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Short communication

Age composition of winter irruptive Snowy Owls in North America

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Patterns of winter irruptions in several owl species apparently follow the 'lack of food' hypothesis, which predicts that individuals leave their breeding grounds in search of food when prey populations do not allow breeding and are too small to ensure survival. Recent analyses, however, suggest an alternative mechanism dubbed the 'breeding success' hypothesis, which predicts that winter irruptions might instead be the result of a very successful breeding season, with a large pool of young birds subsequently migrating south from the breeding grounds. Here we assessed age-class (juvenile vs. non-juvenile) composition of winter irruptive Snowy Owls *Bubo scandiacus* over a 25-year period (winter 1991–1992 to 2015–2016) between regular (North American Prairies and Great Plains) and irregular wintering areas (northeastern North America) using live-trapped individuals and high-resolution images of individual owls. Our results show that the proportion of juveniles (birds less than 1 year of age) varies considerably annually but is positively correlated with irruption intensity in both regions. In irregular wintering areas, it can constitute the majority (up to more than 90%) of winter irruptive Snowy Owls over a large geographical area. These results are consistent with the idea that large winter irruptions at temperate latitudes are not the result of adults massively leaving the Arctic in search of food after a breeding failure but are more likely to be a consequence of good reproductive conditions in the Arctic that create a large pool of winter migrants.

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In mobile species specializing in pulsed resources, i.e. those that are highly variable in distribution and abundance from year to year (Ostfeld & Keesing 2000), irruptive movements can occur during both the breeding and the non-breeding seasons (Newton 2006, 2008). This impressive behaviour has been documented in bird species such as seed-eaters (e.g. crossbills *Loxia* sp., siskins *Spinus* sp.) and small mammal specialists (e.g. owls; reviewed in Newton 2006). In those species, we expect to see breeding and/or wintering dispersal over large distances annually, little apparent fidelity to breeding and/or wintering sites and, in many cases, the capacity to raise large broods sustained by the pulsed resource (Newton 2008). However, empirical observations of these covariates are still scarce for many of those species.

During the non-breeding season, irruptive behaviour is often explained by the 'lack of food' hypothesis, which states that individuals leave their usual breeding range where prey availability is scarce in search of alternate areas where food is more abundant (e.g. Nero & Copland 1997, Koenig & Knops 2001, Cheveau *et al.* 2004, Newton 2006). For instance, winter irruptions of some boreal owl species such as the Great Grey Owl *Strix nebulosa* seem to coincide with periods of low densities of small mammals on the owls' regular distribution range (Nero & Copland 1997, Graves *et al.* 2012). The consequences of such a scenario would be that non-juvenile birds should compose the bulk of the overall population during winter irruptions because the lack of food should have reduced reproductive output during the preceding breeding season and/or fledgling survival.

An alternative hypothesis, dubbed the 'breeding success' hypothesis (Koenig & Knops 2001, Robillard *et al.* 2016), suggests that winter irruptions in some species could actually be the result of a high population density created by highly successful breeding. This could happen when an especially favourable reproductive season due to high food availability creates an unusually large pool of first-year birds that can migrate south at the end of the breeding season (Koenig & Knops 2001). Under this scenario, juveniles should be largely represented in the overall population during years with large winter irruptions.

Winter irruptions of Snowy Owls *Bubo scandiacus* have been reported for more than a century in North America (e.g. Gross 1947). It has long been assumed that those birds were escaping the Arctic tundra during winters when small mammal populations had become scarce (Shelford 1945, Chitty 1950, Lack 1954), as predicted by the 'lack of food' hypothesis. However, in accordance with earlier suggestions by Gross (1947), Keith (1960) and Holt and Zetterberg (2008), recent evidence now points to the 'breeding success' hypothesis to explain such massive movements of individuals (Robillard *et al.* 2016). Indeed, the Snowy Owl relies heavily on lemmings (*Lemmus* and *Dicrostonyx* sp.) for food during the breeding season (Holt *et al.* 2015), a prey whose populations undergo large fluctuations in numbers across the Arctic annually (Krebs 2011). Given that the Snowy Owl can lay relatively large clutches (average of seven eggs per nest, range 1–11; Holt *et al.* 2015, Therrien *et al.* 2015), the number of chicks raised in an area where conditions are favourable (high abundance of lemmings) can be quite high (Gilg *et al.* 2006, Therrien *et al.* 2014).

During the non-breeding season, Snowy Owls can regularly be seen in the Canadian Prairies and the US Great Plains but less so in northeastern North America, where the species is mostly present in large numbers only during larger irruptions, about once every 4 years. If winter irruptions are indeed a consequence of high reproductive success (Robillard *et al.* 2016), then a large proportion of individuals observed during irruptions should be juveniles, as suggested by Smith (1997).

Previous studies have assessed juvenile/non-juvenile ratios of Snowy Owls in regular and irregular wintering grounds of North America and have reported highly varying proportions among regions (Kerlinger & Lein 1986, Chang & Wiebe 2016). However, the annual variation in the proportion of juvenile Snowy Owls has never been studied in relation to irruption intensity across North America. According to the breeding success hypothesis, we would expect Snowy Owl irruptions during the non-breeding season to be mostly composed of juvenile individuals and the juvenile/non-juvenile ratio to be positively correlated with the overall owl abundance in winter. In contrast, if a lack of food on the summer breeding range drives periodic irruption, we would not expect any relation between juvenile/non-juvenile ratio and owl abundance.

METHODS

We used several approaches to assess Snowy Owl abundance during winter. First, we used Christmas Bird Counts (National Audubon Society 2010), a well-known citizen-scientist database that gathers 1-day birding records of thousands of volunteers annually between December 14 and January 5 across North America. The surveys include the number of hours spent in the field per party (i.e. a group of persons counting birds together), and observer effort is thus calculated in party-hours. We used the number of Snowy Owls reported per party-hours across North America for the 1991–2016 period, thus covering 25 winters. We assessed winter owl abundance among regular (North American Prairies/Great Plains: Alberta, Saskatchewan, Manitoba, North and South Dakotas) and irregular wintering areas (using counts from states and provinces where Snowy Owls are known to irrupt during winter: Connecticut, Delaware, Maine, Maryland, Massachusetts, Michigan, Minnesota, New Brunswick, New Hampshire, New Jersey, New York, Nova Scotia, Ohio, Ontario, Pennsylvania, Québec, Rhode Island, Vermont and Wisconsin).

During winter, juvenile Snowy Owls, defined as birds that were born during the previous summer (less than 12 months of age), can be reliably separated from non-juveniles, born at least 1 year before (more than 12 months of age), using distinctive plumage characteristics. Indeed, because moulting of one or two primary flight feathers (starting with P7 and P8) occurs during the summer when individuals reach 1 year of age and continues annually throughout their life (Solheim 2012), we considered individuals to be juveniles when none of their primary feathers showed signs of moult, otherwise they were classified as non-juveniles. Distinctive characteristics discriminate recently moulted feathers from older ones. Indeed, compared with non-juveniles, juvenile feathers exhibit a mottled pattern between dark bands and a narrow or even no white fringe at the tip (Solheim 2012). Moreover, because melanin pigments tend to fade after being exposed to the sun, any new feather contrasts sharply with bleached, older feathers (Solheim 2012), making the assessment highly reliable.

Each year from 1991 and 2015, between November and April, live Snowy Owls (both juveniles and non-juveniles) were routinely trapped and banded in several areas of the species' winter range in North America, including regular and irregular winter areas. The exact number of hours spent in the field in each season is not known precisely but has remained relatively constant throughout the study period. A total of 1017 individuals have been captured using bow-nets and bal-chatri traps (see Table S1 for additional details).

During two winters (2013–2014 and 2014–2015) from November to April, we also obtained more than 600 sets of one to six high-resolution photographs of individual Snowy Owls from birders over northeastern North America (irregular winter areas). All sets of photographs had detailed and precise geographical locations and dates. We retained only the sets of photographs showing individual owls dorsally with open wings ($n = 251$). This position ensured that we correctly assigned the age (juvenile vs. non-juvenile) of the individuals. Two observers separately analysed all retained sets of photographs to assess the age of the individuals and to prevent any duplicates. Indeed, when two or more sets of photographs came from the same vicinity and showed a similar individual (on the basis of age, but also general coloration pattern), we only retained the first one, based on date. We were able to assess confidently the age of 199 (83%) of 240 retained sets of photographs. A third observer assessed the age of a subset of individuals (n = 100). The same age assessment was reached among observers in 97% of the cases.

We first assessed whether there was a difference in the observed proportion of juveniles Snowy Owls recorded annually according to the two techniques (photographed and trapped individuals, assuming that there is no age-class bias associated with photographed ones), using a Chi-square test. We then pooled the values from both techniques and assessed the annual proportion of juvenile Snowy Owls in relation to owl abundance in regular and irregular wintering areas (obtained from Christmas Bird Counts) using linear regressions in R (version 3.1.0; R Core Team 2015). We restricted the analyses using years for which we had age assessment for at least 10 individuals.

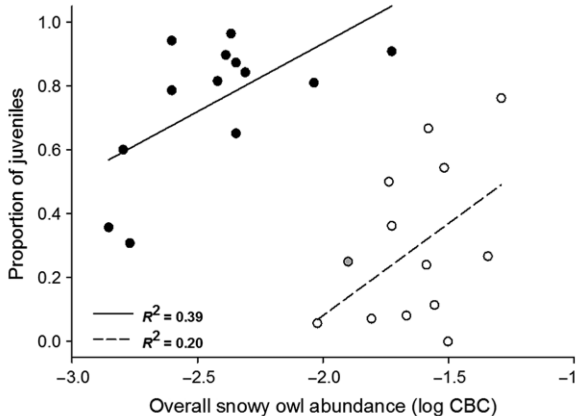

Figure 1. Proportion of juvenile Snowy Owls measured during winter in regular (Canadian Prairies and US Great Plains; open circles) and irregular (northeastern states and provinces; solid circles) wintering areas in North America in relation with overall Snowy Owl abundance assessed from Christmas Bird Counts (CBC) between 1991 and 2015. The solid line represents a significant relation and the dashed line a non-significant one. The grey circle was considered an outlier and was removed from the analysis (see Results and Discussion).

RESULTS

The two techniques (using photographed and trapped individuals) provided similar proportions of juveniles for the 2 years for which we had data (first year: χ^2 = 0.4, df = 1, P = 0.5; second year: χ^2 = 0.6, df = 1, P = 0.4). Overall, the proportion of juveniles varied tremendously among years and regions over the duration of the study. This proportion was lower in the regular wintering area (< 50% in most years) compared with irregular ones (> 60% in most years; Fig. 1). It is also worth noting the overall higher abundance of Snowy Owls in regular wintering areas compared with irregular ones.

The proportion of juveniles tended to increase with increasing owl abundance in both regular and irregular wintering areas (regular: slope ± se = 0.58 ± 0.37, t = 1.57, P = 0.15; irregular: slope ± se = 0.17 ± 0.20, t = 0.86, P = 0.4). The latter slope, however, was strongly influenced by a single point, discussed below. We reran the analysis after removing this single point and observed a strong relation between the proportion of juveniles and an increase in owl abundance in irregular wintering areas (slope ± se = 0.43 ± 0.16, t = 2.67, P = 0.02; Fig. 1).

DISCUSSION

Our results showed that a high proportion of Snowy Owls seen during winter across temperate North America, and especially in the Northeast, are juvenile birds and that this proportion tends to increase in years of high owl abundance (i.e. irruptive years). These results are consistent with the idea that winter irruptions in this species are probably the result of good breeding conditions on the arctic tundra, as predicted by the ‘breeding success’ hypothesis, rather than a generalized lack of food (Koenig & Knops 2001, Robillard *et al.* 2016). These results expand previous reports of a large number of young Snowy Owls detected during winter irruptions at one location in eastern North America over a 15-year period (Smith 1997) and in Manitoba in 1985–1986 (13 individuals; Keith 1960). In the present study, the overall proportion of juvenile individuals was lower in regular than in irregular wintering areas, most probably because the former attracts a certain number of returning adults every year, whereas fewer adults use the irregular wintering areas consistently. Indeed, Robillard *et al.* (2018) have shown that adult Snowy Owls show some degree of site fidelity during winter, with individuals returning in consecutive years in the regular winter areas described in the present study.

We removed one data point, considered an outlier, from the final analysis. This point refers to winter 2014–2015 in the irregular wintering area. That season actually saw a large influx of birds (although not as high as the previous one) but with a relatively low proportion of juveniles (0.25). The potential reason for this result, although speculative, seems to lie in the fact that following the biggest winter irruption ever recorded in eastern North America (2013–2014), many young Snowy Owls born the year before (i.e. in their second winter at that time) came down to the irregular wintering areas. However, because we opted to remain conservative in our age assessment (moult patterns become trickier after the first year; Solheim 2012), those individuals left the juvenile class and the proportion of juveniles seemed lower than usual in the overall population. Even when considering this point, the recorded proportion of juveniles remains relatively high and still supports the breeding success hypothesis.

The proportion of juvenile individuals observed across both regular and irregular wintering areas nonetheless contrasted sharply with what would be expected by the 'lack of food' hypothesis. Indeed, according to this hypothesis, we would expect a very low proportion of juveniles, if any, among wintering birds regardless of the irruption intensity. This has been previously documented in Great Grey Owls during two major winter irruptions. Indeed, 3% and 1% of juveniles have been detected in Manitoba (4 of 126 juveniles during winter 1995–1996, Nero & Copland 1997) and Minnesota (2 of 265 juveniles during winter 2005–2006, Graves *et al.* 2012), respectively. Such a low proportion of juveniles was detected on a few occasions in the present study, but only in the regular wintering areas. Although these results strongly suggest that the overall working mechanism(s) for winter irruptions in owls could be species-specific, they nonetheless remain tightly linked with prey populations on the breeding grounds.

It is worth mentioning that both hypotheses bestow an important role on prey populations and that what ultimately triggers irruptive movements is probably the amount of food available per capita and to some extent the timing of the decline in prey population, as suggested by Svärdson (1957) and Newton (2006). What the results of the present study nonetheless highlight are the dramatic differences in terms of population dynamics between the two suggested hypotheses for the studied species. In the first scenario ('lack of food' hypothesis), prey populations would be too low overall to even allow reproduction in most individuals, and we would expect a very low reproductive success and potentially even a reduced adult survival rate. In the other scenario ('breeding success' hypothesis), prey populations are large enough to allow a good reproductive season, resulting in an important production of young and potentially a high survival rate of adults. Lemming populations typically decline during the autumn following a summer peak (Fauteux *et al.* 2015). The exact timing and speed of this late-season food decline could potentially affect the intensity of winter irruptions. Thus, although a combination of high breeding success followed by a rapid crash in lemming populations may be at play in some irruption years, lack of food alone during the summer cannot explain irruption years in the first place. Further study of juvenile movements and lemming dynamics will help decipher how the phenology of prey abundance can affect irruptions.

Within a species, different age-classes may have different predispositions to migrate. It has been suggested and reported that the most dominant individuals in a partial migratory species tend to migrate less and overwinter closer to their breeding areas (Gauthreaux 1982, Kjellén 1994). As juveniles are often less dominant than adults, they are expected to migrate farther south from their breeding grounds to avoid competition with older, more experienced birds. This phenomenon, called differential migration, has indeed been described in Snowy Owls (Kerlinger & Lein 1986, 1988) and other owl species (Lehikoinen *et al.* 2011), and might explain why the majority of birds reported at the southern edge of the distribution, and especially in irregular wintering areas, are juveniles. Indeed, satellite tracking of individual Snowy Owls has revealed that most non-juvenile individuals remain in the Arctic throughout winter, irrespective of small mammal abundance in the previous summer (Fuller *et al.* 2003, Therrien *et al.* 2011). This further suggests that large winter irruptions at temperate latitudes are not the result of adults massively leaving the Arctic in those years.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Table S1. Annual number of Snowy Owls trapped or photographed in regular (Canadian Prairies and US Great Plains) and irregular (northeastern states and provinces) areas in North America.