

Winter irruptive Snowy Owls (*Bubo scandiacus*) in North America are not starving

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Abstract: Winter irruptions, defined as irregular massive movement of individuals over large distances, have been linked to food supply. Two hypotheses have been put forward: the “lack-of-food” suggests that a shortage of food forces individuals to leave their regular winter range and the “breeding output” suggests that unusually large food supplies during the preceding breeding season allows production of a large number of offspring dispersing in winter. According to the breeding output hypothesis, irruptive Snowy Owls (*Bubo scandiacus* (Linnaeus, 1758)) in eastern North America should not exhibit a lower body condition than individuals in regular wintering regions and individuals on the breeding grounds. Additionally, body condition of irruptive individuals should be unrelated to irruption intensity. Although body condition of juveniles was generally lower than that of adults and improved during the winter, we measured a fair body condition in both juvenile and adult irruptive Snowy Owls across North America. The results showed that Snowy Owls are not in a starving state during winter and that body condition of all age classes was not related to winter irruption intensity. Those results support the breeding output hypothesis suggesting that winter irruptions seem to be primarily the result of a large number of offspring produced when food availability on the breeding grounds is high.

Key words: body condition, body mass, *Bubo scandiacus*, Snowy Owl, winter irruption.

Résumé : Les pullulations hivernales, des déplacements massifs irréguliers d'individus sur de grandes distances, ont été reliées à la disponibilité de nourriture. Deux hypothèses ont été mises en avant, à savoir, celle du « manque de nourriture », selon laquelle une pénurie de nourriture force les individus à quitter leur aire d'hivernage normal, et celle du « rendement de la reproduction », qui postule qu'une disponibilité de nourriture inhabituellement importante durant la période de reproduction précédente permet la production d'une progéniture nombreuse qui se disperse durant l'hiver. Selon l'hypothèse du rendement de la reproduction, des harfangs des neiges (*Bubo scandiacus* (Linnaeus, 1758)) pullulant dans l'est de l'Amérique du Nord ne devraient pas présenter un embonpoint plus faible que les individus dans les régions d'hivernage normales et les individus dans les lieux de reproduction. De plus, l'embonpoint des individus pullulants ne devrait pas être relié à l'intensité de la pullulation. Si l'embonpoint des juvéniles était généralement plus faible que celui des adultes et s'améliorait durant l'hiver, nous avons mesuré un bon embonpoint chez les harfangs des neiges pullulants tant juvéniles qu'adultes à la grandeur de l'Amérique du Nord. Ces résultats démontrent que les harfangs des neiges ne sont pas dans un état affamé durant l'hiver, et l'embonpoint de toutes les classes d'âge n'est pas relié à l'intensité des pullulations hivernales. Ces résultats appuient l'hypothèse du rendement de la reproduction et indiqueraient que les pullulations hivernales sont principalement le résultat d'une progéniture nombreuse produite quand la disponibilité de nourriture dans les lieux de reproduction est élevée. [Traduit par la Rédaction]

Mots-clés : embonpoint, masse corporelle, *Bubo scandiacus*, harfang des neiges, pullulation hivernale.

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Introduction

Irruptive migration, defined as irregular and massive movements of individuals associated with large fluctuations in food supplies, is one of the most dramatic migratory movements observed on land. This phenomenon produces huge concentrations of individuals in given years in some areas followed by a sharp reduction in numbers of individuals in other years at the same location. Irruptive migration usually occurs in species specializing on pulsed resources (Newton 2006, 2008). Examples of irruptive migrants include seed eaters relying on mast fruiting events of a very limited number of coniferous species to reproduce (Larson and Bock 1986; Hochachka et al. 1999) and predatory birds (especially owls) specializing in one or more species of fluctuating small mammals (Sonerud 1997; Robillard et al. 2016).

Two hypotheses have been put forward to explain winter irruptions (Koenig and Knops 2001). The “lack-of-food” hypothesis suggests that a severe shortage of food forces individuals to move out of their regular range in search of food. Under such circumstances, most individuals are expected to be in a suboptimal body condition and (or) in a starving state because the lack of food would have dramatically impacted food acquisition. This has been indeed shown in Great Gray Owls (*Strix nebulosa* J.R. Forster, 1772) during winter irruptions (Graves et al. 2012). Moreover, under this hypothesis, overall body condition should be negatively correlated with irruption intensity. In contrast, the alternate “breeding output” hypothesis suggests that winter irruptions occur when very high food availability during the breeding season results in an unusually large number of offspring dispersing in winter (Koenig and Knops 2001). Under such scenario, these individuals should exhibit a good body condition in winter due to the large food sources available during the previous breeding season, and overall body condition should not be correlated with irruption intensity.

The Snowy Owl (*Bubo scandiacus* (Linnaeus, 1758)) is a top predator of the Arctic tundra and a typical example of an irruptive species. Indeed, during the summer it specializes on lemmings (species of the genera *Dicrostonyx* Gloger, 1841 (collared lemmings) and *Lemmus* Link, 1795 (lemmings)), which exhibit large amplitude fluctuations in abundance annually (Krebs et al. 2011). The Snowy Owl has a high reproductive potential and can benefit from lemming outbreaks by laying one of the largest clutches in birds of prey (up to 11 eggs, mean = 7 eggs; Holt et al. 2015). During the winter season, the species can be regularly seen in the Canadian Prairies and American Great Plains, but less so in eastern North America where it is present in large numbers only in irruptive years. It has long been thought that birds visiting irregular wintering areas were in a starving state, being forced out of their regular range because of a lack of food resources (Shelford 1945; Chitty 1950; Lack 1954; Newton 1970). Recent evidence, however, suggests that winter irruption of this species in North America can be explained by the breeding output hypothesis. Indeed, the winter abundance of Snowy Owls in temperate North America has been positively correlated to the previous summer density of lemmings on Arctic breeding grounds (Robillard et al. 2016). In addition, an apparent large proportion (>80%) of individuals observed in irruption years are juveniles (Smith 1997).

Previous studies have already assessed body condition of Snowy Owls in regular wintering grounds of the Canadian Prairies and have noted that birds are generally in good body condition (Kerlinger and Lein 1988; Chang and Wiebe 2016). However, body condition of owls has never been studied in highly variable or irregular winter areas such as northeastern North America or between years of different irruption intensity. We hypothesized, according to the breeding output hypothesis, that irruptive Snowy Owls outside of their regular winter range should not be in a starving state, just like on regular wintering grounds, and that the body condition should be unaffected by irruption intensity.

Materials and methods

Study areas and field data

Consistently between 1 October and 30 April each year from 1991 to 2016, live Snowy Owls were routinely trapped using bow-net and bal-chatri traps and banded in several areas of the species' winter distribution in North America. This included regular (Saskatchewan and Alberta, Canada) and highly variable or irregular (USA: Delaware, Maryland, Minnesota, New York, and Pennsylvania; Canada: southern Quebec) winter areas, and as part of concomitant research projects on their breeding grounds in northern Quebec and Nunavut, Canada. Periods during which owls were trapped did not differ between the regular and irregular wintering areas. We recorded the age and sex of each individual according to plumage characteristics following Josephson (1980), Seidensticker et al. (2011), and Solheim (2012). Because Snowy Owls start molting their flight feathers when they reach 1 year of age (Solheim 2012), individuals were identified as juveniles (<12 months of age) if they still wore their juvenile feathers and had not molted any flight feathers; otherwise, individuals were considered adults. This classification resulted in four age–sex classes (juvenile female, juvenile male, adult female, and adult male). For each individual, we recorded body mass (± 10 g) using PESOLA spring scales or electronic balances and wing chord (± 1 mm) using rulers. All bird banders used a standardized technique to measure unflattened wing chord. However, the wing-chord measurements differed between the banders, on average, for $4.7 + 6.1$ mm for females and $12.2 + 9.0$ mm for males (linear model: $p < 0.001$, $n = 566$ for females; $p < 0.001$, $n = 462$ for males); therefore, bander ID was used as a random variable in the analyses.

During one winter (2013–2014), we also collected breast muscle samples on a limited number of Snowy Owl carcasses brought to us following airplane or vehicle collisions in irregular wintering areas. We sampled only individuals that were killed instantly by the strike and were kept frozen until sampled. We used those samples to assess the percentage of fat in muscles and the carbon/nitrogen (C/N) ratio, an additional proxy for lipid content (Ehrlich et al. 2011). Muscle samples (about 1 g) were freeze-dried at -50 °C for 72 h and then ground to a fine powder with a mortar and pestle. Lipids were extracted with pure chloroform using a Soxhlet apparatus (Tecator system 1043) and measured as a percentage of sample mass. C/N ratios were determined from percentage element weight measured by mass spectrometry conducted during concomitant stable isotope analyses (for details see Robillard et al. 2017).

To assess annual winter irruption intensity, we used Christmas Bird Count (CBC) data (National Audubon Society, Inc. 2010), a well-known citizen–science database gathering annual birding records of thousands of volunteers made during a single day between 14 December and 5 January 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); observer effort is thus calculated in party-hour. We used the number of Snowy Owls reported per party-hour from 1991 to 2015 across northeastern North America using the states and provinces where Snowy Owls are irregular winter visitors (USA: Connecticut, Delaware, Maine, Maryland, Massachusetts, Michigan, Minnesota, New Hampshire, New Jersey, New York, Ohio, Pennsylvania, Rhode Island, Vermont, and Wisconsin; Canada: New Brunswick, Nova Scotia, Ontario, and Quebec).

Body condition indices

We estimated body condition indices separately for males and females because Snowy Owls exhibit a strong sexual dimorphism (Holt et al. 2015). We corrected body mass for body size using ordinary least squares (OLS) residuals obtained by regressing body mass on wing chord (Labocha and Hayes 2012). The residuals represent positive or negative deviations of body mass values pre-

Table 1. Model selection explaining body condition index (OLS residuals) of Snowy Owls (*Bubo scandiacus*) according to day (day of the winter season from 1 October to 1 April) tested separately by sexes in regular (North America Prairies) and irregular (northeastern North America) wintering areas using linear mixed models fitted with maximum likelihood.

Response variable: Residuals	Predictor variables	K	Δ AIC	AIC weight	Log-likelihood
Change in body condition of female Snowy Owls throughout winter in regular wintering areas ($n = 275$)	Day * Age class + (1 Winter season) + (1 Study area) + (1 Bander ID)	8	0.0	0.6	-1842.4
	Day + Age class + (1 Winter season) + (1 Study area) + (1 Bander ID)	7	0.5	0.5	-1843.7
	Day + (1 Winter season) + (1 Study area) + (1 Bander ID)	6	80.4	0.0	-1884.6
	Null + (1 Winter season) + (1 Study area) + (1 Bander ID)	5	81.3	0.0	-1886.1
Change in body condition of male Snowy Owls throughout winter in regular wintering areas ($n = 138$)	Day + Age class + (1 Winter season) + (1 Study area) + (1 Bander ID)	7	0.0	0.6	-1178.4
	Day * Age class + (1 Winter season) + (1 Study area) + (1 Bander ID)	8	0.4	0.5	-1177.6
	Null + (1 Winter season) + (1 Study area) + (1 Bander ID)	5	35.0	0.0	-1198.0
	Day + (1 Winter season) + (1 Study area) + (1 Bander ID)	6	36.0	0.0	-1197.4
Change in body condition of female Snowy Owls throughout winter in irregular wintering areas ($n = 275$)	Day + (1 Winter season) + (1 Study area) + (1 Bander ID)	6	0.0	0.6	-1801.3
	Day * Age class + (1 Winter season) + (1 Study area) + (1 Bander ID)	8	1.6	0.3	-1800.1
	Day + Age class + (1 Winter season) + (1 Study area) + (1 Bander ID)	7	2.0	0.2	-1801.3
	Null + (1 Winter season) + (1 Study area) + (1 Bander ID)	5	17.0	0.0	-1810.8
Change in body condition of male Snowy Owls throughout winter in irregular wintering areas ($n = 278$)	Day + Age class + (1 Winter season) + (1 Study area) + (1 Bander ID)	7	0.0	0.6	-1802.1
	Day * Age class + (1 Winter season) + (1 Study area) + (1 Bander ID)	8	1.4	0.3	-1801.9
	Day + (1 Winter season) + (1 Study area) + (1 Bander ID)	6	4.9	0.1	-1805.6
	Null + (1 Winter season) + (1 Study area) + (1 Bander ID)	5	25.8	0.0	-1817.1

Note: Winter season is a categorical variable where each level represents one winter from 1991–1992 to 2015–2016. Study area is a categorical variable containing nine locations where data were collected. Bander ID is a categorical variable with 11 levels where each level represents the name of a bander. Age class is a categorical variable with two levels (adult and juvenile). The best selected models where Δ AIC is less than 2 are presented in boldface type. K is the number of parameters and AIC is Akaike's information criterion.

dicted by wing chord where positive residual values represent heavier individuals (assumed in better condition) and negative values represent lighter individuals (assumed in worse condition) than predicted. With this method, residuals of body mass are not correlated with the predictor variable (wing chord) and estimated body condition is therefore not dependent or changeable with body size.

Statistical analysis

First, we assessed whether body condition of male and female Snowy Owls tended to improve during the winter season separately in regular and irregular areas using linear mixed models (LMMs). We performed a separate model for each sex and used OLS residuals as a dependent variable; day (day of the winter season from 1 October to 1 April) and age class as fixed effects; and winter season, study area (categorical variable containing nine locations where data were collected), and bander ID as random effects. Because body condition tended to improve during the winter (see Results), we only used owls measured early in the winter season (before 1 January) in all following analyses, unless specified.

Second, we tested the difference in body condition between irregular and regular wintering areas using LMMs. Separate models for males and females were carried out using OLS residuals as a dependent variable, region (regular vs. irregular wintering areas) and age class as fixed effects, and winter season (categorical variable where each level represents one winter from 1991–1992 to 2015–2016) and bander ID as random effects.

Third, we measured whether body condition of Snowy Owls was linked to irruption intensity in irregular wintering areas using linear models (LMs). We ran a separate model for each sex and used OLS residuals as a dependent variable and CBC value and age class as fixed effects.

Fourth, to assess whether body condition of adult females at irregular wintering areas differs from that of breeding females, we fitted an LMM with OLS residuals as a dependent variable, period (breeding vs. wintering) as a fixed effect, and season (categorical variable where each level represents a winter from 1991–1992 to 2015–2016 or a breeding season from 2007 to 2014) and bander ID as random effects.

Models were ranked according to the Akaike's information criterion (AIC; Burnham and Anderson 2002). Model-averaged estimates and their 95% confidence intervals were computed with multimodel inference on the best models (i.e., Δ AIC < 2) using the AICcmodavg package (Mazerolle 2016). All statistical analyses were performed using R version 3.2.1 (R Core Team 2015) and the package lme4 (Douglas et al. 2015).

Results

Body condition of Snowy Owls was lower in juveniles than in adults and generally improved over time both in regular and irregular wintering areas, especially in juveniles (Table 1; Figs. 1a, 1b; Supplementary Table S1¹). In regular wintering areas, juvenile females increased their body condition index by 132.1 g per month ($n = 88$), whereas the increase was more modest in irregular wintering areas (30.8 g per month, $n = 188$). Adult females in irregular wintering areas increased their body condition index by 14.8 g per month ($n = 88$) and juvenile males by 29.3 g per month ($n = 213$) in the same areas.

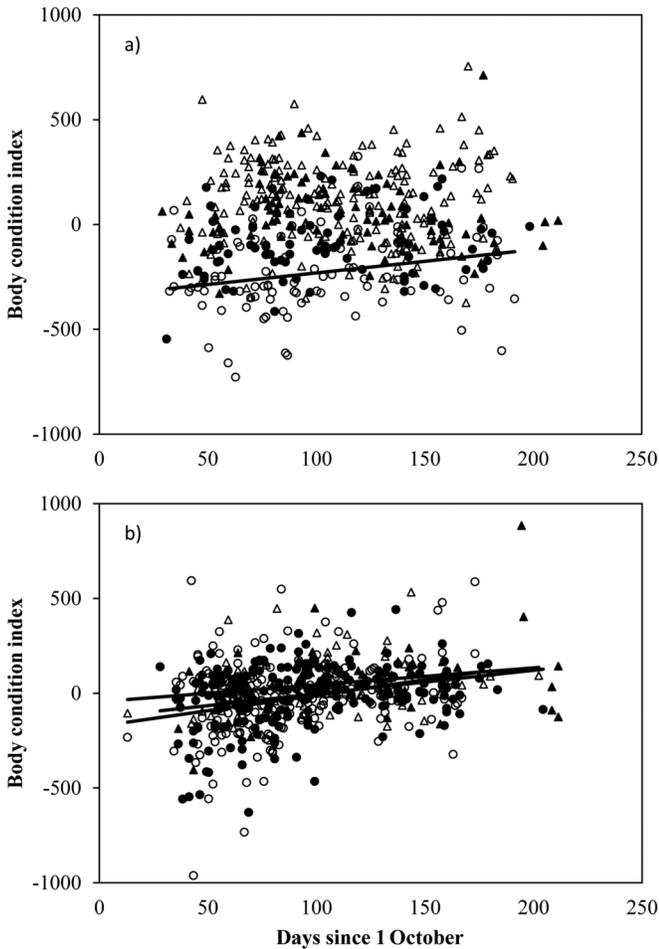
In accordance with our main prediction that wintering Snowy Owls would not be in a starving state in irregular wintering areas, the measured index of body condition was actually better in irregular wintering areas compared with regular ones for most age–sex classes (adult females in regular areas: 116.9 ± 13.8 g (mean \pm SE), $n = 186$; adult females in irregular areas: 21.9 ± 18.7 g, $n = 120$; adult males in regular areas: 22.4 ± 23.3 g, $n = 102$; adult males in irregular areas: 57.8 ± 22.6 g, $n = 65$; juvenile females in regular areas: -215.3 ± 19.6 g, $n = 89$; juvenile females in irregular areas: -35.3 ± 15.5 g, $n = 189$; juvenile males in regular areas: -55.5 ± 15.1 g, $n = 81$; juvenile males in irregular areas: -1.3 ± 9.8 g, $n = 214$) (Table 2, Fig. 2, Supplementary Table S2¹).

Irruption intensity (CBC value) was not related with overall body condition of wintering male and female Snowy Owls captured early in winter in irregular wintering areas (Table 3, Supplementary Table S3¹).

Body condition of adult females was slightly higher in individuals captured during the breeding season than individuals captured early during the winter in irregular areas (breeding season:

¹Supplementary tables are available with the article through the journal Web site at <http://nrcresearchpress.com/doi/suppl/10.1139/cjz-2017-0278>.

Fig. 1. Body condition index (OLS residuals) of Snowy Owls (*Bubo scandiacus*) captured during the winter season in (a) regular wintering areas (North America Prairies) and (b) irregular wintering areas (northeastern North America) in relation with time since 1 October. Juvenile individuals are illustrated with circles and adults with triangles. Females are represented with open symbols and males with solid symbols. Only significant slopes are presented. In panel a, the slope represents juvenile females; in panel b, the top slope represents juvenile female, the middle slope represents adult male, and the bottom slope represents adult female.

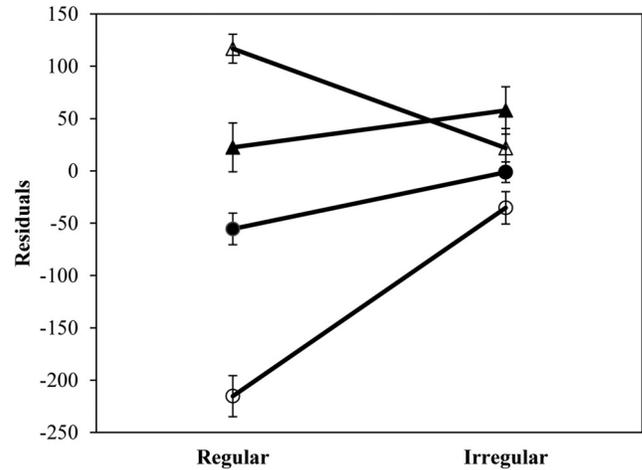


97.1 ± 32.3 g (mean \pm SE), $n = 19$; early in winter season: 12.2 ± 24.8 g, $n = 35$) (Table 4, Fig. 3, Supplementary Table S4¹). The overall body condition index was nonetheless positive for adult females in irregular wintering areas, suggesting an overall fair body condition despite the difference with breeding birds.

Mean (\pm SE) body mass of individuals sampled early in winter in irregular areas was 2086.8 ± 25.4 g ($n = 37$) and 1571.7 ± 28.4 g ($n = 23$) for adult females and males, respectively, and 2027.8 ± 19.3 g ($n = 113$) and 1534.3 ± 18.5 g ($n = 104$) for juvenile females and males, respectively. Considering that body masses of emaciated Snowy Owls during the winter season were established at around 1286 ± 66 g for females and 975 ± 26 g for males (Chang and Wiebe 2016), all individuals from the present study were well above those thresholds. Overall, only four (2%) juvenile females (body mass < 1400 g) and six (3%) juvenile males (body mass < 1100 g) were approaching the emaciated threshold in the irregular wintering areas.

The percentage of fat measured in muscles was high (mean = 15.0%, SD = 12.9%, $n = 24$). In addition, C/N ratios obtained from the

Fig. 2. Mean (\pm SE) body condition index (OLS residuals) of Snowy Owls (*Bubo scandiacus*) captured during the nonbreeding season in regular (North America Prairies) and irregular wintering areas (northeastern North America). Adult females are represented with open triangles, adult males with solid triangles, juvenile females with open circles, and juvenile males with solid circles.



same muscle samples also suggest a rather good body condition (mean = 3.5, SD = 0.2, $n = 24$; Tarroux et al. 2010).

Discussion

Overall, winter irruptive Snowy Owls captured in northeastern North America generally displayed a good body condition, with fewer than 2% of the measured individuals approaching the emaciated threshold. Those results are in agreement with previous studies conducted in regular Snowy Owl wintering areas such as the Canadian Prairies (Kerlinger and Lein 1988; Chang and Wiebe 2016). Those results are also consistent with our prediction that Snowy Owls are not in poor body condition or starving state when they irrupt in northeastern North America during winter. Juveniles of both sexes showed, on average, lower body condition values than adults, which suggests that this age class has an overall lower body condition, especially early in the winter season. This is not surprising because juveniles lose mass after fledgling to develop stronger muscles and bones and only start gaining fat later. In addition, juveniles are expected to be less dominant (Chang and Wiebe 2016) and therefore might have lower access to food than the adults. Juveniles nonetheless improved their body condition throughout the winter season and actually reached a level similar to adults, whereas body condition of adults remained mostly unchanged throughout the winter season. The improvement of body condition throughout the winter season was seen in both regular and irregular wintering areas. Nonetheless, body condition was generally better in irregular than in regular wintering areas. This may be because individuals irrupting in irregular areas do so mostly following periods of high resource availability on the breeding grounds, whereas individuals come in regular winter areas following years of both high and low resource availabilities.

We detected a lower body condition in adult females early in the winter season compared with breeding females. However, none of the individuals approached the emaciated threshold. Breeding individuals are probably those exhibiting the best body condition overall and so we believe that the detected difference should not be interpreted as being a sign of poor body condition during winter in irregular areas. Breeding females were captured in years when food was locally abundant (i.e., high lemming years) and toward the end of the incubation period when they are fed by adult males and food requirements of chicks is minimal. There-

Table 2. Model selection explaining body condition index (OLS residuals) of Snowy Owls (*Bubo scandiacus*) according to region (regular vs. irregular wintering areas) tested separately by sexes using linear mixed models fitted with maximum likelihood.

Response variable: Residuals	Predictor variables	K	ΔAIC	AIC weight	Log-likelihood
Difference in body condition of female Snowy Owls between irregular and regular wintering areas (n = 261)	Region * Age class + (1 Winter season) + (1 Bander)	7	0.0	1	-1740.2
	Region + Age class + (1 Winter season) + (1 Bander)	6	23.4	0	-1753.0
	Region + (1 Winter season) + (1 Bander)	5	61.6	0	-1773.1
	Null + (1 Winter season) + (1 Bander)	4	66.1	0	-1777.3
Difference in body condition of male Snowy Owls between irregular and regular wintering areas (n = 206)	Region * Age class + (1 Winter season) + (1 Bander)	7	0.0	0.9	-1346.6
	Region + Age class + (1 Winter season) + (1 Bander)	6	3.5	0.2	-1349.3
	Null + (1 Winter season) + (1 Bander)	4	18.4	0.0	-1359.8
	Region + (1 Winter season) + (1 Bander)	5	21.7	0.0	-1359.4

Note: Winter season is a categorical variable where each level represents one winter from 1991–1992 to 2015–2016. Bander ID is a categorical variable with 11 levels where each level represents the name of a bander. Age class is a categorical variable with two levels (adult and juvenile). The best selected models where ΔAIC is less than 2 are presented in boldface type. K is the number of parameters and AIC is Akaike's information criterion.

Table 3. Model selection explaining body condition index (OLS residuals) of Snowy Owls (*Bubo scandiacus*) according to winter irruption intensity (i.e., Christmas Bird Count (CBC) value given for each winter season) tested separately by sexes using linear models fitted with maximum likelihood.

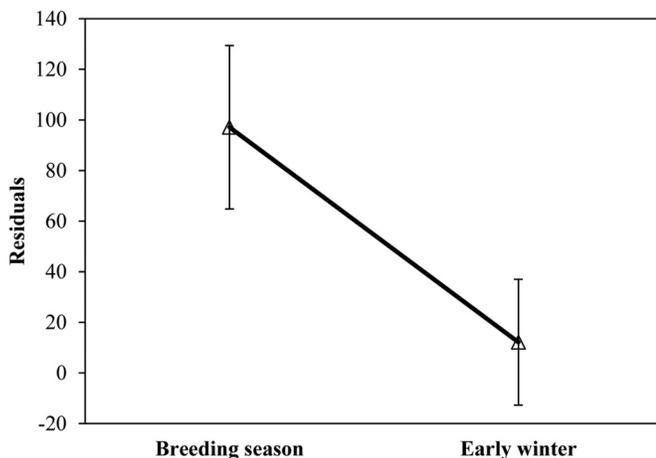
Response variable: Residuals	Predictor variables	K	ΔAIC	AIC weight	Log-likelihood
Effect of irruption intensity on body condition of female Snowy Owls early in the winter in irregular wintering areas (n = 144)	Null	2	0.0	0.4	-972.9
	CBC + Age class	4	0.3	0.3	-971.0
	CBC	3	1.3	0.2	-972.6
	CBC * Age class	5	2.3	0.1	-971.0
Effect of irruption intensity on body condition of male Snowy Owls early in the winter in irregular wintering areas (n = 127)	Null	2	0.0	0.4	-840.4
	CBC * Age class	5	0.3	0.3	-837.5
	CBC	3	1.5	0.2	-840.1
	CBC + Age class	4	2.1	0.1	-839.4

Note: Age class is a categorical variable with two levels (adult and juvenile). The best selected models where ΔAIC is less than 2 are presented in boldface type. K is the number of parameters and AIC is Akaike's information criterion.

Table 4. Model selection explaining body condition index (OLS residuals) of Snowy Owls (*Bubo scandiacus*) according to period (breeding vs. wintering) tested for adult females using linear mixed models fitted with maximum likelihood.

Response variable: Residuals	Predictor variables	K	ΔAIC	AIC weight	Log-likelihood
Difference in body condition of adult females between breeding season and early in winter in irregular wintering areas (n = 55)	Period + (1 Season) + (1 Bander ID)	5	0.0	0.3	-350.7
	Null + (1 Season) + (1 Bander ID)	4	2.1	0.1	-352.7

Note: Season is a categorical variable where each level represents a winter from 1991–1992 to 2015–2016 or breeding season from 2007 to 2014. Bander ID is a categorical variable with 11 levels where each level represents the name of a bander. The best selected models where ΔAIC is less than 2 are presented in boldface type. K is the number of parameters and AIC is Akaike's information criterion.

Fig. 3. Mean (±SE) body condition index (OLS residuals) of adult female Snowy Owls (*Bubo scandiacus*) captured in irregular wintering areas (eastern North America) during the breeding season and early in winter (before 1 January).

fore, it is not surprising that the body condition of these individuals tended to be higher than in early winter.

Our results suggest a good body condition overall for winter irruptive Snowy Owls and apparently very few starving and (or) emaciated individuals. This is in agreement with the breeding output hypothesis (Koenig and Knops 2001), which suggests that a large number of juveniles produced during the breeding season when lemming abundance peaks would lead to winter irruptions (Robillard et al. 2016). A similar situation is to be expected in other mobile species relying on pulse resources for breeding such as seed-eating birds (e.g., crossbills, siskins) and several owl species, but especially for those who have the capacity to lay large clutches. Indeed, during years of high food availability, mean clutch size of both the Snowy Owl and the Northern Hawk Owl (*Surnia ulula* (Linnaeus, 1758)) is around 7 eggs (and up to 11 and 13 eggs, respectively; Holt et al. 2015; Duncan and Duncan 1998). Those two species are thought to irrupt in winter following the breeding output hypothesis. In contrast, the Great Gray Owl, which is a close cousin of the Snowy Owl and also specializes on small mammals during breeding has a mean clutch size of 4.6 eggs (up to 5 eggs) in good food years (Bull and Duncan 1993). This species is thought to irrupt following the lack-of-food hypothesis and body condition recorded in this species in winter supports this assumption (Graves et al. 2012). Whether clutch size is a

predictor of the drivers behind irruptive strategies remains to be tested yet limited empirical data on body condition during winter irruption exist for other owl species and seed-eating birds (but see Korner-Nievergelt et al. 2008).

Irruptive migration might be a strategy to maintain body condition when resource-rich habitats on the breeding grounds become limited due to the large number of individuals. Indeed, small-mammal abundance in peak years often decreases during the summer in response to high predation intensity (Fauteux et al. 2015) and thus food resources may actually become limited during autumn, especially for subordinate juveniles (Chang and Wiebe 2016). Although the breeding output hypothesis may encapsulate the mechanisms behind winter irruptions in several irruptive species such as the Snowy Owl, a decrease in food abundance per capita in late summer may also drive a large number of young to overwinter in temperate regions, so both hypotheses may not be mutually exclusive.

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