat in relation to sex, age and capture date. A few individuals were not aged at capture so I analyzed a larger dataset using a simple chi-square test to compare the proportions of owls with and without fat between the sexes. I subsequently used an ordinal regression to test whether sex, age, or date could predict the amount of fat stores. Similarly, I used an ordinal regression to test whether keel muscle fullness could be predicted based on an owl's sex and age, and date. All interaction terms were included in the initial regressions but were removed if non-significant ($P > 0.05$).

I compared the weights of owls admitted for treatment with weights of live-trapped owls in Saskatchewan with a 2-way ANOVA. Years were pooled as there were too few cases per year to allow an examination of annual effects. A sex ratio for each cause of death was also calculated and compared to the average sex ratio of wild-trapped owls observed on the 60 km transect route. I assumed that members of the public turned in sick and injured owls which they encountered irrespective of the sex of the bird and so that the sex ratios of the veterinary birds were unbiased estimates of the sex ratios of owls actually suffering distress. Data were analyzed using SPSS 22.0 with significance at $\alpha = 0.05$.

4.4 Results

During 18 winter field seasons of trapping in south-central Saskatchewan, male owls averaged 1611 ± 12 g SE, $n = 222$ whereas females averaged 2149 ± 14 g SE, $n = 315$, with ages pooled.

An ANCOVA on the body condition index of female owls found that adults ($n = 216$) were significantly heavier than juveniles ($n = 53$, $F_{1, 264} = 8.97$, $P = 0.003$) but there was no effect of trapping date ($F_{1, 264} = 0.39$, $P = 0.53$; Figure 4.1). Similarly for males, adults ($n = 113$) were heavier than juveniles ($n = 65$; $F_{1, 174} = 9.81$, $P = 0.002$) with no effect of trapping date ($F_{1, 174} = 0.33$, $P = 0.57$; Figure 4.1). Interactions between age class and trapping date on body condition were not significant for either sex (females: $F_{1, 264} = 0.00$, $P = 0.99$; males: $F_{1, 174} = 1.36$, $P = 0.25$).

Using a dataset which included individuals which were not aged, a greater proportion of males (56%, $n = 66$) than females (31%, $n = 147$) completely lacked furcular and wing pit fat ($X^2 = 12.46$, $P < 0.001$). A similar result was found using the logistic regression on owls with recorded ages; females were more likely to have furcular and wing pit fat than males (odds ratio = 0.92, Wald $X^2_1 = 8.14$, $P = 0.004$) and adults were more likely to have such fat than juveniles (odds ratio = 1.16, Wald $X^2_1 = 5.46$, $P = 0.02$). The likelihood of having furcular and wing pit fat deposits increased over the winter season (odds ratio = 0.012, Wald $X^2_1 = 8.11$, $P = 0.004$). In an analysis of the seven categories of fat with an ordinal regression, females had more fat than males (odds ratio = 0.732, Wald $X^2_1 = 6.56$, $P = 0.01$) and adults had more fat than juveniles (odds ratio = 1.04, Wald $X^2_1 = 4.93$, $P = 0.026$), with fat deposits again increasing over the season (odds ratio = 0.012, Wald $X^2_1 = 12.22$, $P < 0.001$; Figure 4.2). The percentages of females lacking furcular and wing pit fat during early (up to Dec 31), mid (Jan 1 to Feb 28/29), and late winter (Mar 1 and onwards), were 43% (44), 25% (80), and 26% (23) respectively (sample sizes in brackets). The percentages for males in the same periods were 65% (31), 52% (25), and 40% (10).

An ordinal regression on keel scores showed that adult owls had thicker breast muscle than juveniles (odds ratio = 2.61, Wald $X^2_1 = 100.11$, $P < 0.001$), and there was a trend that females had thicker breast muscle than males (odds ratio = 0.36, Wald $X^2_1 = 3.16$, $P = 0.08$). Unlike fat deposits, there was no relationship between trapping date and keel scores (odds ratio = 0.00, Wald $X^2_1 = 0.02$, $P = 0.90$).

Of 134 sightings of wild owls on the transect in 2013-14, 45% were males and of 369 sightings in 2014-15, 44% were males. This sex ratio did not differ between years ($X^2_1 = 0.004$, $P = 0.95$), so I pooled years for an average ratio in the wild of 45% males. Sex ratios (% male) for owls from veterinary clinics varied according to the cause of distress (Figure 4.3). There was a higher proportion of males in the emaciated class compared to wild-trapped owls or owls with trauma ($X^2_3 = 13.52$, $P = 0.004$; Figure 4.3). Of the 238 owls submitted for rehabilitation, the most common cause was emaciation (43% of cases; Figure 4.3). In addition to the significant effect of sex on body mass ($F_{1, 602} = 264$, $P < 0.001$), a 2-way ANOVA found that the four different health categories of owls had different body masses ($F_{4, 602} = 228$, $P < 0.001$), and a significant interaction between sex and health category ($F_{4, 602} = 6$, $P < 0.001$, Figure 4.4). Tukey's post-hoc contrasts showed that all health categories except for trauma and wild-trapped juveniles differed significantly from each other. Wild-trapped adult females were 73% heavier than emaciated females which weighed on average 1286 ± 66 g SE and wild-trapped adult males were 73% heavier than emaciated ones at 975 ± 26 g SE. Wild-trapped juvenile females and males were 46% and 54% heavier than emaciated ones, respectively.

4.5 Discussion

There were differences in body condition between sex and age classes in the wild, free-living population consistent with our predictions. In addition, the male bias in mortality rate suggests that males and juveniles face greater challenges than females and adults in meeting energetic demands during winter. However, our findings are counter to the idea that Snowy Owls that winter south of the Arctic breeding range are mostly in very poor condition and in agreement with Kerlinger and Lein (1988b). Namely, I found that average body masses of overwintering owls on the prairies were substantially above those of starving owls turned into rehabilitation facilities.

4.5.1 Dominance and body reserves in Snowy Owls

I found that the dominant sex and age classes (females and adults) had more fat reserves than subordinates, similar to the pattern found in some other relatively large-bodied birds which do not rely on flight to escape predators (e.g. Hohman et al. 1992, Moon and Haukos 2009). In such birds, fat stores may be consumed and diminish over winter (Massemin et al. 1997, Thouzeau et al. 1997), and fat stores, up to a point, are positively correlated with overwinter survival (Thomas 1987). In contrast, some studies on passerines with high predation risk show that dominant individuals maintain lower fat reserves than subordinates (Witter and Swaddle 1995, Pravosudov et al. 1999, Polo and Bautista 2002) presumably because fat deposits reduce escape ability and require longer foraging time in areas exposed to predation (Lima 1986, Lilliendahl 1997, Rogers 2015). Apparently Snowy Owls as apex predators (Holt et al. 2015) have a strategy of maximizing body reserves in harsh and unpredictable climactic conditions and dominant individuals are most able to achieve this.

Indeed, counter to our expectation, subcutaneous fat stores seemed to increase in adults during the winter, although the weight of deposited fat may be small relative to total body mass because no temporal change was detected in the body condition residuals over time. Apparently the older owls which are probably skilled hunters may be able to build up or at least maintain energy reserves during the winter months. This ability may occur because Snowy Owls are well insulated and adapted to withstand very cold temperatures (Gessaman 1972). Furthermore, winter is also a time when owls are not engaged in energetically costly activities such as reproduction, and movements on the landscape may be reduced. Thus, given sufficient food sources, winter may actually be a time for owls on the prairies to increase energy stores prior to migration, especially in adult females preparing for reproduction.

4.5.2 Age- and sex-related differences in body reserves

Consistent with our second prediction, adults had better body condition than yearlings as would be expected if adults are more capable foragers than yearlings or are more able to identify high quality habitat (high prey availability) and defend it. I did not quantify hunting success of owls but a study of Missouri raptors showed that adults had higher hunting success than juveniles in 8 of 9 species (Toland 1986). The only species for which juveniles had greater hunting success was the Sharp-shinned Hawk (*Accipiter striatus*), and this difference disappeared when controlling for prey type, as only juveniles attacked invertebrates, and only adults successfully hunted birds. Thus, some young raptors may compensate for being in poorer quality habitat and for poor hunting ability by pursuing less rewarding, but easier prey, but easy and abundant prey such as insects are not available to wintering Snowy Owls. Rather, alternative prey are likely more difficult to capture than small mammals and include game birds, waterfowl, and shorebirds

(Williams and Frank 1979, Boxall and Lein 1982b). Thus, any hunting disadvantage experienced by yearlings is likely to manifest in decreased physical condition.

For overwintering raptors hunting small mammals in fluctuating snow depths and temperatures, maintaining a reserve in the form of muscle or fat on the body is a way to buffer unpredictable food shortages (Rogers and Heath-Coss 2003). Our data showed that females maintained significantly more body fat than males and tended to also have more breast muscle mass although the sex effect was less apparent for the latter measure. A larger variance in fat stores compared to muscle stores may be expected if fat is the primary fuel metabolized in conditions of reduced food availability or increased food variability. Indeed, other birds such as overwintering Mallards (*Anas platyrhynchos*) in Edmonton (Pawlina et al. 1993) and migrating Short-tailed Shearwaters (*Puffinus tenuirostris*, Baduini et al. 2001) consumed breast muscle only after fat stores were nearly depleted. Thus, adult male Snowy Owls may be more food stressed compared to females because they have less fat, but juvenile owls may be the most severely stressed of the sex-age classes because they lack both furcular and wing pit fat and protein (breast muscle).

Within each sex, adult Snowy Owls had a higher body condition index and carried more fat and breast muscle than yearlings. Similarly, in many populations of large birds in winter, adults have been found to have higher mass than juveniles, including ducks (Hohman and Weller 1994, Kestenholz 1994), shorebirds (O'Reilly and Wingfield 2003), Red-Tailed Hawks (Schoenbeek et al. 2014), and Eurasian Kestrels (Dijkstra et al. 1988). The specific relationship between age and wintering protein levels has been studied mostly in waterfowl, and many studies have found higher protein stores in adults than juveniles (Morton et al. 1990, Hohman and Weller 1994, Jamieson et al. 2013).

4.5.3 Overwinter mortality and its relationship to sex and body condition

Of the owls brought into veterinary and rehabilitation facilities, the leading cause was emaciation, followed closely by physical trauma, mostly from vehicle collisions. The proportion of emaciated owls in our veterinary data (43%) is substantially greater than the 14% starving owls reported by Kerlinger and Lein (1988b) who found the main cause of distress was trauma. However, one cannot make strong conclusions about the frequencies of the various causes of death in the veterinary data because there are may be biases in the types of injured/ sick owls found by the public. For example, there is probably a positive bias in owls found near roadsides, likely over representing the influence of vehicle collisions. Furthermore, one is unable to assess the actual (absolute) mortality rate in the wild population based on the number of owls turned into rehabilitation facilities.

In the sample of veterinary owls, disease and starvation were hard to separate as ultimate cause of death, as they both entailed low weights relative to the wild-trapped owls. Experimental food-restriction has been shown to reduce immune function in other species of birds (Alonso-Alvarez and Tella 2001) and conversely, experimental infection by bacteria may also reduce feeding rate and body mass (Johnson et al. 1993, Owen-Ashley et al. 2006). I found no sex-bias in traumatic injuries suffered by Snowy Owls in winter, so such injuries happened to owls irrespective of body condition or sex. In contrast, the significant male-bias in owls suffering from disease and especially emaciation supports the prediction that the subordinate sex (males), with their lower average body condition than females in winter, are more likely to succumb to food shortages than females. Some field studies have shown that winter mortality among raptors is

often greater in juveniles than adults (Anders and Marshall 2005) because adults are better hunters and competitors (Kjellen 1994).

Clearly, some owls of both sexes became emaciated while wintering on the Canadian prairies but the average body mass of adult wild-trapped owls was 73% above the emaciation threshold so most overwintering owls on the prairies were not starving. However, further information is needed on owls which appear in the south sporadically during "irruption years" from other regions of the continent, because those cohorts may contain a higher proportion of food-stressed juveniles (Holt and Zetterberg 2008, Robbins and Otte 2013). As well, I know little about carry-over effects and seasonal changes in mass although the average mass of females in the current study (2149 g) seems similar to nesting females trapped in Nunavut in 2007 (2170 ± 45 g SE, $n = 11$, Therrien et al. 2008). I found that body condition and starvation risk in winter was aligned with dominance and perhaps hunting skill between sex and age classes so the next step is to determine how females gain better access to food, whether they hold better quality territories than males or whether they can capture larger and perhaps more rewarding prey items by virtue of their larger body size than males (Boxall and Lein 1982b, Toland 1986). Thus, further data on differences in movements, space use, and diet between male and female Snowy Owls would be helpful in illuminating aspects of their energetics during winter.

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Ethics Statement: Owls were trapped under permit numbers 10736 and 10737.

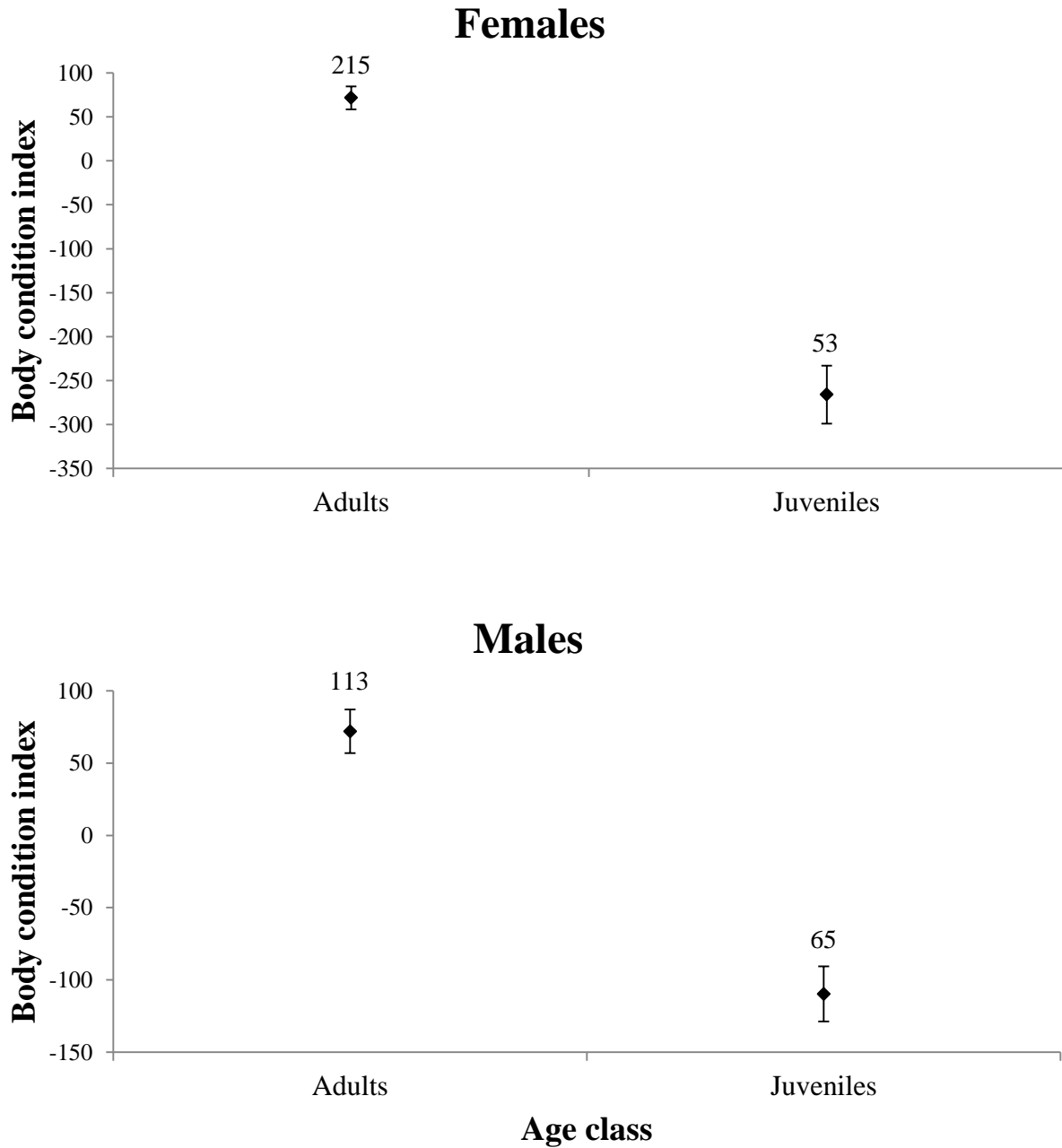


Figure 4.1. Mean body condition (+/- SE) of wild-trapped female ($n = 269$, top panel) and male Snowy owls ($n = 178$, bottom panel) over 18 winters during 1997/98-2014/15 in south-central Saskatchewan. Numbers above the points indicate sample size.

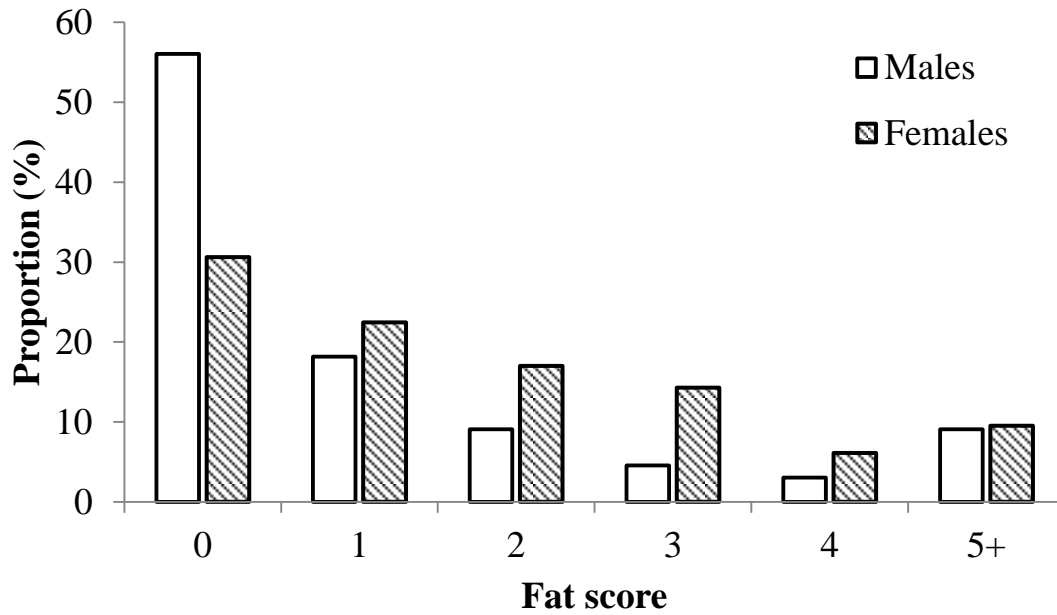


Figure 4.2. The distribution of male ($n = 66$) and female ($n = 147$) Snowy Owls according to the relative amount of body fat deposits. A score of zero signifies that no visible fat was observed.

The birds were live-trapped during winter in Saskatchewan during 2004/5-2014/15.

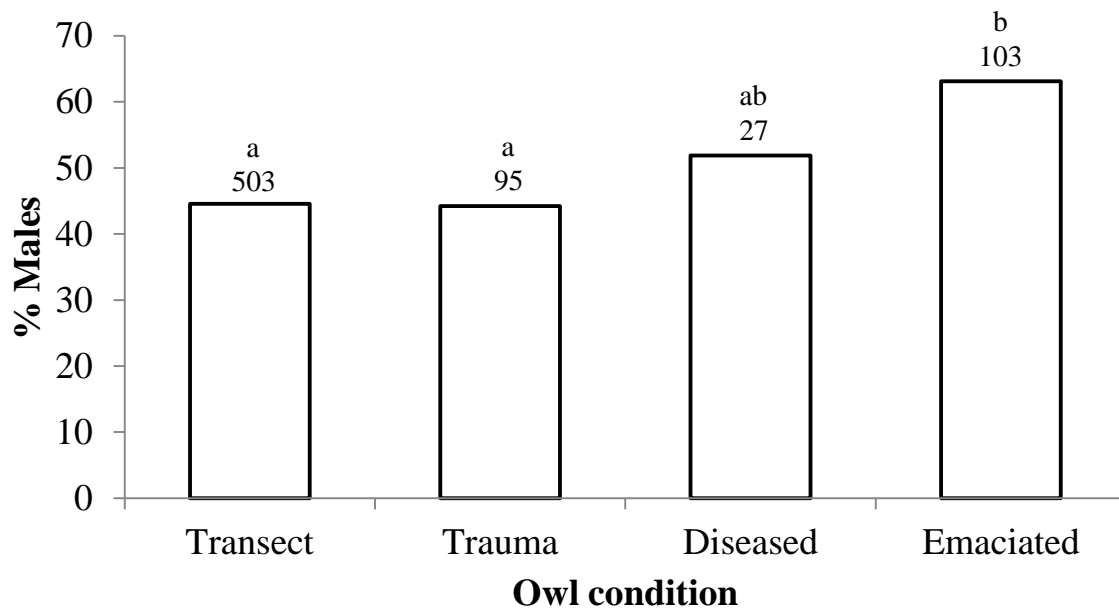


Figure 4.3. Sex ratios of wild Snowy Owls seen during transect surveys in Saskatchewan conducted along grid roads during winter, 2013-14 and 2014-15, versus those brought to rehabilitation facilities for various causes. Numbers above the bars indicate sample size. Owls in different health categories with different letters above the bars indicate significant differences according to Tukey's test at $P < 0.05$.

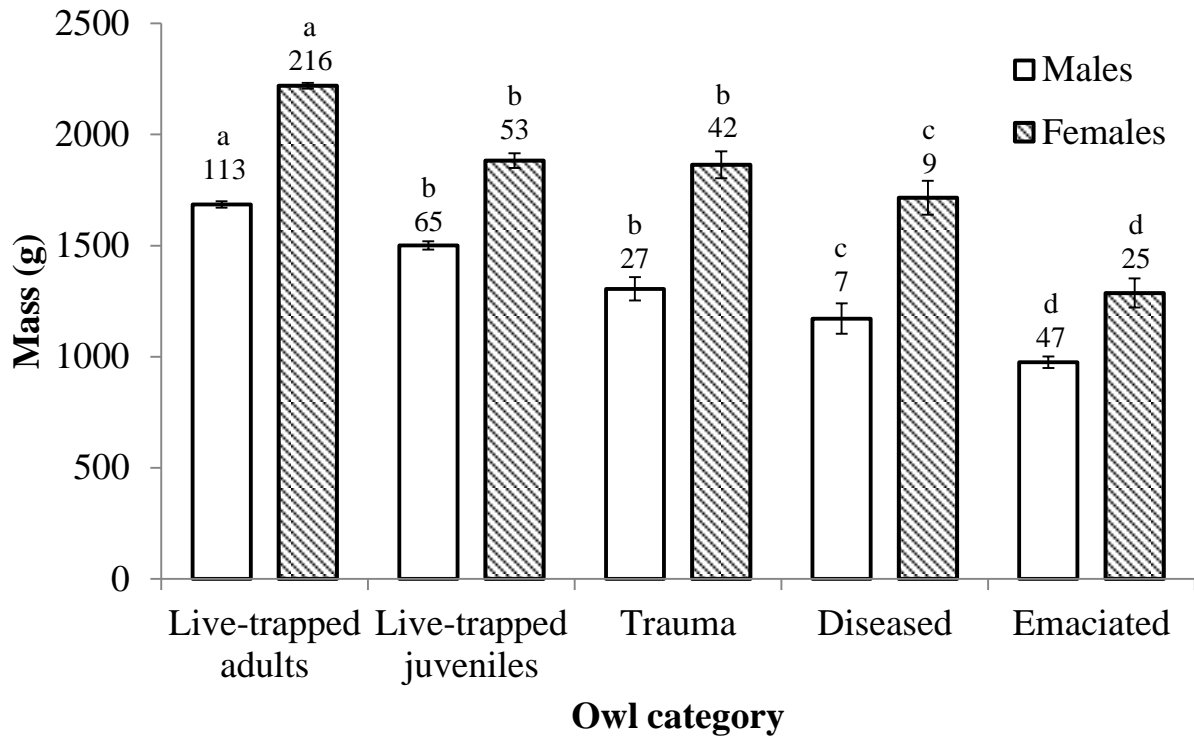


Figure 4.4. Mean body mass (+/- SEM) of Snowy Owls live-trapped in Saskatchewan versus those brought to rehabilitation facilities on the Canadian prairies for various causes. Age classes are pooled for the birds admitted for treatment but are shown separately for the wild trapped owls and numbers above the bars indicate sample size. Within each sex, owl categories with different letters above the bars indicate significant differences according to Tukey's test at $P < 0.05$.

CHAPTER 5: GENERAL DISCUSSION

5.1 Overview

The goal of this research was to broadly understand the relationship between wintering male and female Snowy Owls on the prairies in terms of competitive dominance, its effects on space and habitat use, and consequently body condition and survival. In agreement with previous studies on Snowy Owls and other raptors (e.g. Boxall and Lein 1982a; Ardia and Bildstein 1997, 2001; Buij et al. 2012), we found evidence that the larger females were competitively dominant over males (Appendix 1). Based on this knowledge, we sought to know whether females assert their dominance to achieve priority access to resources on the landscape. First, I looked at differences between males and females in the type of winter habitat they used (Chapter 2). Although prey abundance did not differ greatly between habitat types (pastures had fewer prey in one year, but there was no difference between the three crop types), the sexes differed in habitat selection on different scales, both selecting for legumes and against canola. I found that females placed home ranges in areas with a lower proportion of canola, and that the males, being relegated to areas with higher proportions canola, nonetheless avoided canola within their home ranges. There are many ways by which subordinate individuals of different species attempt to compensate for reduced access to high quality habitat, and whereas male Snowy Owls do place their home ranges in less ideal landscapes (based on the proportional availability of different habitats), they appear to concentrate more on legume fields with the least vegetative cover and where small mammal prey may be most accessible. .

I also quantified and compared the scale of winter movements between males and females in winter (Chapter 3). Using new GPS-GSM satellite telemetry technology, I was able to

regularly and precisely locate Snowy Owls at all times, and was thus able to generate more accurate estimates of home range size and movements in winter than was previously known for the species. Although the difference in average home range size between males and females is not statistically significant, possibly because of small samples, the direction of our data agree with the prediction that dominance is negatively correlated with home range size.

Finally, lest we mistakenly assume that males are able to fully compensate for their subordinate status and reduced access to resources by using alternative habitat or having larger home ranges, I compared winter body condition and survival between the sexes (Chapter 4). I sought to extend the findings of the first two data chapters to test if female dominance manifests in better body condition and survival in wintering female Snowy Owls. Combining field surveys, a large historical database of wild-trapped owls, and records from veterinary colleges and rehabilitation centers, I was able demonstrate a male bias toward lower winter body condition and reduced survival.

My research in Snowy Owls generally aligns with previous results on the winter ecology and habitat use of a few other raptor species, namely that female are socially dominant and can exclude males from the most productive winter habitats. I extended this knowledge about raptors' use of winter habitat by confirming speculation that such habitat segregation has fitness consequences for the sexes (Massemin et al. 1998; Ardia 2002). Using new technology, my research sheds some light on the biology of an iconic and well recognized species that has nevertheless not been the subject of much study, to date.

5.2 Future research, directions, and considerations

I was able to answer some questions about the winter ecology of Snowy Owls in Saskatchewan, increasing our understanding about how the sexes relate to each other in competition, and the population level effects of female dominance. However, as is often the case, my findings lead to further, unanswered, questions. Now that it is known that the average body condition of males is compromised more than that of females during the winter, it would be interesting to extend this study by monitoring individuals into the summer to test for carryover effects of this lower condition where one might predict female-biased sex ratios overall unless, the mortality of females is higher than that of males during other times (e.g. during breeding). For example, it would be interesting to investigate the relationship between winter body condition and the quality of breeding territory obtained in the Arctic by both sexes, and consequently their reproductive productivity. It would also be interesting to compare sex and age ratios in winter between Snowy Owls in the arctic and the prairies.

My thesis focused on differences between the sexes but further research on the winter ecology of Snowy Owls could apply similar techniques to study the relationship between age and dominance, and test whether younger age classes have lower access to habitats and resources than older individuals, and whether differences in winter body condition and survival are also related to age.

From a strictly behavioural point of view, we still know little about the signals or cues that individuals may use to determine or enforce dominance relationships. Owls clearly do interact with one another in direct competition using aggressive chases and physical contact, but the comparative role of visual signalling from a distance in maintaining dominance or territorial boundaries are yet unknown.

Finally, some patterns of male and female territory size and movements were consistent with predictions of space use associated with dominance, but were not statistically significant. I maximized the number of transmitters within the constraints of my budget and the 2-year time frame of the study, but as technology becomes cheaper a greater sample size of owls carrying transmitters would be more feasible and helpful in confirming the extent of any difference in home range size between the sexes.

In sum, my study has begun to illuminate aspects of the winter ecology of a well-known, but understudied species. This work will hopefully spur on additional research on Snowy Owls on the prairies but hopefully will also be integrated with studies of irruptive movements which occur continent wide (Holt and Zetterberg 2008; Robbins and Otte 2013) so we can better understand the habitat requirements and population dynamics of Snowy Owls on much larger scales, in order to mitigate threats linked to rapidly changing landscapes and climates (Samson and Knopf 1994).

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APPENDIX 1: Behavioural interactions between male and female Snowy Owls

To learn the mechanism by which female Snowy Owl dominance over males is established and maintained, I wanted to observe behavioural interactions between individuals. For example, some species engage in direct physical contests to establish dominance (Meese and Ewbank 1973; Issa et al. 1999) whereas other species avoid aggressive encounters by assessing visual cues of rivals such as body size or plumage colour (Searcy 1979; Crowhurst et al. 2012; Dwyer 2014). Observing interactions between individual Snowy Owls also gives insight into their winter spacing behaviour, whether they are territorial or tolerant of nearby conspecifics. Because direct interactions between live individuals may be difficult to observe in the field, other studies have used taxidermy mounts to simulate these situations (Elliot 1985; Van Lanen et al. 2011).

I searched for Snowy Owls along rural roads near Rosetown, Saskatchewan. Upon finding an owl perched close to a roadside, I drove towards it and placed a taxidermy mount of either a male or a female Snowy Owl 200 m away from the target owl (the sex of the mount was alternated systematically between trials and the mounts resembled typical adult Snowy Owls in plumage colouration and size). I recorded the sex of the live owl, and the sex of the mount. After placing the mount, I backed away to a distance of 500 m from the mount, and 700 m away from the live owl, and after turning off the vehicle, observed reactions of the live owl for 10 minutes through a spotting scope. Behaviours were classified as submissive (flying away from the mount, or flying to a lower perch), neutral (no change in position), or aggressive (any approach toward the mount, including fly-overs or direct physical contact). After 10 minutes, I picked up the mount. If the owl reacted prior to the stopping and turning off of the vehicle, the trial was not included in analysis.

Aggressive behaviour was more common towards male than female taxidermy mounts (Table 1), and submissive behaviour was more common in response to female than male mounts, but these differences were not significant (Fisher's Exact Test: $P = 0.17$). There was a pattern that male owls were more likely to react submissively towards mounts than females, and female live owls were more likely to behave aggressively towards mounts than males, but this was not significant (Fisher's Exact Test: $P = 0.15$). Most owls showed no reactions to the mounts so the sample size of reactions was small, nevertheless the patterns are consistent with the idea that males, more so than females, are threatened by female intruders and are more likely to flee or avoid contact with conspecifics.

Table 1. Counts (and proportions) of live male and female Snowy Owls exhibiting different behaviours when presented with a male (a) or female (b) Snowy Owl taxidermy mount 200 m away.

a) Reaction to male mount			
Live owl: Sex	Submissive	Neutral	Aggressive
Male	3 (23%)	9 (69%)	1 (8%)
Female	0 (0%)	8 (80%)	2 (20%)
b) Reaction to female mount			
Live owl: Sex	Submissive	Neutral	Aggressive
Male	6 (50%)	6 (50%)	0 (0%)
Female	3 (21%)	10 (71%)	1 (7%)