Canadian Journal of Zoology
Revue canadienne de zoologie

**Movement patterns and home ranges of male and female
Snowy Owls (*Bubo scandiacus*) wintering on the Canadian
prairies**

Journal:	<i>Canadian Journal of Zoology</i>
Manuscript ID	cjz-2017-0280.R1
Manuscript Type:	Article
Date Submitted by the Author:	30-Nov-2017
Complete List of Authors:	Chang, Alex; University of Saskatchewan, Biology Wiebe, Karen; University of Saskatchewan, Biology
Keyword:	BEHAVIOUR < Discipline, SEX DIFFERENCES < Discipline, telemetry, OWLS < Taxon, HOME RANGE < Habitat

Movement patterns and home ranges of male and female Snowy Owls (*Bubo scandiacus*)
wintering on the Canadian prairies

Alexander. M. Chang¹ (alex.chang@usask.ca)

Karen. L. Wiebe^{1,2} (karen.wiebe@usask.ca)

¹ University of Saskatchewan

Department of Biology

112 Science Place, Saskatoon SK, S7N 5E2

² Corresponding author

Tel: 306-944-4406

Fax: 306-944-4461

Draft

Movement patterns and home ranges of male and female Snowy Owls (*Bubo scandiacus*) wintering on the Canadian prairies.

By: Alexander M. Chang and Karen L. Wiebe

Abstract: Meeting energy requirements during the non-breeding season is important for many animals and some defend winter territories to secure a food supply. In birds of prey, females, the larger and competitively dominant sex may monopolize areas with higher prey abundance than males. We thus predicted that female Snowy Owls (*Bubo scandiacus* L., 1758) which might acquire the high quality habitats and individuals in better body condition would be able to persist on smaller home ranges, travel shorter distances, and spend proportionally more time on a home range than males, during the winter. On the prairies in central Saskatchewan, we deployed satellite transmitters on 11 male and 12 female Snowy Owls over two winters. There were no significant differences between the sexes in home range size or the amount of travelling during the winter months. Average first home range (95% minimum convex polygon) size was 54.4 km² for males, 31.9 km² (estimated marginal means) for females and 53.8 km² for the sexes combined. However within sexes, home range size was negatively correlated with body condition as predicted. A lack of defense of home range perimeters against conspecifics could increase variation in home range size and movement patterns and reduce differences between the sexes.

Key words: *Bubo scandiacus*, Snowy Owl, competition, home range, space use, movement, satellite transmitters, winter

Introduction

The non-breeding season is increasingly being recognized as an important period in the annual cycle of animals, with its own challenges that affect an individual's lifetime fitness. Individuals overwintering at northern latitudes, for example, have high metabolic demands resulting from thermoregulation (Gessaman 1972; Buck and Barnes 2000) which may be more difficult to meet if snow cover reduces food availability (Kostrzewa and Kostrzewa 1991; Korslund and Steen 2002; Ueda et al. 2002; 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. Some mammals (Gurnell 1984) and birds (Stutchbury 1994) defend territories in winter, presumably to assure priority access to limited food supplies. Learning how individuals settle or move on the landscape during the non-breeding period can reveal behavioural adaptations to a challenging environment and indicate mechanisms involved in carryover effects across seasons (O'Connor et al. 2014).

Brown's (1964) model of economic defendability suggests that the size of a territory used for obtaining food 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 (*Lynx rufus* Schreber, 1977) was inversely correlated with stem cover density and estimated snowshoe hare (*Lepus americanus* Erxleben, 1777) density (Litvaitis et al. 1986). In birds, a similar relationship was found between Spotted Owl (*Strix occidentalis* Xantus, 1860) home range size and wood rat (*Neotoma* spp.) density (Zabel et al. 1995) and between prey abundance and winter territory size in Sanderlings (*Calidris alba* Pallas, 1764), because areas of higher prey abundance were more costly to defend (Myers et al. 1979). 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, Barrette and Vandal 1986), mates (McElligott et al. 2001; Cockburn et al. 2008; Magana et al. 2011) and good quality habitat (Bruinzeel et al. 2006; Murray et al. 2007). If home range size is inversely related to food abundance, one would predict that dominant individuals or those in good body condition would use smaller home ranges in higher quality habitat, relegating poor competitors to poor quality habitat or perhaps forcing them to adopt different foraging strategies. For example, in American Redstarts (*Setophaga ruticilla* L., 1758), the sexes segregate into different wintering habitat types, 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). Similarly, male and female Red Deer (*Cervus elaphus* L., 1758) occupy different habitats in times of decreased food availability because of intersexual competition (Clutton-Brock et al. 1987). 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 also more likely to be used as a strategy by large 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* L. 1758) which include extended periods at sea may be evidence of nomadism during an annual period of decreased food availability (Burnham and Newton 2011).

Birds of prey with reversed sexual size dimorphism can provide special insight into the effects of dominance on territoriality and movements because it is the larger females which are the dominant sex in contrast to the pattern in most other vertebrates (reviewed in Kruger 2005). Snowy Owls (*Bubo scandiacus* L. 1758) typify raptors in this regard, with females weighing on average 33% more than males (Chang and Wiebe 2016) and chasing and displacing males

during interactions observed in the wild (Evans 1980; Boxall and Lein 1982a). In some species of raptors, females 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). In previous work, we documented a higher body condition (greater stores of fat) in female than in male Snowy Owls (Chang and Wiebe 2016) and found that home ranges of females contained less dense vegetation cover which may give them better access to prey (Chang and Wiebe, in review). Here, our goal was to expand on this work by studying the home range size and the movements of wintering Snowy Owls.

Boxall and Lein (1982a) found that adult female Snowy Owls had smaller ranges than the subdominant juveniles because home range size was regulated to provide individuals with a constant supply of food. Here, we compare home range size between the sexes rather than age classes and predicted that the dominant female owls would have smaller home ranges than males. Within sexes, we predicted that individuals in relatively good body condition would also subsist on smaller home ranges. Further, since previous studies of space use in wintering Snowy Owls relied solely on opportunistic observations, we used Global Positioning System - Global System for Mobile Communications (GPS-GSM) satellite transmitters to generate locations unbiased by detectability and road access. We also predicted that females, if they are more able to acquire and defend desirable home ranges, would travel shorter distances and spend less time moving nomadically during the winter than males.

Materials and methods

Study site and study species

We studied Snowy Owls during the three winters from 2014/15 to 2016/17 in south-central Saskatchewan. Owls were trapped (see below) 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 strains (*Brassica*), legumes, 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.

Deployment of transmitters

We searched for Snowy Owls in rural areas with consistently high densities of the birds in previous winters. Owls were caught by licensed banders between December and February in all 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. Mass, 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 mass over flattened wing chord length (Chang and Wiebe 2016). Body condition index was calculated separately for the sexes because there was no overlap in mass between them. 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).

Solar powered GPS-GSM transmitters (Ecotone Telemetry, model Saker H, 25 g) were attached, backpack style, to 23 individuals (11 males, 12 females) using teflon ribbon. The owls were handled according to Animal Care permit (20090025); the lightest owl we equipped with a transmitter was 1646 g, so the transmitter never exceeded 2% of the body mass of the owl. We deployed transmitters on three owls during the first winter, 14 owls in the second, and six owls in the third. Data collected for owls which returned in subsequent winters were included in the Linear Mixed Effect (LME) models as separate observations with "individual owl" as a random

factor. These included five males and two female owls, each having data for two winters. All male owls and all but one female were adults, i.e. > 1 year old.

Transmitters recorded locations (accurate to 20 m) every 6 h. We considered an owl to be settled on a home range if fixes were not consistently moving in one direction and thus resulted in a cluster of points during a period lasting at least 10 days. This amount of time provided at least 40 spatial locations which is generally regarded as a sufficient sample size for calculating home range size (e.g. Seaman et al. 1999). Travelling was defined when successive 6 hour GPS fixes were consistently directional such that an owl did not return to its previous home range for 5 days. 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). Some studies have used kernel methods (e.g. Roth et al. 2008) but we found that the least squares cross-validation smoothing algorithms of such models (Worton 1989) did not converge for our data, so used the widespread MCP calculation which also facilitates comparisons between studies. We rejected kernel methods that use the HREF smoothing parameters because they tend to overestimate home range sizes (Worton 1995). The use of MCP rather than more data-intensive models (e.g. Walter et al. 2015) was also appropriate for our data which contained substantially fewer than 1000 fixes per owl. For all owls, only locations taken prior to 15 March were used, because later in spring, the long distances which many owls moved were likely related to spring migration.

Statistical analyses

Snowy Owls often showed complex movement patterns involving more than one apparent home range during the winter (see results). For example, some individuals moved within a fixed, local area, revisiting locations over a period of time (we defined this as a typical "home range") before moving directionally some distance to settle again in a new area that did not overlap with the previous range. We therefore quantified space use using two main

methods. The first was to calculate a "total used area" which was simply the MCP of all points collected for an individual during the winter, including any home ranges and the distance between them. The second was to break down the data into separate (sequential) home ranges if they existed and to calculate MCPs only for those. In the latter analysis we compared home range size between the sexes using: 1) first home ranges only and also 2) a dataset with all sequential home ranges, using individual as a random factor to control for multiple observations per individual within and among years. Total winter areas, home range sizes and the proportion of the total time the bird was observed during which it moved on the landscape versus remained stationary on a home range, over the entire winter, were compared between the sexes using Linear Mixed Effect models (LME) with restricted maximum likelihood (REML). The initial models included year and sex as fixed factors and their interaction but the interaction term was dropped if not significant. The qualitative results of models did not change with removal of the interaction term. The analyses which incorporated multiple home range estimates per individual also used individual as a random term. Home range sizes were log-transformed to achieve normality. Similarly, distances travelled over the landscape during winter (from first to second home range only and total distance) and duration travelled were compared between the sexes using LME models. Data were analyzed using SPSS 22.0 with significance set at $\alpha = 0.05$.

Results

Total used area and home range size

The size of the total area an individual used during the winter did not differ between years (LME; year effect, 95% MCP: $F_{2,23} = 0.15$, $p = 0.86$) or between sexes ($F_{1,23} = 1.89$ $p = 0.18$). The size of the first home range in a season for males (estimated marginal means, 95% MCP = $54.4 \text{ km}^2 \pm 22.2 \text{ SE}$, $n = 16$) averaged 22% larger than that of females ($31.9 \text{ km}^2 \pm 21.6 \text{ SE}$, $n = 14$) and the corresponding 50% MCP ranges of males ($8.4 \text{ km}^2 \pm 2.9 \text{ SE}$) averaged 25% larger than for females ($6.3 \text{ km}^2 \pm 2.8 \text{ SE}$; Figure 1). There was a significant year effect on home

range size (LME; year effect: 95% MCP: $F_{2,26} = 3.9$, $p = 0.03$; 50% MCP: $F_{2,26} = 2.7$, $p = 0.09$) with ranges in the second winter being larger than those in the third. However, there was no significant difference between the sexes (sex effect: 95% MCP: $F_{1,26} = 0.014$, $p = 0.91$; 50% MCP: $F_{1,26} = 0.003$, $P = 0.96$). Pooling the sexes, the mean size of first home ranges, 95% and 50% MCP respectively, were $53.8 \text{ km}^2 \pm 14.0 \text{ SE}$ and $7.2 \text{ km}^2 \pm 1.8 \text{ SE}$.

Of the 30 calculated home ranges, 13 owls (8 females, 5 males) had more than one home range within a winter season (12 had two ranges and 1 had three). For those owls with multiple home ranges, the size of the first established range was not significantly different from the size of their next range for females (paired t-tests, 95% MCP: $t_7 = 0.60$, $p = 0.56$; 50% MCP: $t_7 = 0.99$, $p = 0.36$) whereas ranges of males tended to become larger over the season but not significantly so (paired t-tests, 95% MCP: $t_4 = 2.25$, $p = 0.09$, 50% MCP: $t_4 = 2.33$, $p = 0.08$). Similar results were obtained by pooling all home ranges within and among years and using individual as a random factor. There was a year effect, such that 95% and 50% MCP home ranges in the third field season were smaller than in the second (LME; year effect: 95%: $F_{2,41} = 3.7$, $p = 0.03$; 50%: $F_{2,41} = 4.5$, $p = 0.02$). However, there was no overall difference in home range size between the sexes (LME; sex effect: 95% MCP: $F_{1,41} = 0.09$, $p = 0.76$; 50% MCP: $F_{1,41} = 0.28$, $p = 0.60$, Fig.1).

Within sexes, for both females and males, body condition had a negative relationship with logged home range size at the 95% MCP level, for first home ranges (LME females: $F_{1,7} = 8.3$, $p = 0.024$; males: $F_{1,7} = 13.2$, $p = 0.008$, Fig.2) and all pooled home ranges (females: $F_{1,13} = 21.6$, $p < 0.001$; males: $F_{1,11} = 15.3$, $p = 0.002$). This negative relationship between body condition and home range size was also found in males but not females at the 50% MCP level, for first home ranges (females: $F_{1,7} = 1.4$, $p = 0.28$; males: $F_{1,7} = 9.7$, $p = 0.02$) and all pooled home ranges (females: $F_{1,13} = 4.2$, $p = 0.06$; males: $F_{1,11} = 8.1$, $p = 0.02$).

Movement patterns

Some owls were fairly stationary on one home range all winter (23% of 30 observations), whereas the others were more nomadic, using multiple home ranges or wandering on the landscape after leaving the first home range (Figure 3). The sexes did not differ in the average amount of time spent on the first home range before moving (males: 36 days, females 38 days, T-test; $t_{28} = 0.26$, $p = 0.80$). The direction of the movement from first home ranges depended on date. When owls moved off home ranges in early winter (December or January), most (10 of 12 individuals) went south. In February, about half of the movements from home ranges were northward (3/7) while the others moved south. In late winter (first 15 days of March) almost all movements from home ranges were northward (14/16) and only 2 of the owls which moved travelled southward.

There was also variation in the timing and speed of movements of owls that moved from home ranges during winter. Some moved gradually and consistently from one home range to another whereas others moved rapidly in bouts separated by short periods of reduced movement. For example, one owl moved a total of 116 km over 60 hours, in 3 spurts of 28 to 46 km lasting 6 to 12 hours, stopping for 6-18 h between moves, whereas another moved 42 km over 66 hours at a consistent rate (Figure 4). The sexes did not differ in the average distance moved after leaving the first home range to the second home range, or to the cut-off date before migration, 15 March, whichever came first (males: 110 km $\pm$ 40 SE, females: 90 km $\pm$ 39 SE; LME sex effect: $F_{1,26} = 0.16$, $p = 0.69$; year effect: $F_{2,26} = 0.98$, $p = 0.39$). 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: 6.9 days $\pm$ 3.7 SE, females: 6.2 days $\pm$ 4.5 SE; LME sex effect: $F_{1,24} = 0.03$, $p = 0.87$, year effect: $F_{2,24} = 0.94$, $p = 0.40$). The greatest distance moved over winter from December to March was 521 km by a male but the sexes did not differ in total distance travelled among home ranges over the whole winter (males: 215 km $\pm$ 84 SE, females: 211 km $\pm$ 89 SE; LME sex effect $F_{1,25} = 0.001$, $p = 0.97$, year effect: $F_{2,25} = 0.43$, $p = 0.65$). Over the whole winter, there was no difference between the sexes

in the proportion of time spent on a home range (LME males: $84\% \pm 5 \text{ SE}$, females $90\% \pm 5 \text{ SE}$; sex effect: $F_{1,26} = 1.0$, $p = 0.32$, year effect: $F_{2,26} = 1.9$, $p = 0.16$).

Discussion

We found mixed support for the idea that social dominance in Snowy Owls is linked to home range size and patterns of movement in winter. The size of home ranges averaged about 25% larger for males than females in the direction predicted, but not significantly so, and when comparing large scale winter movements, the sexes did not differ in distances moved after leaving the first home range or total distance moved over winter or total land area covered. Neither did males and females differ in the proportion of time spent stationary on a home range versus travelling during the winter months. However, our finding that body condition was negatively correlated with home range size within both sexes at the 95% MCP level, and within males at the 50% MCP could suggest that dominance, or perhaps individual quality may indeed affect home range size.

Because breeding pairs form in the Arctic on the breeding grounds (Holt et al. 2015), movements of the owls during winter are unlikely to be for the purpose of mate searching and owls would not be establishing home ranges or territories to attract the opposite sex. Instead, home range size and movements of owls are likely to be explained in relation to finding food and maintaining energy balances during the harsh winter. Significant annual variation in home range size likely reflects differences in small mammal numbers and distributions in the province which vary annually (Chang and Wiebe, unpublished data). There are several reasons for the large variance in the size of home ranges within the sexes. First, in another study, we found that the home ranges of males and females were characterized by different proportions of land cover types consistent with the idea that females monopolized somewhat more profitable habitats (Chang and Wiebe, unpublished data). However, the habitat types used by each sex overlapped extensively so the difference in quality (prey abundance) experienced by male and

female owls may be relatively minor compared to other bird species with distinct segregation of sexes by habitat type.

Furthermore, although we observed two direct aggressive encounters in the field between the sexes (the female chased the male in both cases) there is no evidence that owls regularly patrol and defend exclusive territory boundaries. Home ranges averaging 30-55 km² are too large to scan from a single perch and defense of exclusive boundaries would thus entail energy costs of flying the perimeter regularly to monitor a large landscape. Thus, there could be some overlap of males and females on the landscape which may reduce differences in habitat quality the sexes experience. Indeed, Snowy Owls might be characterized as living on undefended home ranges during winter, but engaging in direct interference competition over smaller spatial scales than a home range. Such direct aggressive encounters between owls may occur when the individuals are within visual contact and be centred over specific resources like possession of prey items. Intraspecific attempts at kleptoparasitism were commonly directed to victims of equal or younger age in Lesser Black-backed Gulls (*Larus fuscus* L., 1758) (Galvan 2003), suggesting an important role of dominance. In raptors, Bald Eagles (*Haliaeetus leucocephalus* L., 1766) often steal prey from conspecifics (Jorde and Lingle 1988) and kleptoparasitism is directed from the larger females towards males in Common Kestrels (*Falco tinnunculus* L., 1758) (Kitowski 2005) and Lesser Kestrels (*Falco naumanni* Fleischer, 1818) (Negro et al. 1992).

When we presented taxidermy mounts of conspecifics to wild owls in an experiment, a greater proportion of females than males acted aggressively to the rival (approach/attack), whereas a greater proportion of males than females flew away (Chang 2017). 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 (Chang 2017). This suggests that social dominance does play a role in access to food and space but over relatively small spatial scales when owls are in visual contact.

Another explanation for similar average home range size between the sexes might be that the dietary niches differ sufficiently between males and females. In that case, although dominant individuals might exclude subordinates from some areas, optimal home range sizes would be based on different types of prey species and hence the sexes of Snowy Owls might focus on different foraging techniques and different habitats. With different dietary niches, movement patterns and the relationship between home range size and food abundance could be variable and difficult to compare. In other birds of prey, niche separation between the sexes reduces competition for food (Reynolds 1972; Andersson and Norberg 1981; Massemin et al. 2000). For example, in three harriers (*Circus* spp.) males and females preferred different winter foraging habitats associated with smaller and larger prey, respectively (Buij et al. 2012). Female Snowy Owls include more large prey in their diets than males, such as Richardson's ground squirrels (*Spermophilus richarsonii* Sabine, 1822), white-tailed jackrabbits (*Lepus townsendii* Bachman, 1839), weasels (*Mustela* spp.), and Grey Partridge (*Perdix perdix* L., 1758; Boxall and Lein 1982b). Nevertheless, the prey niches of the sexes still overlap greatly as both feed predominantly on small mammals in winter on the Canadian prairies (males: 85%, females 79%, Boxall and Lein 1982b). Furthermore, if anything, the ability to exploit a wider diversity of prey suggests females could meet their energy requirements within a smaller area compared to males but this was not the pattern we found.

Counter to our prediction the subordinate male Snowy Owls did not spend more time moving on the landscape or travel longer distances than did females. In contrast, Brown Skuas (*Stercorarius antarcticus* Lesson, 1831), dominant breeders defended feeding territories whereas sub-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* L., 1758), 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). Common Ravens (*Corvus corax* L., 1758) in the Arctic are more nomadic because of reduced food availability compared to temperate regions where ravens hold winter territories (Restani et al. 2001).

We found that for adult (≥ 2 year old) owls, individuals in better body condition had smaller home ranges. The effect of body condition and age on social dominance may be confounded because adult owls are generally in better body condition than yearlings (Chang and Wiebe 2016). We could not address age-related effects with our sample but Boxall and Lein (1982a) found that adult females used smaller areas than juveniles, consistent with the idea that dominant individuals can secure better quality areas with more food and hence need to defend less space. Irrespective of social dominance, it is possible that the better body condition of individuals reflected hunting skills, and hence owls in good condition could meet their energy requirements in a smaller area with less movement and travelling. The relationship between social dominance and home range size has not been investigated in many other birds but the same negative relationship between dominance and home range size within sexes was found in Wild Turkeys (*Meleagris gallopavo* L., 1758; Badyaev et al. 1996).

In sum, we did not find significant differences between the sexes in home range size and distances moved during the winter, although the direction of the differences were consistent with our predictions. Our sample sizes were not large enough to detect small differences between the sexes but should have been sufficient to elucidate distinct sex-specific behaviour had it existed. Future studies should monitor agonistic encounters between neighbouring owls fitted with transmitters to see whether individuals defend exclusive territories in the winter, or only behave aggressively to others in close range. Annually, a large number of Snowy Owls winter on the North American prairies (Potapov and Sale 2012) so it is important to understand how habitat characteristics and prey abundance affects survival during this part of the annual cycle. More information on the spatial distribution and predictability of small rodent prey during winter

would be useful to better understand how individuals use and track food resources and whether owls are adapting to the rapidly changing agricultural habitats on the prairie landscape.

Acknowledgements

This research would not have been possible without assistance in Snowy Owl trapping from M. Stoffel and D. Zazelenchuk and we are indebted to their patience and perseverance in the field. Owls were trapped under banding permit numbers 10736 and 10737. The study was funded by a Natural Sciences and Engineering Research Council of Canada (Discovery Grant 203177) and by a grant from the Kenneth M. Molson Foundation

References

- Allen, C.R., and Saunders, D.A. 2002. Variability between scales: Predictors of nomadism in birds of an Australian Mediterranean-climate ecosystem. *Ecosystems*, **5**: 348–359.
- Andersson, M., and Norberg, R.A. 1981. Evolution of reversed sexual size dimorphism and role partitioning among predatory birds, with a size scaling of flight performance. *Biol. J. Linn. Soc.* **15**: 105–130.
- Ardia, D.R., and Bildstein, K.L. 1997. Sex-related differences in habitat selection in wintering American Kestrels, *Falco sparverius*. *Anim. Behav.* **53**: 1305–1311.
- Ardia, D.R., and Bildstein, K.L. 2001. Sex-related differences in habitat use in wintering American Kestrels. *Auk*, **118**(3): 746–750.
- Badyaev, A.V., Etges, W.J., and Martin, T.E. 1996. Ecological and behavioral correlates of variation in seasonal home ranges of Wild Turkeys. *J. Wildl. Manage.* **60**: 154–164.
- Baker, M.C., Belcher, C.S., Deutsch, L.C., Sherman, G.L., and Thompson, D.B. 1981. *Anim. Behav.* **29**: 137–142.
- Banks, E.M., Wood-Gush, D.G.M., Hughes, B.O., and Mankovich, N.J. 1979. Social rank and priority of access to resources in Domestic Fowl. *Behav. Proc.* **4**: 197–209.

- Barrette, C., and Vandal, D. 1986. Social rank, dominance, antler size, and access to food in snow-bound wild Woodland Caribou. *Behaviour*, **97**: 118–145.
- Boxall, P.C., and Lein, M.R. 1982a. Territoriality and habitat selection of female Snowy Owls (*Nyctea scandiaca*) in winter. *Can. J. Zool.* **60**: 2344–2350.
- Boxall, P.C., and Lein, M.R. 1982b. Feeding ecology of Snowy Owls (*Nyctea scandiaca*) wintering in southern Alberta. *Arctic* **35**(1): 282–290.
- Brown, J.L. 1964. The evolution of diversity in avian territorial systems. *Wilson Bull.* **76**(2): 160–169.
- Bruinzeel, L.W., van de Pol, M., and Trierweiler, C. 2006. Competitive abilities of Oystercatchers (*Haematopus ostralegus*) occupying territories of different quality. *J. Ornithol.* **147**: 457–463.
- Buck, C.L., and Barnes, B.M. 2000. Effects of ambient temperature on metabolic rate, respiratory quotient, and torpor in an arctic hibernator. *Am. J. Physiol. Regulatory Integrative Comp. Physiol.* **279**: 255–262.
- Buij, R., van der Goes, D., de longh, H.H., Gagare, S., Haccou, P., Komdeur, J., and de Snoo, G. 2012. Interspecific and intraspecific differences in habitat use and their conservation implications for Palaearctic harriers on Sahelian wintering grounds. *Ibis* **154**: 96–110.
- Burnham, K.K., and Newton, I. 2011. Seasonal movements of Gyrfalcons *Falco rusticolus* include extensive periods at sea. *Ibis* **153**: 468–484.
- Chang, A.M. 2017. Habitat use, movement patterns, and body condition of male and female Snowy Owls (*Bubo scandiacus*) in winter. M.Sc. Thesis. Department of Biology, University of Saskatchewan, Saskatoon, SK.
- Chang, A.M., and Wiebe, K.L. 2016. Body condition in Snowy Owls wintering on the prairies is greater in females and older individuals and may contribute to sex-biased mortality. *Auk*, **133**: 738–746.

- Clutton-Brock, T.H., Iason, G.R., and Guinness, F.E. 1987. Sexual aggression and density-related changes in habitat use in male and female Red deer (*Cervus elaphus*). *J. Zool. (Lond.)* **211**: 275–289.
- Cockburn, A., Osmond, H.L., Mulder, R.A., Double, M.C., and Green, D.J. 2008. Demography of male reproductive queues in cooperatively breeding Superb Fairy-wrens *Malarus cyaneus*. *J. Anim. Ecol.* **77**: 297–304.
- Evans, D.L. 1980. Vocalizations and territorial behavior of wintering Snowy Owls. *Am. Birds* **34**(5): 748–749.
- Fretwell, S.D., and Lucas, H.L.Jr. 1970. On territorial behavior and other factors influencing habitat distribution in birds. I. Theoretical development. *Acta Biotheor.* **19**:16–36.
- Galvan, I. 2003. Intraspecific kleptoparasitism in Lesser Black-backed Gulls wintering inland in Spain. *Waterbirds* **26**(3): 325–330.
- Gessaman, J.A. 1972. Bioenergetics of the Snowy Owl (*Nyctea scandiaca*). *Arct. Alp. Res.* **4**(3): 223–238.
- Gurnell, J. 1984. Home range, territoriality, caching behaviour, and food supply of the red squirrel (*Tamiasciurus hudsonicus fremonti*) in a subalpine lodgepole pine forest. *Anim. Behav.* **32**: 1119–1131.
- Hahn, S., and Bauer, S. 2008. Dominance in feeding territories relates to foraging success and offspring growth in Brown Skuas *Catharacta antarctica lonnbergi*. *Behav. Ecol. Sociobiol.* **62**: 1149–1157.
- Heisler, L.M., Somers, C.M., and Poulin, R.G. 2014. Rodent populations on the northern Great Plains respond to weather variation at a landscape scale. *J. Mammal.* **95**: 82–90.
- Holt, D., Larson, M.D., Smith, N., Evans, D., and Parmelee, D.F. 2015. Snowy Owl (*Bubo scandiaca*), *The Birds of North America Online Edited by A. Poole*. Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America Online: <http://bna.birds.cornell.edu/bna/species/010>.

- Jorde, D.G., and Lingle, G.R. 1988. Kleptoparasitism by Bald Eagles wintering in south-central Nebraska. *J. Field Ornithol.* **59**: 183–188.
- Josephson, B. 1980. Aging and sexing Snowy Owls. *J. Field Ornithol.* **51**: 149–160.
- Kitowski, I. 2005. Sex skewed kleptoparasitic exploitation of Common Kestrel *Falco tinnunculus*: The role of hunting costs to victims and tactics of kleptoparasites. *Folia Zool.* **54**(4): 371–378.
- Korslund, L., and Steen, H. 2006. Small rodent winter survival: Snow conditions limit access to food resources. *J. Anim. Ecol.* **75**: 156–166.
- Kostrzewa, R., and Kostrzewa, A. 1991. Winter weather, spring and summer density, and subsequent breeding success of Eurasian Kestrels, Common Buzzards, and Northern Goshawks. *Auk*, **108**: 342–347.
- Kruger, O. 2005. The evolution of reversed sexual size dimorphism in hawks, falcons and owls: A comparative study. *Evol. Ecol.* **19**: 467–486.
- Littlefield, C.D., and Johnson, D.H. 2005. Habitat preferences of migrant and wintering Northern Harriers in northwestern Texas. *Southwest. Nat.* **50**(4): 448–452.
- Litvaitis, J.A., Sherburne, J.A., and Bissonette, J.A. 1986. Bobcat habitat use and home range size in relation to prey density. *J. Wildl. Manage.* **50**(1): 110–117.
- Magana, M., Alonso, J.C., and Palacin, C. 2011. Age-related dominance helps reduce male aggressiveness in Great Bustard leks. *Anim. Behav.* **82**: 203–211.
- Marra, P.P. 2000. The role of behavioral dominance in structuring patterns of habitat occupancy in a migrant bird during the nonbreeding season. *Behav. Ecol.* **11**(3): 299–308.
- Massemin, S., Korpimäki, E., and Wiehn, J. 2000. Reversed sexual size dimorphism in raptors: Evaluation of the hypotheses in kestrels breeding in a temporally changing environment. *Oecologia*, **124**: 26–32.

- McElligott, A.G., Gammell, M.P., Harty, H.C., Paini, D.R., Murphy, D.T., Walsh, J.T., and Hayden, T.J. 2001. Sexual size dimorphism in fallow deer (*Dama dama*): Do larger, heavier males gain greater mating success? *Behav. Ecol. Sociobiol.* **49**: 266–272.
- Murray, C.M., Mane, S.V., and Pusey, A.E. 2007. Dominance rank influences female space use in wild chimpanzees, *Pan troglodytes*: Towards an ideal despotic distribution. *Anim. Behav.* **74**: 1795–1804.
- Myers, J.P., Connors, P.G., and Pitelka, F.A. 1979. Territory size in wintering Sanderlings: The effects of prey abundance and intruder density. *Auk*, **96**(3): 551–561.
- Negro, J.J., Donazar, J.A., and Hiraldo, F. 1992. Kleptoparasitism and cannibalism in a colony of Lesser Kestrels (*Falco naumanni*). *J. Raptor Res.* **26**(4): 225–228.
- O'Connor, C.M., Norris, D.R., Crossin, G.T., and Cooke, S.J. 2014. Biological carryover effects: linking common concepts and mechanisms in ecology and evolution. *Ecosphere*, **5**: 1–11.
- Ponjoan, A., Bota, G., and Manosa, S. 2012. Ranging behaviour of Little Bustard males, *Tetrax tetrax*, in the lekking grounds. *Behav. Processes* **91**: 35–40.
- Potapov, E., and Sale, R. 2012. *The Snowy Owl*. T & AD Poyser, London.
- Restani, M., Marzluff, J.M., and Yates, R.E. 2001. Effects of anthropogenic food sources on movements, survivorship, and sociality of Common Ravens in the Arctic. *Condor*, **103**(2): 399–404.
- Reynolds, R.T. 1972. Sexual dimorphism in accipiter hawks: A new hypothesis. *Condor*, **74**: 191–197.
- Riegert, J., and Fuchs, R. 2011. Fidelity to roost sites and diet composition of wintering male urban Common Kestrels *Falco tinnunculus*. *Acta Ornithol.* **46**(2): 183–189.
- Roth, T. C. II, Vetter, W. E., and Lima, S. L. 2008. Spatial ecology of wintering *Accipiter* hawks: Home range, habitat use, and the influence of bird feeders. *Condor*, **110**: 260–268.

- Seaman, D. E., Millspaugh, J. J., Kernohan, B. J., Brundige, G. C., Raedeke, K. J., and Gitzen, R. A. 1999. Effects of sample size on kernel home range estimates. *J. Wildl. Manage.* **63**: 739–747.
- Storer, R.W. 1966. Sexual dimorphism and food habits in three North American accipiters. *Auk*, **83**: 423–436.
- Stutchbury, B.J. 1994. Competition for winter territories in a neotropical migrant: The role of age, sex and color. *Auk*, **111**: 63–69.
- Ueda, H., Takatsuki, S., and Takahashi, Y. 2002. Bark stripping of hinoki cypress by sika deer in relation to snow cover and food availability on Mt Takahara, central Japan. *Ecol. Res.* **17**: 545–551.
- Walter, D. W., Onorato, D. P. and Fischer, J. W. 2015. Is there a single best estimator? Selection of home range estimators using area under the curve. *Movement Ecol.* 3: 1-11.
- Worton, B.J. 1989. Kernel methods for estimating the utilization distribution in home-range studies. *Ecology*, **70**: 164-168.
- Worton, B.J. 1995. Using Monte Carlo simulation to evaluate kernel-based home range estimators. *J. Wildl. Manage.* **59**: 794-800.
- Zabel, C.J., McKelvey, K., and Ward, J.P.Jr. 1995. Influence of primary prey on home-range size and habitat-use patterns of Northern Spotted Owls (*Strix occidentalis caurina*). *Can. J. Zool.* **73**: 433–439.

Figure Captions

Figure 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 2. Relationship between body condition residuals and first home range size (95% MCP) for female and male Snowy Owls wintering in Saskatchewan.

Figure 3. Movements of two female Snowy Owls demonstrating stationary home range (A, 20 Jan 2016 to 15 Mar 2016) and nomadic (B, 08 Jan 2016 to 15 Mar 2016) winter movement patterns. Locations were taken every 6 hours.

Figure 4. Cumulative distanced moved between winter home ranges over time for four male Snowy Owls. Each line represents a different individual.

Fig.1

Fig.2

Fig.3

Fig.4