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POPULATION ECOLOGY – ORIGINAL RESEARCH

Pulsed resources at tundra breeding sites affect winter irruptions at temperate latitudes of a top predator, the snowy owl

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Abstract Irruptive migration is mostly observed in species specialized on pulsed resources and is thought to be a response to unpredictable changes in food supply. We assessed two alternative hypotheses to explain the periodic winter irruptions of snowy owls *Bubo scandiacus* every 3–5 years in temperate North America: (a) the lack-of-food hypothesis, which states that a crash in small mammal abundance on the Arctic breeding grounds forces owls to move out of the tundra massively to search for food in winter; (b) the breeding-success hypothesis, which states that high abundance of tundra small mammals during the summer allows for high production of young, thus increasing the pool of migrants moving south the following winter. We modeled winter irruptions of snowy owls in relation to summer food resources and geographic location. Winter abundance of owls was obtained from citizen-based surveys from 1994 to 2011 and summer abundance of small mammals was collected in summer at two distant sites in Canada: Bylot Island, NU (eastern High Arctic) and Daring Lake, NWT (central Low Arctic). Winter owl abundance was positively related to prey abundance during the previous summer at both sites and tended to decrease from western to eastern temperate North America. Irruptive migration of snowy owls was therefore best explained by the breeding success hypothesis and was apparently caused by large-scale summer variations in food. Our results, combined with previous findings, suggest that the main determinants of irruptive migration may be species specific even in a guild of apparently similar species.

Keywords *Bubo scandiacus* · Irruptive migration · Wintering range · Small mammal · Zero-inflated negative binomial model

Introduction

Migrants are found in a wide diversity of taxa in the animal kingdom, from insects [e.g., dragonflies (Wikelski et al. 2006; Dingle 1972)] to large mammals [e.g., African elephant, *Loxodonta Africana* (Thouless 1995)] and in both terrestrial [e.g., blackpoll warbler, *Setophaga striata* (DeLuca et al. 2013); caribous, *Rangifer tarandus* (Le Corre et al. 2014)] and aquatic species [e.g., eels (Miller et al. 2015); humpback whale, *Megaptera novaeangliae* (Zerbini et al. 2006)]. Despite the fact that animal migration patterns are often characterized by regularity and predictability, they are complex and take many forms. These patterns are often regarded as continua that vary in terms of distance (short- to long-distance migration), intensity (partial to complete migration), or obligation to move

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(facultative to obligate migration) (Newton 2006a, 2008). Irruptions (or invasions) are an extreme and often spectacular form of facultative migration characterized by unusual and massive movements of individuals to a given area, a phenomenon that can sometimes attract considerable public attention (Holland 2013; Kaufman 2013). Movement patterns during irruptive migrations can be highly variable in terms of number of migrants, the distance they travel, the area they occupy and the duration of their travel (Newton 2008). Irruptive migration is mostly observed in species that specialize on unpredictable or pulsed resources and their movements are generally thought to be a response to irregular fluctuations in their food supply (Newton 2006a).

Irruptive migration is common in two groups of birds, boreal seed-eating birds and several raptors, especially owls. Seed eaters typically specialize on a limited or a single food plant, which often include mast-fruiting species like coniferous trees (Newton 2008). Examples include common redpolls *Acanthis flammea*, which feed primarily on birch and alder seeds (Hochachka et al. 1999), and common crossbills *Loxia curvirostra*, which specialize on conifer seeds, especially spruce (Newton 2006b). Irruptive migrations of these species have been suggested to be related to periodic failure in the seed crop of their preferred food for a long time (Svardson 1957; Bock and Lepthien 1976). Koenig and Knops (2001) pointed out that two hypotheses could actually explain winter irruptions in seed-eating birds: the seed-crop failure and the population density hypotheses. According to the first hypothesis, a widespread failure of the seed crop on the northern breeding grounds would force individuals to move overwhelmingly to southern areas in winter due to lack of food. Alternatively, a good seed crop could lead to a high survival and especially a high reproductive success, resulting in an unusually large number of first-year birds being produced and moving south in winter. Results presented by Koenig and Knops (2001) for several species of seedeater suggest a combination of both hypotheses as irruptions were often best explained by a large seed crop resulting in high population densities due to a high breeding success followed by a poor seed crop the following year but with some species-specific differences.

Among owls, several species feed primarily on small mammals, which show large-amplitude, cyclic fluctuations in abundance in many northern areas (Stenseth 1999; Korpimäki et al. 2004; Ims and Fuglei 2005; Fauteux et al. 2015a, b). Species like the great gray owl *Strix nebulosa*, the boreal owl *Aegolius funereus* and especially the snowy owl *Bubo scandiacus* exhibit irruptive migration during winter in several areas, sometimes with a periodicity similar to the one of small mammals (Bull and Duncan 1993). It has therefore long been thought that these large-scale movements were related to the periodic fluctuations in small mammal abundance (Shelford 1945; Cheveau et al. 2004; Morrissette et al. 2010). Winter irruptions of several boreal owls were found to be negatively related to abundance of small mammals during the previous summer, suggesting that owl irruptions were a response to a lack of food (Cheveau et al. 2004; Côté et al. 2007), which is analogous to the seed-crop failure hypothesis of Koenig and Knops (2001) for boreal seedeaters.

The snowy owl is probably the species for which periodic winter irruptions are most spectacular and have been known for a long time in North America (Gross 1927, 1931; Shelford 1945; Kerlinger et al. 1985). This Strigidae irrupts in large numbers every 3–5 years [mean ± SE = 3.9 ± 0.13 (Newton 2002)] in southern Canada and northern USA during winter. Snowy owls breed in the Arctic tundra where they feed primarily on lemmings and voles (subfamily Arvicolinae) and their local breeding density and reproductive success are highly dependent on the abundance of small mammals (Gauthier et al. 2004; Gilg et al. 2006; Therrien et al. 2014b). Unlike many birds, including other owl species, snowy owls can lay clutches of up to 14 eggs in small mammal peak years [mean ± SD, 7.0 ± 2.1 eggs (Potapov and Sale 2012)]. In winter, their diet is more diversified though small mammals remain a prey of choice (Keith 1963; Boxall and Lein 1982; Detienne et al. 2008). It has long been thought that snowy owls were also escaping areas where food had become scarce, such as during the low period of lemming cycles, and that winter irruptions were thus caused by a lack of food in the north (Shelford 1945; Chitty 1950; Lack 1954; Newton 1970). However, recent evidence has not been consistent with this suggestion. Satellite tracking revealed that many adult owls remain in the Arctic tundra during the winter, irrespective of lemming abundance in the previous summer (Fuller et al. 2003; Therrien et al. 2011, 2014b). During invasion years, a greater proportion of juveniles are observed compared to non-irruptive years and individuals are generally in good body condition (Smith 1997; J. F. Therrien, unpublished data). These observations were more in agreement with the hypothesis that a large production of young due to a high lemming abundance in summer were responsible for winter irruptions of owls, an idea already put forward by Gross (1947).

Our goal was to assess two alternative hypotheses to explain periodic winter irruptions of snowy owls in temperate areas of North America. The lack-of-food hypothesis states that a crash in small mammal abundance in the Arctic creates a shortage of food and forces owls to move out of the tundra massively in winter. The breeding-success hypothesis states that a peak in small mammal abundance during the summer allows for a production of numerous young in the Arctic tundra, which considerably increases the pool of migrants in the following winter.

The lack-of-food hypothesis predicts that owl abundance in winter should be negatively related to the abundance of tundra small mammals in the previous summer whereas the breeding-success hypothesis predicts a positive relation. Studying irruptive migration is challenging due to the continental scale of this phenomenon but citizen-based surveys such as the Christmas Bird Count (CBC) are powerful tools with which to colligate long-term, pan-continental observations (Koenig and Knops 2001), especially for an easily observable species like the snowy owl. Our study combined, for the first time, continental-scale data from the CBC with field data of annual fluctuations of small mammals at two distant sites in the Canadian Arctic to test the contrasting predictions of these two hypotheses.

Materials and methods

Snowy owl abundance data

Data on the abundance of wintering snowy owls were obtained from the CBC records for the 1994–2011 period. The CBC is conducted annually across North America by volunteer bird watchers and consists of a 1-day survey performed in the weeks around Christmas. Volunteers select a "circle" (i.e., survey site) of 24.1 km (15 mi) in diameter, and report every bird seen or heard while walking or driving routes crisscrossing the survey area [mean = 28.5 volunteers/circle, range = 1–200 (Butcher 1990)]. Circle locations are predefined and permanent although each circle may not be visited every year, as the visits depend on the volunteers' enrollment at each site. They also report the number of hours spent in the field per party (i.e., a group of persons counting birds together), for each transportation method used (e.g., car, foot, boat). Observer effort is thus calculated in party-hours. Among the 2300 circles included in the CBC database, 616 have reported at least one snowy owl observation during the 18 years of our study. To evaluate the influence of small mammal abundance on winter irruptions of owls and reduce the noise resulting from anecdotal observations, we only selected sites that showed irruptive patterns, i.e., at least 3 years with three or more owl observations recorded at a site between 1994 and 2011. This allowed us to eliminate sites where presence of owls is only accidental and which are unlikely to show irruptive patterns. The selection was performed prior to any analyses. We found 84 sites that met this criterion. The sites were concentrated in southern Canada and northern USA and spanned the whole continent from east to west (Fig. 1; see Appendix S1 for the list of sites).

Previous studies that used CBC data to assess bird population trends have emphasized the need to correct for observer effort (Link and Sauer 1999; Dunn et al. 2005). To evaluate the relevance of accounting for observer effort in our study, we verified the relationship between owl counts and effort (calculated as party-hours; see Appendix S2), but we could not detect any trend. We also compared models with and without the effort variable in our subsequent analysis (results not shown). Models not accounting for effort performed better based on Akaike information criterion (AIC) and the confidence intervals of the effort variable always included zero when effort was added as a covariate.

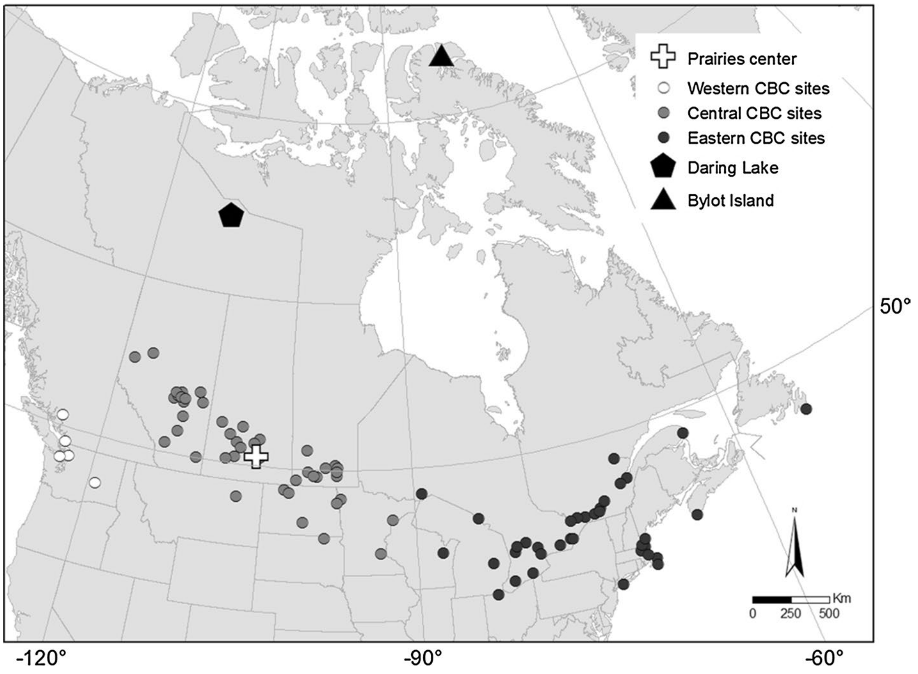

Fig. 1 Location of study sites for summer small mammal abundance in the Canadian Arctic (Bylot Island and Daring Lake), and of Christmas Bird Count (*CBC*) sites selected to detect an irruptive pattern in winter abundance of snowy owls in temperate North America. The *white cross* depicts the center of the Prairies calculated as the mean coordinates of CBC sites located in the Canadian Prairies and US Great Plains and Midwest

Therefore, an increased observation effort apparently did not lead to higher owl counts. This counterintuitive result can likely be explained by the fact that snowy owls are large, charismatic and conspicuous birds found in open habitats, which facilitates their observation. Moreover, their presence, like that of other birds of prey (Dunn et al. 2005), is often known by observers prior to the CBC survey. We thus only report the results based on raw counts.

Small mammal abundance data

Reliable, long-term time series of small mammal abundance in the Arctic tundra of North America, where snowy owls breed, are very scarce. We obtained data on annual small mammal abundance from two Arctic sites from 1994 to 2011: Bylot Island, Nunavut (73°08N 80°00W), and Daring Lake (64°52N 111°35W), Northwest Territories, separated by 1555 km (Fig. 1). These were the only two tundra sites that provided a consistent record of annual abundance of small mammals using standard methods for the whole period. Both sites are known breeding grounds for snowy owls. Bylot Island is a High Arctic, coastal study site where two species of small mammals are found: brown lemmings *Lemmus trimucronatus*, the most abundant species, and collared lemmings *Dicrostonyx groendlandicus*. Ninety-one percent of individuals caught in peak years were brown lemmings and 31 % in crash years [percentages are based on live-trapping data from 2004 to 2011 (Fauteux et al. 2015b)]. The landscape at this site is dominated by herbaceous tundra and composed of a mosaic of mesic (85 %) and wet (15 %) environments. Snap-trapping has been conducted at the site since 1994 and live-trapping since 2004 (see Gruyer et al. 2008, 2010; Fauteux et al. 2015b for details of the methods). Snap-trapping provides an index of annual abundance while live-trapping allows accurate determination of densities using capture-recapture method. For our analyses, we used population density estimates (number per hectare), measured directly from 2004 onward and transformed from the annual snap-trap index before 2004 using the equation provided by Gauthier et al. (2013).

Daring Lake is a Low Arctic, continental site where multiple species of small mammals are observed: northern red-backed vole *Clethrionomys rutilus* (68 %; percentages are based on snap-trapping captures across the study years), meadow vole *Microtus pennsylvanicus* (15 %), collared lemming (12 %), brown lemming (3 %), and different species of shrews (*Sorex* spp.; 1 %). Small mammal abundance at Daring Lake were estimated using snap-trapping methods and were provided by the Northwest Territories Small Mammal Survey (Government of the Northwest Territories 2008). Snap-trap indices (number caught by 100 trap-nights) usually provide a good index of mammal abundance (Gauthier et al. 2013). Small mammal abundance at the two sites were not correlated ($r = -0.03$, $p = 0.9$), which indicates an absence of synchrony in small mammal populations at that spatial scale (1555 km). Although small mammal *density* was estimated on Bylot, the term “abundance” will be used hereafter to simplify the text. However, due to differences of methods, absolute abundance values cannot be compared between the two sites.

Statistical analyses

Analyses of count data represent a challenge as they often depart from normal distributions due to the presence of excess zeroes or overdispersion. A visual inspection of the frequency distribution of our count data suggested that an excess of zeroes was the case (Appendix S3). Therefore, to assess the predictors of snowy owl irruptions, we used zero-inflated negative binomial (ZINB) models, a class of generalized linear models (GLMs) that account for data with excess zeroes and overdispersion. ZINB models are derived from a mixture of two distributions where a logistic regression models the structural zeroes (i.e., presence/absence) and a negative binomial regression is used for the counts [i.e., abundance; $y > 0$ (Hilbe 2011)]. Covariates can be added to each component to model the excess of zeroes and/or the count (see Appendix S4 for details).

ZINB models can extend GLMs by including random effects to the existing fixed effects in the linear predictor, thus producing mixed-effect models (McCulloch and Searle 2001). To account for the non-independence of data collected annually at a given site in our analyses, we added the site as a random effect. We adjusted models with a random effect on the presence/absence component only, the abundance component only and on both. Models with a random effect on both components performed better than models with random effects on each component separately (ΔAIC = 123.8) and we therefore retained the site as a random effect on both components. Models were fitted with the NLMIXED procedure (release 9.3; SAS 2010, NC). We found no evidence for spatial auto-correlation in our data (Moran’s I statistic, $p = 0.37$) (Dormann et al. 2007).

Predictor variables included in the ZINB model were: abundance of small mammals on Bylot Island and at Daring Lake, and the longitudinal distance between CBC sites and the center of the North American Prairies (see Fig. 1). The latter variable was included to account for the fact that snowy owl irruptions could be asynchronous between eastern and western North America. We chose the center of the Prairies as our reference point (distance = 0) because this region of the continent receives the highest densities of snowy owls in winter and is considered a favorable winter habitat for them (Boxall and Lein 1982; Kerlinger and Lein 1986). The distance variable was expressed in kilometers and represents the longitudinal distance from each site to the reference point (50.57°N–104.88°W), which was the average coordinate of the 43 CBC sites located in the Canadian Prairies and the US Great Plains and Midwest (gray circles in Fig. 1). This distance ranged from −1354 km for our westernmost site to 3589 km for our easternmost site. In the analyses, the distance was divided by a constant (i.e., 100) to minimize the magnitude difference between variables. Because snowy owl abundance may not be related to prey densities at our tundra sites equally across the continent, interactions between small mammal densities at each site and distance were also tested. Abundance of small mammals were standardized (i.e., $(x - x)/\mathrm{sd}$) because they had different units.

Models were built by combining different groups of variables: (1) food resources in the Arctic (i.e., abundance of small mammals on Bylot Island and at Daring Lake), (2) geographic location in winter (i.e., distance of the sites from the center of the Prairies), and (3) the interactions between these two first groups. Each of these effects had to be applied simultaneously to both components (i.e., presence/absence and abundance) of the model. We compared models using AIC corrected for small sample size (AICc) and performed multi-model inference following Burnham and Anderson (2002).

Results

Between 1994 and 2011, a total of 1298 counts were performed at the 84 CBC sites retained in our analysis (mean ± SD = 15.5 ± 3.9 counts/site). Of these counts, 494 counts reported no owls (38.1 %), whereas 3357 snowy owls were observed during the other 804 counts. Total owl abundance (mean ± SD = 186.5 ± 105.0 owls/year, excluding zeros) fluctuated annually and suggested a cyclical pattern of fluctuations during this period (Fig. 2). Owl abundance also varied spatially (annual mean ± SD = 2.1 ± 2.0 owls/site; Fig. 3). In decreasing order of abundance, the five sites where the most owls were counted are: Regina, Saskatchewan; Ladner, British Columbia; Kingston, Ontario; Winnipeg, Manitoba; and Oak Hammock Marsh, Manitoba (see Appendix S1 for details on each site). However, these values should not be considered representative of the mean winter abundance of owls throughout their range considering that we only selected sites where they occurred regularly and showed an irruptive pattern (see "Materials and methods").

Model selection provided strong evidence for an effect of lemming abundance at both study sites on the probability of occurrence and abundance of snowy owls in winter and weak evidence for an effect of the distance to the prairies (cumulative AICc weight = 0.58; Table 1). Probability of occurrence in winter was positively related to small mammal abundance on Bylot Island, but confidence intervals of the other model-averaged estimates included zero (Table 2). Owl abundance in winter was positively related to small mammal abundance the previous summer both on Bylot Island and at Daring Lake, and based on its confidence interval, the distance variable nearly excluded zero (Table 2). We based our subsequent interpretations on the abundance data (rather than the probability of occurrence), as we considered these most relevant to our initial hypotheses. Winter abundance of snowy owls increased when summer abundance of small mammals increased at either of the two Arctic sites and the slopes of the relationships

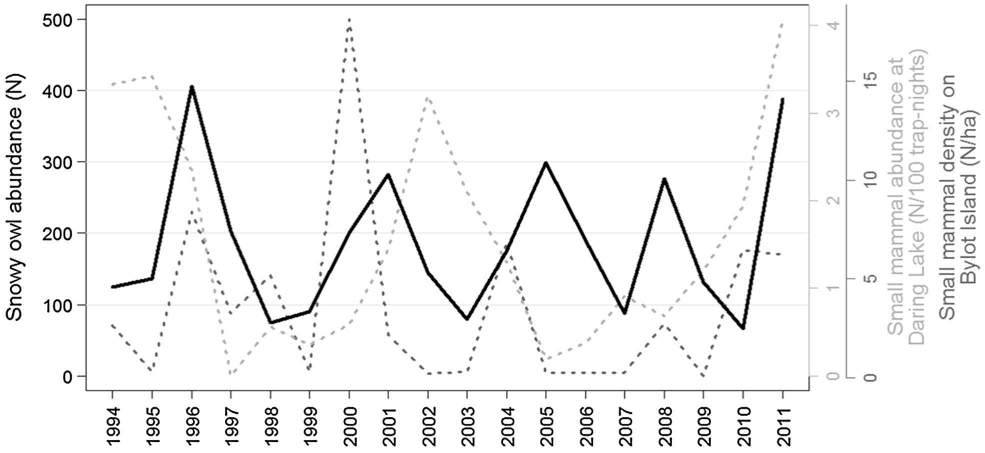

Fig. 2 Annual variation of snowy owl winter abundance at selected CBC sites in temperate North America (*black line*), small mammal abundance in summer at Daring Lake, Northwest Territories (*light gray dashed line*) and small mammal densities on Bylot Island, Nunavut (*dark gray dashed line*). Note the different axes' scales and units for lemming numbers at each study site. Lemming abundance values are not directly comparable between the two sites because of different units

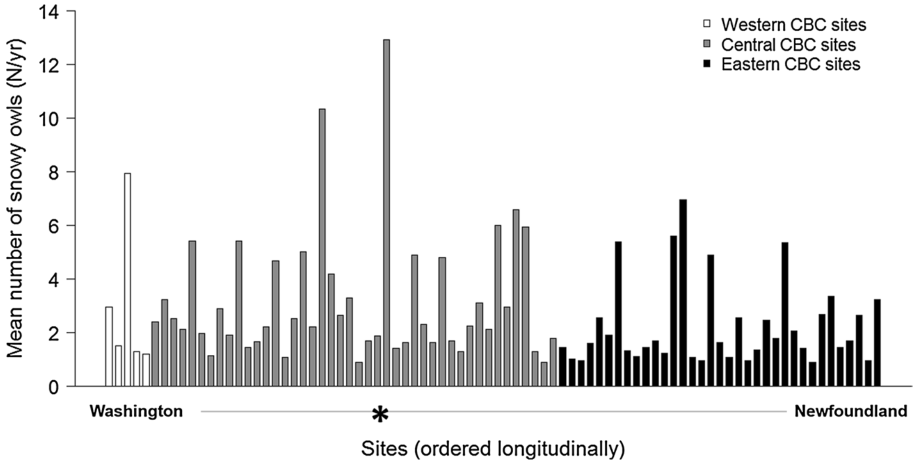

Fig. 3 Mean number of snowy owl observations at each selected CBC site 1994–2011. Sites are ordered longitudinally, from the westernmost site in Washington State, USA, to the easternmost site in Newfoundland, Canada. These 84 sites were selected based on the presence of irruptive numbers of owls, and exclude sites where the presence of snowy owls was accidental or sporadic (see "Materials and methods"). The center of the Prairies region (see Fig. 1) is depicted by a *black asterisk*

Table 1 Model selection of the effect of small mammal abundance at two Arctic sites in summer and geographic location in winter on the probability of occurrence (presence/absence) and abundance of snowy owls in the Christmas Bird Count in southern Canada and northern USA between 1994 and 2011 using zero-inflated negative binomial (ZINB) models

Variables	*K*	−2 × log lik.	ΔAICc	w_i
mamBylot + mamDaring + Dist.	11	5084.5	0	0.44
mamBylot + mamDaring	9	5088.5	0.1	0.42
mamBylot + Dist.	9	5091.5	3.2	0.09
mamBylot + mamDaring + Dist. + Dist.× mamBylot + Dist. × mamDaring	15	5081.5	5.4	0.03
mamBylot + Dist. + Dist. × mamBylot	11	5091.1	6.9	0.01
mamDaring + Dist.	9	5117.2	28.8	0.00
mamDaring + Dist. + Dist. × mamDaring	11	5114.4	30.1	0.00
Dist.	7	5124.4	32.0	0.00

ZINB models used for this analyses are derived from a mixture of two distributions where a logistic regression models the structural zeroes (i.e., presence/absence) and a negative binomial regression is used for the counts (i.e., abundance; see "Materials and methods"). The same effects were modeled on the probability of occurrence and abundance. Site identify was entered as a random factor in the analysis

mamBylot Small mammal abundance on Bylot Island, *mamDaring* small mammal abundance at Daring Lake, *Dist.* distance to the center of the Prairies, *K* number of parameters, *Log-lik.* log-likelihood, *AICc* Akaike information criterion corrected for small sample size, w_i AICc weight

Table 2 Factors influencing the probability of occurrence (presence/absence) and abundance of snowy owls in the Christmas Bird Count of southern Canada and northern USA between 1994 and 2011

Model component	Variable	Coefficient	Unconditional SE	Lower CI	Upper CI
Occurrence	Intercept	1.327[a]	0.214[a]	0.907a	1.747[a]
	MamBylot	0.434[a]	0.117[a]	0.204[a]	0.664[a]
	MamDaring	−0.012	0.084	−0.176	0.152
	Dist.	−0.015	0.013	−0.040	0.009
	Dist. × mamBylot	−0.002	0.007	−0.017	0.013
	Dist. × mamDaring	−0.004	0.006	−0.016	0.008
Abundance	Intercept	1.202[a]	0.075[a]	1.054[a]	1.350[a]
	MamBylot	0.064[a]	0.027[a]	0.011[a]	0.117[a]
	MamDaring	0.068[a]	0.026[a]	0.017[a]	0.119[a]
	Dist.	−0.007	0.005	−0.017	0.002
	Dist. × mamBylot	−0.001	0.002	−0.005	0.003
	Dist. × mamDaring	−0.003	0.002	−0.007	0.001

Model-averaged coefficients of the ZINB models (from Table 1) are presented with their unconditional SE and 95 % confidence intervals (*CI*) (*df* = 82). For other abbreviations, see Table 1

[a] Variables with 95 % CI excluding zero

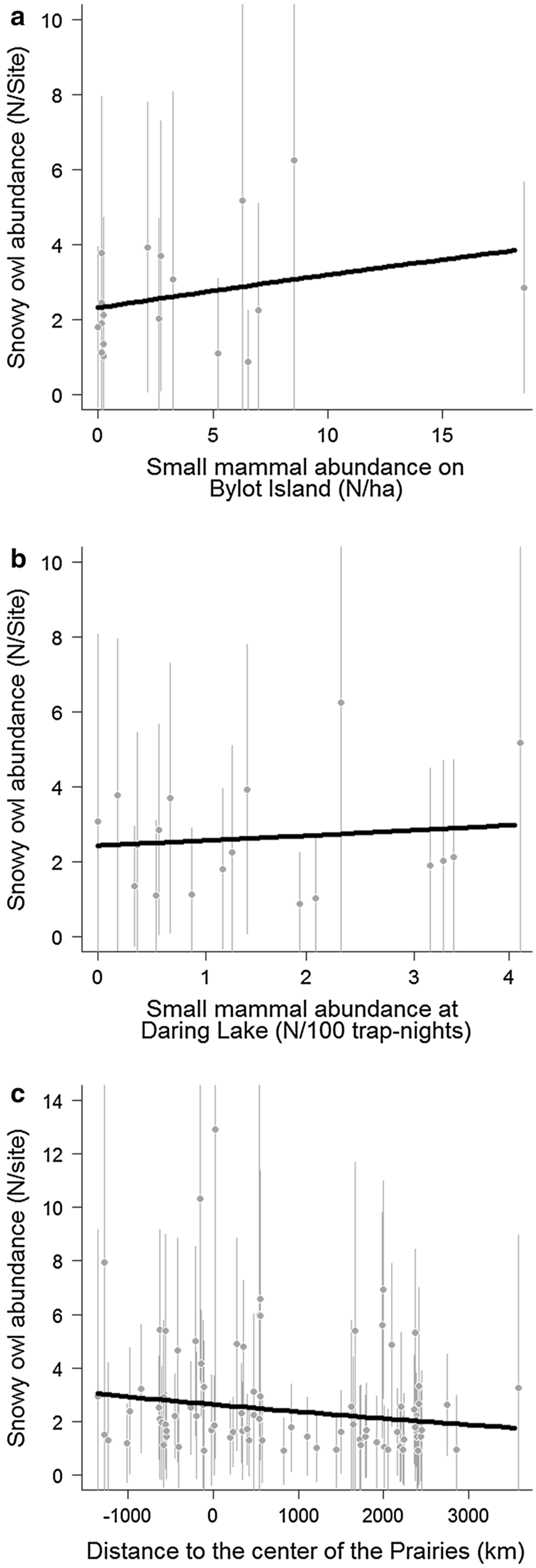

Fig. 4 Relationships between abundance of wintering snowy owls in southern Canada and northern USA predicted by the model-averaged coefficients (from the second component of the zero-inflated negative binomial model; see Table 2) and **a** small mammal abundance on Bylot Island, **b** small mammal abundance at Daring Lake, and **c** longitudinal distance from the Prairies' center. Mean ± SD annual abundance of snowy owls is presented to illustrate the fit of the model. Abundance values on the *x*-axis are not directly comparable between the two sites (**a**, **b**) because of different units

were similar at both sites (Fig. 4a, b). Owl abundance at individual sites also tended to decrease with the longitudinal distance from west to east (Fig. 4c).

Discussion

Irruptive migration of some bird species in temperate areas is thought to be a response to unpredictable changes in food supply in northern regions. Our study is the first to document conclusively a link between summer abundance of small mammals in the Arctic tundra and the winter irruptions of the snowy owl in North America. Our results showed a positive relationship between summer food resources and winter abundance of owls, thereby supporting the breeding-success hypothesis but not the lack-of-food one. We also found weak evidence for geographic variation in winter abundance of snowy owls.

Owl irruption and small mammal abundance

The pattern of winter fluctuations of snowy owl abundance that we detected in temperate North America over the past 2 decades showed periodic irruptions every 3–5 years, which is similar to observations reported earlier during the twentieth century (e.g., Shelford 1945; Gross 1947; Chitty 1950), despite some critics of these studies (Boxall and Lein 1982; Kerlinger et al. 1985). These irruptions have long been thought to be linked to the cyclic fluctuations of small mammal populations in the Arctic breeding grounds of this species (Gross 1927, 1931, 1947). However, the lack of long-term monitoring of small mammal abundance in the Canadian Arctic strongly limited the ability of previous studies to formally test hypotheses that could explain this pattern (Morrissette et al. 2010; Potapov and Sale 2012). Our results, based on rare long time series, were not consistent with the most commonly accepted hypothesis, the lack of food, which suggests that winter irruption of owls in temperate regions is caused by a crash in small mammal populations in the north (Shelford 1945; Chitty 1950; Lack 1954; Newton 1970). On the contrary, we found a positive relationship between summer abundance of small mammals at our two study sites and owl abundance during the following winter.

High abundance of small mammals, and in particular lemmings, is essential for successful owl reproduction (Therrien et al. 2014a; Holt et al. 2015). Lemming abundance typically follows a 3- to 5-year cycle in many parts of the Canadian Arctic (Elton 1924; Chitty 1950; Gruyer et al. 2008; Krebs 2011), but populations may not fluctuate synchronously over the whole range. Potential asynchrony at relatively large spatial scale was the main reason that led Kerlinger et al. (1985) to conclude that rodent abundance was unlikely to explain fluctuations in winter abundance of owls in North America. However, in both North America and Eurasia, rodent population cycles can be synchronous at the scale of several 100 km, though usually not at scales ≥1000 km (Erlinger et al. 1999; Angerbjörn et al. 2001; Predavec et al. 2001; Krebs et al. 2002). The asynchronous fluctuations in small mammals between our two selected Arctic sites located 1555 km apart are thus in agreement with the scale at which spatial synchrony disappeared in these studies.

Since snowy owls will only settle to breed in areas of high lemming abundance (Therrien et al. 2014a), the average breeding dispersal distance recorded for this species in North America [i.e., 725 km (2007–2010) (Therrien et al. 2014b); 1042 km (2013–2015) (Robillard, unpublished data)] provides an idea of the spatial scale at which they have to move to find a high abundance of lemmings following a crash at their previous nesting site. Considering this high dispersal distance, years of high lemming abundance at either of our two selected Arctic sites should result in a good production of young over a relatively large area, which would explain the occurrence of an irruption in the following winter. This interpretation is consistent with the predominance of juveniles reported in years of owl irruption (Smith 1997), indicative of a high production of young in the north. Moreover, owls observed in winter are generally in good body condition, suggesting that birds moving south in years of irruptions are not starving (Kerlinger and Lein 1988). It is also quite unlikely that an owl in poor condition could even migrate 1000 km. Finally, the temporal variability in the amplitude of irruptions could partly be explained by chance events [e.g., weather (Krebs et al. 2002)] that may play a role in synchronizing small mammal populations across distant regions of the Arctic such as between our two study sites.

Recent satellite-tracking studies in the eastern Canadian Arctic revealed that most adult female owls remain in the Arctic during the winter [>75 % (Therrien et al. 2011, 2014b)]. These birds spent much of the winter on or near sea ice and likely had a diversified diet, including marine prey (seabirds). Remaining in the Arctic during the non-breeding season may be beneficial for adults as they are close to the breeding ground in spring and can initiate prospecting earlier for a site with high lemming abundance to breed (Therrien et al. 2014b, 2015). In contrast, young birds, which may not breed before several years, may find it easier to move to southern latitudes where (1) conditions are milder, (2) prey may be more abundant and easier to catch, and (3) there is less competition with adult owls that remain in the Arctic. Every year, independently of the phase of the lemming cycle, the onset of the Arctic winter likely results in a reduction of the overall prey abundance or accessibility (due to snow or darkness) which may trigger movements of young owls toward southern latitudes.

Geographic variation

Snowy owls can winter in different places like the Arctic tundra (Gessaman 1972) and on or near sea ice (Gilchrist and Robertson 2000; Therrien et al. 2011), but for those that move to temperate areas in winter, the North American Great Plains and Prairies are a prime wintering habitat (Boxall and Lein 1982; Kerlinger et al. 1985; Holt et al. 2015). The vast, open areas of the Prairies are similar to the tundra in terms of vegetation structure and abundance of rodent species (Boxall and Lein 1982; Holt et al. 2015). Moreover, the thin snow accumulation in the Prairies, as in the tundra, is likely another factor facilitating capture of small mammals. Indeed, snow cover and depth have been shown to affect hunting efficiency (Chamberlin 1980) as well as movements and settlement decisions in snowy owls (Therrien et al. 2015). It is thus surprising that we only found a weak trend for an increase in abundance from east to west, especially considering that Kerlinger et al. (1985) reported a higher abundance in the Prairies than elsewhere in winter based on an analysis of CBC data. A possible explanation for this discrepancy is that in our study, we only selected sites where snowy owls were regularly observed and showed an irruptive pattern in order to test our main hypotheses (see "Materials and methods"). Based on our criteria, we retained 28 % of CBC sites (44/158) located in the Prairies (Central region) but only 12 % (35/303) in the Eastern region among sites where owls had been observed at least once (Fig. 1). This selection led to the exclusion of a much greater proportion of sites where owls were rarely observed in the East than in the Prairies, thereby dampening the spatial variation in abundance between the Prairies and the Eastern region. This could explain why distance from the Prairies had only a weak effect in our analysis. Therefore, our results should not be considered representative of the mean abundance of snowy owls across their temperate wintering range.

Determinants of irruptive migration

The observed pattern of irruptive migration of snowy owls in temperate North America was most consistent with the breeding success hypothesis. This pattern of migration involves a mechanism similar to that of the population density hypothesis of Koenig and Knops (2001), which can explain invasions of the common redpoll and black-capped chickadee *Parus atricapillus*, as well as that of another Strigidae, the northern saw-whet owl *Aegolius acadius* (Confer et al. 2014). In contrast, the migration patterns of other seedeaters like the white-winged crossbill *Loxia leucoptera* appear to be better explained by the seed-crop failure hypothesis (Koenig and Knops 2001) and the ones of boreal owl, northern hawk owl and great gray owl by the lack-of-food hypothesis as formulated here (Koenig and Knops 2001; Cheveau et al. 2004). Therefore, although several seedeaters and owls feed on pulsed resources that can fluctuate up to 100-fold from one year to the next, species within each of these groups can apparently respond to these fluctuations in different ways. It thus appears that no unique hypothesis can explain irruptive migrations even in species that specialize on similar food resources. Perhaps the strictness of the specialist behavior (i.e., high specialist vs. mild specialist), the type of food exploited, the flexibility in habitat use, the breeding strategy, and the body size are all factors that could influence the response of irruptive migrant to resources fluctuations (Cheveau et al. 2004). Weather has also been proposed to play a role in explaining irruptive patterns (Kerlinger et al. 1985; Krebs et al. 2002). These factors are perhaps not mutually exclusive, and may interact in shaping the migration patterns of irruptive migrants.

Although our study is the first one to model the influence of summer prey abundance on winter abundance of owls using long-term field data, some limitations must also be acknowledged. First, because of the limited availability of long-term monitoring data, only two Arctic small mammal survey sites could be used to assess irruptive patterns of snowy owls. It may look like a sparse data set considering the size of the Canadian Arctic. Nevertheless, these two sites were far apart and asynchronous, which eliminated the problem of pseudo-replication and helped us to determine the response of owls at the continental scale to opposite variations in small mammal abundance. Secondly, working with citizen-based data such as CBC is challenging in many ways. CBC surveys were not initially designed nor intended for scientific purposes, but the interest in these large-scale and long-term data has rapidly grown despite the many sources of variability [e.g., number and experience of participants, weather, habitat, modes of travel, area covered, use of attracting devices (Dunn et al. 2005)] that introduce background noise to the data set. Despite these potential sources of variability, CBC data also have some advantages such as the large number of survey sites available and the continental-scale coverage. CBC data therefore offer an enormous and unique potential for large-scale studies, as long as limitations are considered.

Despite all these drawbacks, our analysis revealed unique and novel links between pulsed resources during the summer and irruptive migration in winter of an Arctic-nesting predator. For the first time, we provide direct evidence that a good production of young during the summer due to a high abundance of food, rather than a lack of food, is the main mechanism leading to periodic irruptions of snowy owls in temperate North America. Future work on irruptive migration should include more birds tracked by satellite telemetry to compare among age and sex classes, multi-year study of migratory routes and seasonal dynamic of irruptive movements, an assessment of the geographic origin of irruptive birds and the influence of winter habitat selection on breeding success. Ultimately, combining long-term studies of inter-seasonal prey dynamics and extensive satellite tracking of individuals could unravel the details of inter-annual movements associated with irruptive migration and their determinants.

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Author contribution statement J. B. originally formulated the idea; A. R. and J. F. T. conceived and designed the experiments. G. G., K. C. and J. F. T. conducted fieldwork; A. R. developed the mathematical models and performed statistical analyses; A. R., J. B. and G. G. wrote the manuscript and all other authors revised it and provided editorial advice.

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