Articles

Irruptive movements and breeding dispersal of snowy owls: a specialized predator exploiting a pulsed resource

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Mobility and irruptive movements have been proposed as mechanisms that could allow some diet specialists to inhabit and breed in environments with highly unpredictable resources, like the arctic tundra. The snowy owl, one of the main avian predators of the tundra, is known to specialize on lemmings during the breeding season. These small mammals are also well known for their tremendous spatial and temporal variations in abundance. We examined the spring (pre-breeding, from March to June) movements of snowy owls by tracking 9 breeding females in the Canadian Arctic for up to 3 yr with satellite transmitters. We used state-space modeling to assess searching behavior and measure breeding dispersal distances. We also ascertain lemming abundance at some of the sites used by the marked owls. Tracked owls displayed searching movements for extended periods (up to 108 d) and traveled over large distances (up to 4093 km) each spring. The distance between furthest apart searching areas in a given year averaged 828 km (range 220 to 2433 km). Settlement date, distance between searching areas, traveled distance and the duration of prospecting movements were longer in the year where density of lemmings recorded in the eastern High-Arctic (Bylot Island) was lowest. Nonetheless, snowy owls settled in areas where local lemming abundance was relatively high. Individual breeding dispersal distance between consecutive years averaged 725 km (range 18 to 2224). Overall, the high mobility of female snowy owls allowed these diet specialists to behave as irruptive migrants and to sustain their reproductive activities during consecutive years even under highly fluctuating resources.

Predators living in seasonal and heterogeneous environments rely on resources that vary spatially and temporally in availability. Pulsed resources represent an extreme case because they typically become super abundant for a very short and often unpredictable period of time (Ostfeld and Keesing 2000). Examples include the blooming of plankton in ephemeral ponds, the massive and periodic emergence of some insects and mast fruiting by several trees. In all these cases, resources can be plentiful in a given year but virtually non-existent in others (Ostfeld and Keesing 2000). Consumers have developed several strategies to cope with variable or pulsed food sources. Indeed, in the presence of highly variable resources, some species broaden their diet in order to maximize energy gain (Terraube and Arroyo 2011) while others rely on hoarded resources (Careau et al. 2008) or reduce metabolic (or reproductive) activities until the next resource pulse (Stearns 1992).

Consumers are not expected to specialize on ephemeral food supply. Instead, diet generalists are more likely to exploit pulsed resources because they can switch to alternative food sources during periods of low availability of the former (Ostfeld and Keesing 2000). However, high mobility and irruptive movements have been proposed as mechanisms that could allow some diet specialists to inhabit and breed in environments with highly unpredictable resources despite the inherent uncertainties and associated costs of locomotion (Newton 2006a). Long-distance movements of individuals in response to variation in local food supplies would thus result in large fluctuations in numbers of a given species at the local or even the regional scale. Individuals exhibiting irruptive migration are expected to breed in widely spaced localities in different years (Newton 2006a).

The Arctic tundra is a highly seasonal environment well-known for the high-amplitude, multi-annual variations in population densities of small mammals such as lemmings (*Lemmus* and *Dicrostonyx* sp., Elton 1924, Ims and Fuglei 2005, Krebs 2011). Those cyclic fluctuations affect local breeding densities and reproductive success of several avian and mammalian predators, which exhibit strong numerical responses to lemming densities (Reid et al. 1997, Wiklund et al. 1998, Gilg et al. 2006, Therrien et al. 2014). Although high lemming abundance can occur synchronously over relatively large areas (ca up to 1000 km; Erlinge et al. 1999, Angerbjörn et al. 2001, Krebs et al.

2002), numerous biotic and abiotic factors can affect the periodicity and amplitude of these outbreaks, rendering them rather unpredictable on a year to year basis (Myrberget 1973, Ims and Andreassen 2011).

The snowy owl, one of the main avian predators of the tundra, is known to specialize on lemmings during the breeding season (reviewed by Parmelee 1992). This species can exhibit large variations in breeding numbers, ranging from 0 to 17 nests 100 km^{-2}, in relation to changes in local lemming abundance (Gauthier et al. 2004, Gilg et al. 2006, Therrien et al. 2014). These local fluctuations in numbers are most likely due to movements of individuals because years with high breeding numbers are typically preceded or followed by years of total (or near total) absence of individuals in a given area (Gauthier et al. 2004). The limited information coming from ring recoveries and satellite tracking of a small number of birds has revealed the high mobility of this species (Fuller et al. 2003, Dunn et al. 2009), which is often presented as the classic example of a nomadic species (Greenwood and Harvey 1982, Parmelee 1992, Newton 2006a). However, the paucity of information on their movements and their determinants hinders considerably our understanding of their role in the structure and functioning of the tundra food web (Korpimäki and Krebs 1996).

In this paper, we examined the spring (pre-breeding) movements and breeding dispersal of female snowy owls. We specifically assessed annual movement parameters such as migration phenology, search and settlement patterns and breeding dispersal distance, and examined the influence of spatial and temporal variability in food resource availability (i.e. lemmings) on those movements. We hypothesized that 1) snowy owls exhibit extensive, large-scale searching behavior during spring as they seek areas of high lemming abundance, 2) snowy owls settle to breed in areas with a relatively high abundance of lemmings, and 3) breeding dispersal of owls occurs at the continental scale because lemming population cycles tend to be synchronized regionally.

Methods

Field activities primarily occurred on the southern portion of Bylot Island, Nunavut, Canada (73°N, 80°W), over a 400 km² area of Arctic tundra. The landscape is made of gently rolling hills and river valleys and is a prime breeding habitat for snowy owls and lemmings (see Gauthier et al. 2004 for details). Every year from 2004 to 2010, we assessed the density of snowy owl nests in a core study area of 100 km² through systematic searches (see Therrien et al. 2014 for details).

From 27 June to 11 July 2007, we captured 12 adult female snowy owls on their nest using a bow-net trap. All of these birds were captured outside our core study area because none nested in that specific area that year (except one that abandoned during egg-laying; see results). Birds were captured after hatching had started (i.e. when eggs were cracking or nests had at least one hatched young) and no bird abandoned their nest following capture. We marked owls with 30-g satellite transmitters (Microwave Telemetry, MD, USA; PTT-100) attached with back-pack harnesses

(Steenhof et al. 2006) made of teflon ribbon. Tracking of these birds for up to 3 yr suggested no impact of the transmitter on their subsequent survival or reproduction (Therrien et al. 2012).

Transmitters were programmed to transmit continuously for an average of 5 h and then turned off for an average of 125 h from marking to the end of the following winter (February 2008). During the first spring and summer period (March to July 2008), transmitters were programmed to transmit for 5 h and then turned off for 49 h. Finally, cycles of 4 h of transmission and 142 h off were programmed for the remaining battery life of the transmitters. We received locations of marked owls via the Argos system (Collecte Localisation Satellites 2011). Each location was assigned by CLS Argos to a class (0, 1, 2, 3, A, B, or Z) according to its estimated precision. The estimated accuracy of location classes 0, 1, 2, and 3 followed a normal distribution with a standard deviation of >1000 m, <1000 m, <350 m, and <150 m, respectively. There is no accuracy estimate associated with the remaining classes (A, B and Z). From 1 March to 30 June, we received an average of 440 (range: 347–546), 161 (range: 121–226) and 135 (range: 98–216) locations per bird from CLS Argos in 2008, 2009 and 2010 respectively. Overall, 9%, 19%, 29%, 29%, 6%, 7% and 1% of locations were of quality 3, 2, 1, 0, A, B and Z respectively.

Both the brown (*L. trimucronatus*) and collared (*D. groenlandicus*) lemmings have a widespread distribution across North American tundra and are present on Bylot Island. From 2004 to 2010, we measured lemming density by live-trapping them on two trapping grids (11 ha each) spaced by 2 km. Grids were set up in areas representative of the main habitats found at the study site, one in wet meadow and one in mesic tundra. Each trapping grid had 144 Longworth traps placed at 30-m interval in a Cartesian plan and were opened for three or four consecutive days at each trapping period. Traps were baited with apples and checked at 12 h intervals. We conducted three trapping sessions each summer (mid-June, mid-July and mid-August). All captured animals were identified to the species level, individually marked with PIT tags and released following capture (see Gruyer et al. 2010 for details). The trapping grids were located at the center of our 100 km² core study area.

In 2008, we visited by helicopter distant sites (n = 8) where satellite-tracked owls had settled and searched for these birds and their nest. This allowed us to confirm whether these birds were breeding or not. Only one site selected by a tracked female in 2008 could not be visited because it was located in the western Canadian Arctic (>1200 km away from Bylot Island). We assessed lemming abundance using snap traps at two sites on Baffin Island where the marked owls had settled to breed; Mary River (71.3°N, 79.4°W) and Dewar (69.1°N, 70.8°W), 200 and 560 km south of Bylot Island, respectively. At each site, we set 240 traps at 80 stations along two transects 100 m apart. We set three traps within 2-m of each station and each station was spaced by 15 m along transects. Traps were baited with peanut butter and rolled oats. Trapping lasted 48 h at Mary River (6–8 July) and 24 h (8–9 July) at Dewar.

Statistical analyses

Because Argos transmitters emitted at irregular intervals (see above), we used a state-space modeling (SSM) approach (state-space hierarchical switching model; Jonsen et al. 2005) to estimate daily locations during each annual journey of individual birds using all locations provided by CLS Argos. This Bayesian approach allows the estimation of the most probable locations at fixed time steps (1-d in the present case) based on the previous and forthcoming locations while taking into account the precision of each location provided by CLS Argos as described above (see Jonsen et al. 2005 for further details). All movement analyses were then run on those estimated daily locations. For each location, the SSM also assigns the probability that a bird was in a 'searching' or a 'moving' behavioral state according to its speed and turning angle. A bird was considered in a moving state when it exhibited a high travel speed and a low turning angle (score close to 0) or in a searching state when its movements were characterized by a low speed and a high turning angle (score close to 1). We used a cut-off value of 0.5 to classify the behavioral state associated with each estimated location (i.e. 0–0.5: moving; 0.5–1: searching; Jonsen et al. 2005).

SSM estimations were made using the R package bsam (Jonsen 2013) under the R 2.15.2 environment (R Core Team) with the Markov Chain Monte Carlo (MCMC) sampler of program JAGs (Plummer 2012) and basic movement analyses were done using the trip package (Sumner 2012). To ensure accurate and faster estimates with the SSM, we applied a speed filter (McConnell et al. 1992) before running estimations to remove extreme error locations. The state-space hierarchical switching models were fitted to the dataset using 2 chains of 250 000 MCMC samples; the first 100 000 samples were discarded as a burn-in and the remaining 150 000 were thinned out to 3000 samples by retaining only every 50th sample to reduce autocorrelation. Estimated locations were based on these final 3000 samples. For each estimated location, convergence and absence of autocorrelation were graphically checked, and we also applied the convergence diagnostic of Gelman and Rubin (1992).

Pre-breeding movements were those occurring between the areas where birds had settled for winter, as described in Therrien et al. (2012), and where they eventually settled for the summer. We defined individual departure date from wintering sites when behavior state switched for the first time from searching (1) to moving (0) after 1 March. Since two birds did not settle at all during winter 2009, we selected the average departure date of the other tracked individuals for that year as the reference date for the calculation of the different movement parameters (duration, distance traveled). A bird was deemed to have settled on a potential breeding site when it entered a 5 km radius area into which it stayed throughout July (Ganusevich et al. 2004; see Therrien et al. 2012 for details on how summer home range was calculated). Based on summer movement patterns, we were able to infer that all tracked females bred in all years, which was confirmed by ground visits conducted in 2008 (Therrien et al. 2012).

Pre-breeding movements typically showed the following pattern. After departure from the wintering ground, birds often remained in the moving state for an average of 12 d; we called this component the directional movement. The birds eventually exhibited searching behavior, often alternating between the moving and searching state over a few days, before eventually settling for the summer. We defined prospecting movements as those occurring between the first time a bird switched to a searching state over potential breeding habitat and the time of settlement (as defined above). Breeding habitat refers to the arctic tundra as extracted from the Global Ecological Zones database from FAO; < www.fao.org/geonetwork/srv/en/metadata.show? id = 1255>, accessed 20 June 2013). We defined a searching area as the distance covered by a bird while remaining in a searching state during consecutive locations over breeding habitat. As birds could alternate between searching and moving states during prospecting, a single bird could patrol several searching areas in a given year. We calculated the duration and total distance traveled for each component of the pre-breeding movements (i.e. directional and prospecting). We evaluated the linear distance between furthest apart searching areas for each individual in a given year as an index of prospecting scale. We calculated the annual breeding dispersal distance of individuals as the distance between the center of their summer home range once they had settled (or their nest site when known) in year i and $i + 1$. We compared the date of settlement, duration, total distance traveled, linear distance between furthest apart searching areas and breeding dispersal among years using general linear mixed models and a posteriori Tukey tests. An individual's ID was used as a random factor in the model to account for the fact that the same individuals were sampled more than one year. Because our sample size is limited, we used a more liberal significant threshold value of $p = 0.1$ to reduce the risk of type II errors.

We estimated summer densities (individuals ha^{-1}) of live-trapped lemmings at each trapping session using mark–recapture techniques with the program DENSITY 4 (Efford et al. 2004, Efford 2009) as described by Bilodeau et al. (2013). All parameter settings in DENSITY were similar to those used by Krebs et al. (2011). We averaged densities of each species between the two grids for the first two trapping sessions (mid-June and mid-July) each year in order to have a global measure of lemming density on the study area during the breeding period. All animal manipulations were conducted in accordance with the animal care committee of Univ. Laval (CPAUL permit #84921).

Results

We successfully tracked 9 of the 12 marked female snowy owls during the first year and 7 of them for an additional 2 yr. Departure dates from the wintering sites were variable among individuals although birds generally departed in late March (mean ± SD; 30 March ± 19 d, n = 9 in 2008, 21 March ± 15 d, n = 5 in 2009 and 24 March ± 6 d, n = 7 in 2010). Settlement dates on the breeding grounds were also variable among individuals and years. Birds settled in early May in 2008 (8 May) and 2010 (4 May) but settled later in 2009 (25 May; $F_{2,8} = 3.2$, p = 0.08; Fig. 1).

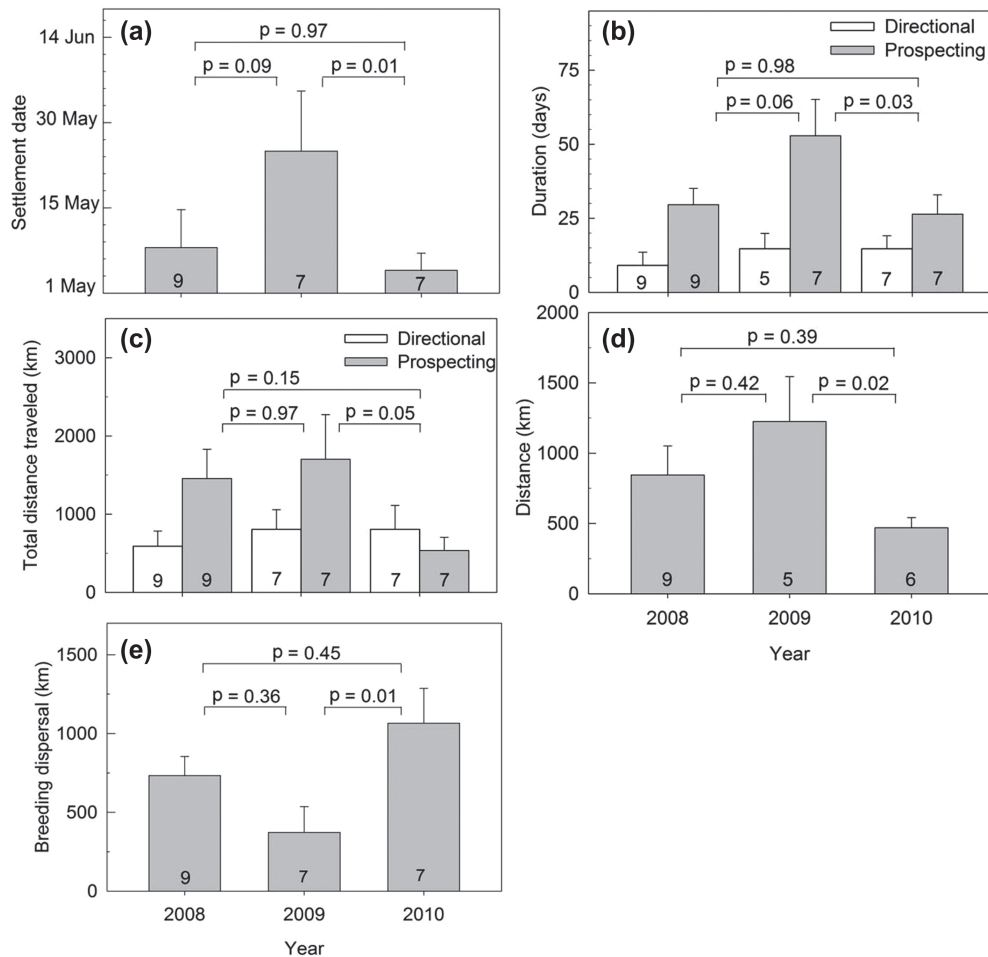Following departure from their wintering site in early spring, birds generally took a northward orientation (Fig. 2)

Figure1. Settlement date (a), duration (b), total distance traveled (c), linear distance between furthest apart searching areas (d) and breeding dispersal (e) during the pre-breeding period of nine adult female snowy owls marked with satellite transmitters on Bylot Island, NU, Canada in 2007 and tracked for up to 3 yr. Mean ± SE. Tukey tests were done between years for the prospecting period only. Sample sizes are shown on bars.

and maintained directional movements, though for a relatively short period of time, usually ≤ 10 d (Fig. 2, Supplementary material Appendix 1). Birds that showed the longest directional movements (e.g. birds F8 and F9) were generally those that wintered the furthest south (Fig. 2, Supplementary material Appendix 1). Tracked owls exhibited a broad range of exploratory behavior in spring as distance traveled and time spent prospecting were highly variable among birds and years (Fig. 2, Supplementary material Appendix 1). On average, birds prospected between 1 and 2 months in spring, which was at least 3 times longer than the time spent in directional movements (Fig. 1). The duration of the prospecting period was longer in 2009 (53 d) than in 2008 (30 d) and 2010 (26 d; $F_{2,8} = 3.9$, $p = 0.04$; Fig. 1). The total distance traveled each year during prospecting ranged from 536 to 1702 km on average, which was usually longer than the distance traveled during directional movements (Fig. 2, Supplementary material Appendix 1). Mean total distance traveled during prospecting differed among years ($F_{2,8} = 3.1$, $p = 0.08$) and was highest in 2009 (1702 km) and lowest in 2010 (536 km, Fig. 1). Similarly, the linear distance between furthest apart searching areas differed among years ($F_{2,8} = 3.6$,

$p = 0.07$) and was highest in 2009 (1225 km) and lowest in 2010 (470 km; Fig. 1).

Except in 2007 when one nest, which failed during laying, was found in the searched area of 100 km^2 on Bylot Island, snowy owls only settled to breed on our core study area when average lemming numbers during the summer were over 4.0 ind. ha^{-1} (equivalent to ~1.5 ind./100 trap-nights, Gauthier et al. 2013). In those years, density of nesting snowy owls reached 10 ± 2 nests 100 km^{-2} (Fig. 3). Similarly, lemming abundance was relatively high in the two areas where snowy owls settled in 2008 and where lemmings could be trapped (Mary River: 4.0 ind./100 trap-nights, Dewar: 2.3 ind./100 trap-nights).

After breeding on Bylot Island in 2007, marked females settled to breed in far apart areas during the three subsequent summers. Noteworthy is one bird (F4) that came back to breed on Bylot Island in 2010, 1.1 km from where it nested in 2007, after breeding on Baffin Island (2008) and northern Greenland (2009) during the previous summers (Fig. 4). Most birds settled to breed on Baffin Island in summers 2008 and 2009 but one settled on Prince Patrick and Borden Islands in the western Canadian Arctic (Fig. 4). In summer 2010, birds generally settled further south, in northern
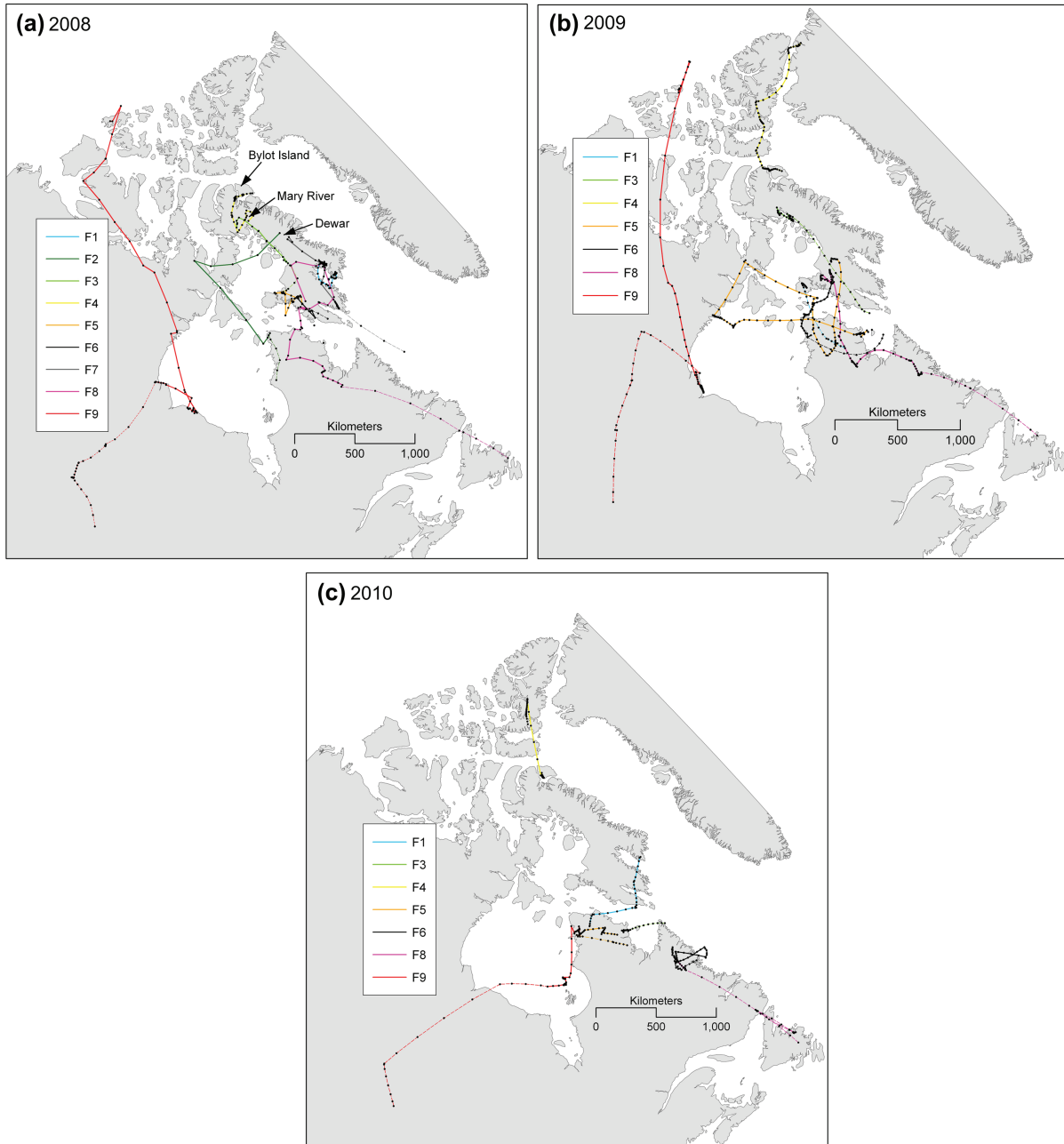
Figure 2. Pre-breeding movements of adult female snowy owls tracked with satellite transmitters in northern Canada from 5 March to 24 June in 2008 (a), 2009 (b) and 2010 (c). Each point represents the estimated location based on state-space modeling (Methods). Dashed lines represent directional movements and solid lines represent prospecting movements.

Quebec, thereby showing an almost complete lack of site fidelity. Individual breeding dispersal distance between consecutive years ranged from 18 to 2224 km and averaged 725 km over the 4 breeding seasons (Fig. 4, Supplementary material Appendix 1), which represents the longest confirmed mean breeding dispersal ever recorded for a bird species.

Discussion

The movements of female snowy owls recorded by satellite-tracking for up to three consecutive years generally supported

our three hypotheses. First, owls showed a prolonged (1–2 months) period of prospecting over a broad scale (mean distance between furthest apart searching areas of 828 km) as they search for potential breeding sites in spring and these movements were generally tortuous in accordance with the observed spatial unpredictability of small mammal outbreaks (Myrberget 1973, Ims et al. 2011). Moreover, the prospecting period lasted longer, distance traveled was lengthier and settlement date at the breeding site was later in the year where summer abundance of lemmings was lowest on Bylot Island. Considering the scale of spatial synchrony in lemming cycles (see below), we presume that the situation
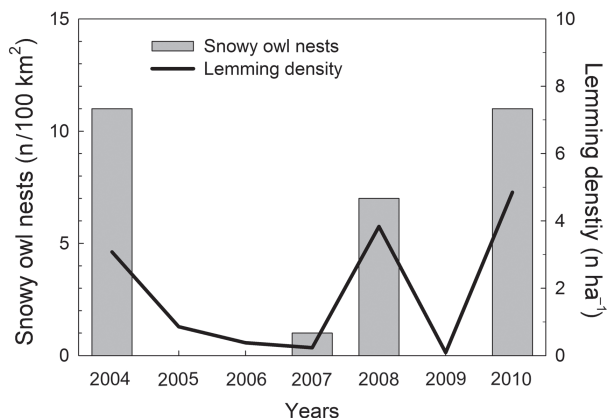
Figure 3. Average lemming density measured annually with live-trapping in June and July and number of snowy owl nests monitored in the 100 km² core study area systematically searched on Bylot Island, Nunavut, Canada from 2004 to 2010.

encountered on Bylot Island was representative of the eastern Canadian Arctic (as confirmed by lemming trapping conducted at three distant sites in 2008). Second, owls settled in our main study area almost exclusively when lemming abundance was relatively high, as observed in other tundra areas (Pitelka et al. 1955, Wiklund et al. 1998, Gilg et al. 2003, 2006). Trapping conducted at two other sites in 2008 further confirmed that owls had moved to areas of high lemming abundance to settle that year. Third, the scale at which annual breeding dispersal occurred was very large, approaching the continental scale (>700 km on average). This value provides an order of magnitude of the average linear distance that owls need to move annually to find suitable areas to breed. Interestingly, this value seems to correspond to the scale of spatial synchrony of lemming cycles reported in previous studies, with phase synchrony in lemming populations at distances ranging from 500 to 1000 km but asynchronous phases in populations separated by ≥ 1000 km (Erlinge et al. 1999, Angerbjörn et al. 2001, Predavec et al. 2001, Krebs et al. 2002).

Despite those results, some issues regarding the mechanisms involved in the settling decisions of snowy owls remain unclear. Indeed, in 2007, estimated lemming density was low in our core study area where lemming trapping and intensive searches for owl nests occurred. Nonetheless, some snowy owls bred on Bylot Island outside of our core study area that year and we marked 12 of them. Local lemming density in those areas remains unknown but was apparently not very high based on casual field observations. A possible explanation for that apparently contradictory result may be that the decision to settle and initiate a nest might not depend solely on absolute local lemming density but also on the relative lemming density in the surrounding regions, which may have been low in 2007. None of the owl came back to our study site one year after marking even though lemming density was high in 2008 and numerous unmarked snowy owls nested there. However, lemming abundance was apparently high over a large portion of the eastern Canadian Arctic in 2008 and individuals may have encountered numerous suitable nesting site locations during

their pre-breeding prospecting movements. In spring 2010, owls traveled over a short distance compared to other years when they settled in the low Arctic (northern Quebec), an area close to their wintering area (Therrien et al. 2011). Field observations indicative of high lemming density (e.g. browsing damage on shrub stems and extensive cutting of graminoid shoots) were reported in northern Quebec that year (J.-P. Tremblay pers. comm.). Overall, our observations suggest that females starting to move northward in spring may settle as soon as they find suitable breeding conditions, such as high lemming density and sites unoccupied by conspecifics.

Irruptive migration seemed to have evolved in highly mobile consumers in response to the unpredictability of resources. Similar behaviors are thus expected in other avian species feeding primarily on temporally and spatially unpredictable resources (Newton 2006a). Indeed, Newton (2006b) reported long-distance dispersal movements over consecutive breeding seasons in common crossbills *Loxia curvirostra*, apparently tracking the production of coniferous seeds over more than 2000 km. Newton (2008) also reviewed similar long-distance dispersal movements in other owl species following variation in prey populations. This strategy is however not universal. Indeed, annual movements of great-horned owls *Bubo virginianus*, a strigidae of similar size than the snowy owl inhabiting the boreal forest, are very limited even if its main prey, snowshoe hares *Lepus americanus*, vary considerably in abundance from one year to another (Rohner 1996). Its capacity to turn to alternative prey (Rohner 1995) and the benefits of remaining on territory likely outweigh the potential gains of moving.

As a behavioral strategy, irruptive migration has many potential drawbacks. Indeed, such large-scale movements require a large energy expense associated with locomotion and may entail some costs such as uncertainty, hazards and the risk of 'moving for nothing'. Furthermore, by moving extensively from one year to the next, individuals loose detailed knowledge and familiarity with a given area, which has been identified as a prime advantage of breeding site fidelity in many species (Hinde 1956, Gavin and Bollinger 1988). In the short-term, all of those issues could hinder resource acquisition and ultimately reproductive output and survival, which would not promote the evolution of such behavior. However, irruptive migration may also provide some benefits for specialist species living in seasonal environments such as the snowy owl (Newton 2006a). Indeed, being a diet specialist can increase foraging efficiency and compensate some of the previously described disadvantages (Terraube et al. 2011). Moreover, the potential access to plentiful resources and the possibility to sustain reproductive activities every year, despite a strong reliance on an unpredictable food supply, likely outweigh the potential costs of irruptive migration for female snowy owls.

Several adaptations may have contributed to the success of the snowy owl as an irruptive migrant. First, the relatively low wing-loading characteristic of strigidae reduces their costs of locomotion compared to birds with higher wing-loading (Poole 1938, Johnson 1997). This also means that owls can accumulate energy reserves without impairing their flight capability and then fast for several days if needed.
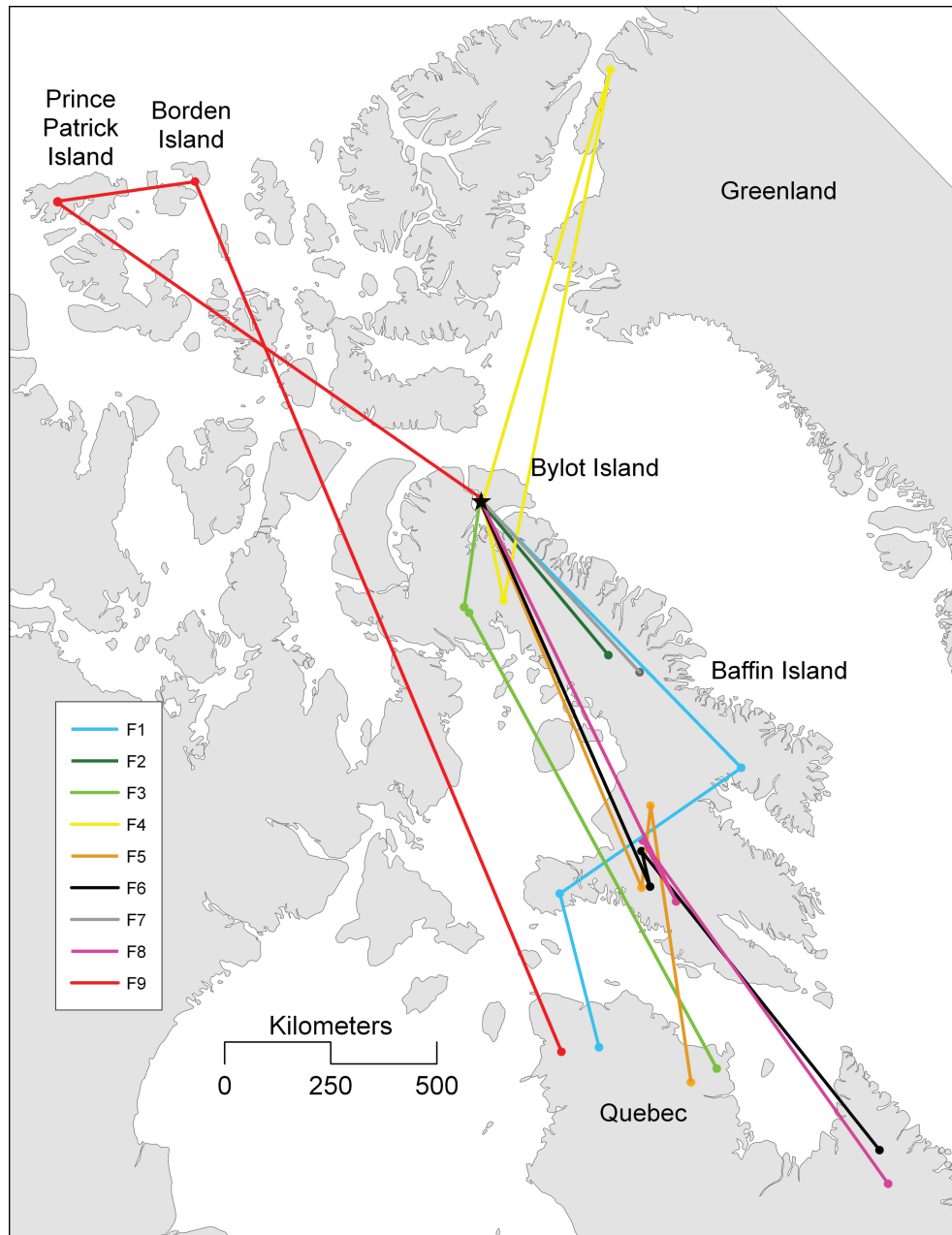
Figure 4. Breeding site locations of nine adult female snowy owls originally marked on Bylot Island (large star) and tracked with satellite transmitters over four consecutive breeding seasons (2007–2010) in northern Canada. Breeding sites are chronologically displayed and linked by a line for each individual.

Second, its 'sit and wait' hunting strategy should reduce foraging costs compared to actively foraging predators. Third, large body size and especially powerful talons allow snowy owls to feed opportunistically on a large variety of prey if lemmings are scarce in a given region (reviewed by Parmelee 1992; see also Therrien et al. 2011). Fourth, adult birds face limited threats from other predators of the tundra, at least when not incubating, thus reducing the risks associated with exploration of unfamiliar areas. Fifth, previous knowledge on the presence of potentially competing neighbors in its breeding area may be of limited importance because snowy owls can efficiently defend a large breeding territory from any species competing for similar resources on the tundra

(Parmelee 1992). Finally, snowy owls can raise large clutches (from 6 to 10 chicks) when resources are abundant (Parmelee 1992, Therrien et al. 2012) and thus the reproductive benefits of finding an area with a high density of lemmings is relatively high.

At the ecosystem level, it has been suggested that irruptive predators could affect prey populations if they exhibit strong aggregative responses with no time-lag to an increase in prey abundance (Janzen 1971, Korpimäki 1985, Korpimäki and Norrdahl 1991). Avian predators inhabiting the tundra such as the snowy owl can consume large quantities of lemmings. Indeed, consumption rates can sometimes exceed the maximum growth rate of lemming populations, thereby

potentially limiting their growth in a top-down manner (Gilg et al. 2003, 2006, Therrien et al. 2014). Such a phenomenon has been documented in the boreal grasslands of Finland where an assemblage of owl species can regulate rodent populations (Korpimäki 1985, Korpimäki and Norrdahl 1991). Our study provides evidence that the snowy owl is a predator that can act in this manner as it can explore large expanses of the tundra every spring to find areas of high lemming abundance and settle in those areas to breed without any time-lag even if this entails net linear movement of up to 1000 km or more between consecutive years. Such large-scale irruptive movements combined with their high consumption rates could in turn promote synchronization among fluctuating small mammal populations over a wide area (Norrdahl and Korpimäki 1996, Ims and Andreassen 2000, Krebs et al. 2002). Predation by this irruptive migrant could therefore have a dampening effect on the amplitude of lemming population cycles over a broad continental scale. This suggests that the snowy owl could play a major role in the tundra food web structure and functioning.

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Supplementary material (Appendix JAV-00426 at <www.avianbiology.org/readers/appendix>). Appendix 1.