The irruptive nature of Snowy Owls: an overview of some of the recent empirical evidence

A natureza irruptiva da coruja-das-neves: visão geral de algumas das recentes evidências empíricas

Jean-François Therrien[1*], Gilles Gauthier[2], Tom McDonald[3], Norman Smith[4], Scott Weidensaul[5], David Brinker[6], Rebecca McCabe[1,7], Audrey Robillard[2], Joël Bêty[8], Nicolas Lecomte[9]

1 Hawk Mountain Sanctuary, PA, USA

2 Université Laval, QC, Canada

3 Rochester, NY, USA

4 Massachussetts Audubon, MA, USA

5 Ned Smith Center, PA, USA

6 Department of Natural Resources, MD, USA

7 McGill University, QC, Canada

8 Université du Québec à Rimouski, QC, Canada

9 Université de Moncton, NB, Canada

*** Corresponding author:** therrien@hawkmountain.org

ABSTRACT

Irruptive movements resulting in large and periodical fluctuations in number of a species in a given area is thought to happen in some owl species. Although impressive, empirical details of such a phenomenon remains however very limited. The Snowy Owl is a classic example of such a species but until recently, the limited empirical evidence did not allow a thorough description of its behavioral ecology over its complete life cycle. We have studied Snowy Owls for 25 years in North America using nest monitoring, diet analyses and individual tracking to understand the species' movement ecology over a full annual cycle. On the Arctic breeding grounds, nesting density of Snowy Owls varies tremendously annually, mirroring the high-amplitude variations in abundance of its main prey (lemmings). Indeed, during the breeding season, Snowy Owls have a highly specialized diet almost entirely made of lemmings. Tracking individuals revealed that adults are displaying some of the greatest breeding dispersal distances ever measured annually

in a bird species and that most of them breed every year, in areas where lemmings are abundant. Individual fidelity to a breeding area is thus very low. During winter, most adults remain at high latitudes and individuals tend to be more faithful to their wintering than their breeding areas. Periodic winter irruptions south of the boreal forest occurring roughly every 4 years follow successful breeding conditions in the Arctic and are mainly composed of juvenile individuals. Body condition of winter irruptive individuals is usually good. Even if some aspects of the behavioral ecology of the Snowy Owl still remain to be assessed, those results provide a clear overview of its irruptive nature over a complete annual cycle.

Keywords: *Bubo scandiacus,* behavioral ecology, breeding dispersal, prey abundance, satellite telemetry

RESUMO

Pensa-se que os movimentos irruptivos que resultam em grandes flutuações periódicas na abundância de uma espécie numa determinada área ocorram em algumas espécies de aves de rapina noturnas. Embora impressionante, esse fenómeno ainda está associado a detalhes empíricos muito limitados. A coruja-das-neves é um exemplo clássico de uma dessas espécies mas, até há pouco tempo, as poucas evidências empíricas não permitiam uma descrição completa da sua ecologia comportamental ao longo de todo o seu ciclo de vida. Estudamos a coruja-das-neves na América do Norte há 25 anos, através de monitorização dos ninhos, análise da dieta e seguimento de indivíduos, para compreender a ecologia dos movimentos da espécie ao longo de um ciclo anual completo. Nas áreas de reprodução do Árctico, a densidade de corujas-das-neves nidificantes varia muito anualmente, refletindo a grande amplitude das variações na abundância das suas principais presas (lemingues). Durante a época de reprodução, as corujas-das-neves têm uma dieta altamente especializada, quase inteiramente composta por lemingues. O seguimento de indivíduos revelou que os adultos apresentam algumas das maiores distâncias de dispersão de reprodução alguma vez medidas anualmente numa espécie de ave, e que a maioria deles reproduzem-se todos os anos em áreas onde os lemingues são abundantes. A fidelidade dos indivíduos a uma área de reprodução é, assim, muito reduzida. Durante o Inverno, a maioria dos adultos permanece em latitudes elevadas, e os indivíduos tendem a ser mais fiéis às suas áreas de invernada do que de reprodução. As irrupções periódicas de Inverno a sul da floresta boreal, que ocorrem aproximadamente de 4 em 4 anos, decorrem de condições de elevado sucesso reprodutivo no Árctico e são compostas principalmente por indivíduos juvenis. Os indivíduos que fazem movimentos irruptivos no Inverno estão, geralmente, em boa condição corporal. Apesar de alguns aspetos da ecologia comportamental da coruja-das-neves ainda estarem por avaliar, estes resultados fornecem uma visão clara da sua natureza irruptiva ao longo de um ciclo anual completo.

Palavras-chave: abundância de presas, *Bubo scandiacus*, dispersão de reprodução, ecologia comportamental, telemetria por satélite

Introduction

Irruptive movements resulting in large and periodical fluctuations in the number of individuals of a given species, in a given area (Newton 2006, 2008), occur in species specializing their diet on pulsed resources (i.e. highly variable and unpredictable; Ostfeld and Keesing 2000). Irruptive behavior has been described in seed-eaters (e.g. crossbills, *Loxia* sp. siskins, *Spinus* sp.) which feed heavily on cone crops varying greatly in abundance from one year to the next in a given area, and some raptor species (especially owls) specializing their diet on fluctuating small mammals (reviewed in Newton 2008). Empirical details of such behavior however remains very limited for any of those species.

The Snowy Owl (*Bubo scandiacus*) is a classic example of an irruptive species, but until recently, the limited empirical evidence did not allow a thorough description of its behavioral ecology over a complete annual cycle. Indeed, several authors have already described the highly specialized diet almost entirely composed of lemmings (*Lemmus* and *Dycrostonyx* spp.) during the breeding season across its circumpolar range (reviewed in Holt et al. 2015) as well as the highly variable breeding densities recorded over consecutive years on a given area for this species (Gilg et al. 2006, Therrien et al. 2014). In addition, several authors have also suggested that the varying abundance of Snowy Owls recorded annually in the southern part of their range in North America (southern Canada, northern United States) were related to the abundance of prey on their breeding grounds (Holt and Zetterberg 2008, Robillard et al. 2016).

The 5th World Owl Conference held in Evora, Portugal in 2017, provided us with an opportunity to look back at the last 25 years of monitoring Snowy Owls and to connect the different pieces of information we have collected over time. We hereby provide an overview of some of the recent empirical evidence in Snowy Owl movements by combining breeding density in relation to prey abundance, breeding dispersal over consecutive years and age composition and body condition of Snowy Owls irrupting in the southern part of their range in winter. We acknowledge that many of those aspects have previously been published in the scientific litterature, but are combined here for the first time in a complete annual cycle story.

Methods

We have monitored Snowy Owl and lemming populations for 25 years (1993-2017) on their breeding grounds at our long-term study site of Bylot Island, Nunavut (Canada; 73°N, 80°W; see Therrien et al. 2014 for details). Every year in mid-June, we measured nesting density of Snowy Owls by covering on foot a 100 km2 area to record each nest. Nesting white Snowy Owls are quite conspicuous on the greenish tundra and display territorial defense behaviors. We are thus confident that our detection probability is close to 100%. In addition, we have conducted opportunistic surveys at two additional sites in the eastern Canadian Arctic (Mary River 71°N, 79°W in 2008 and 2011, and Deception Bay 62°N, 74°W, in 2013). For all nests found, we estimated the clutch size (minimum number of eggs and/or chicks) and revisited nests periodically to assess diet, by identifying and counting the number of prey at the nest and, when possible, by collecting pellets of prey remains.

We measured annual lemming abundance at our main study area using a combination of snap- and live-trapping on two permanent grids (see Bilodeau et al. 2013 for details). Lemming abundance was also estimated at the two additional sites using snap traps (see Therrien et al. 2014b for details).

We have installed a total of 31 satellite transmitters on breeding Snowy Owls. On Bylot Island, we deployed 12 transmitters in

July 2007 and 8 transmitters in July 2014, all on females. One transmitter was put on a male in Mary River in July 2011 and 10 transmitters in Deception Bay in July 2013. All transmitters (30g, battery-powered; Microwave Telemetry and Northstar Technologies) were affixed using a harness made of Teflon ribbon following Steenhof et al. (2006; see Therrien et al. 2012 for details).

Between 1991 and 2017, live Snowy Owls were routinely trapped and banded in several areas of the species' wintering range in temperate North America, including regular (Alberta, Manitoba, North Dakota, Saskatchewan, South Dakota) and irregular (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) wintering areas. We assessed sex, age class and body condition of all trapped birds (see Curk et al. 2018 and Santonja et al. 2018 for details).

To assess annual winter population abundance, we used Christmas Bird Count (CBC) data (National Audubon Society 2010), a well-known citizen-science database gathering annual birding records of thousands of volunteers made during a single day 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-hr. We used the number of Snowy Owls reported per party-hr from 1991 to 2015 in regular and irregular winter areas. We assessed if the abundance of Snowy Owls during winter was synchronized among the two areas by correlating the residual values annually for each area (Buonaccorsi et al. 2001). Since none of the areas exhibited any trend with time, the residual values were simply the difference to the mean. We did the graphs and analyzes using SigmaPlot 11.0.

Results

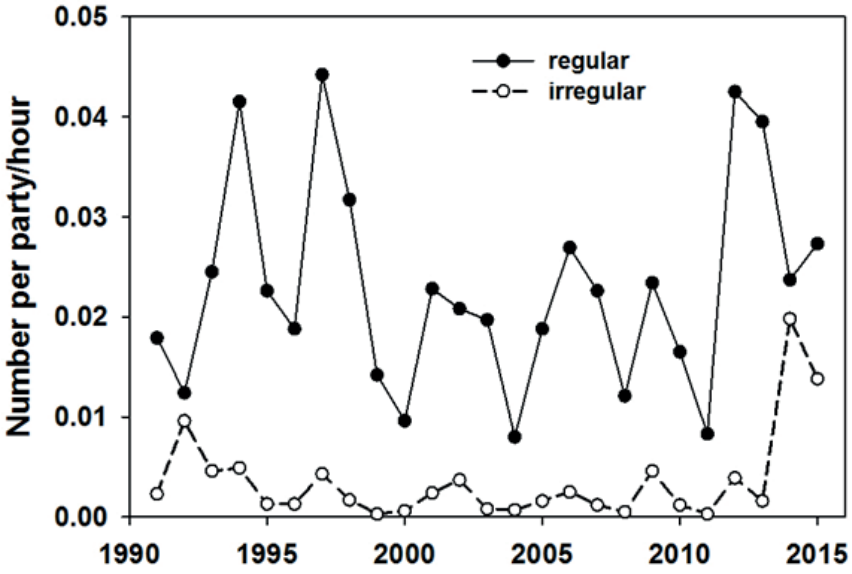
Nesting density of Snowy Owls varied annually, mirroring the high-amplitude variations in lemming abundance (Therrien et al. 2014a). Over the years, the average clutch size (±SE) remained relatively high for an owl species at all studied sites (Bylot Is. = 7.1 ± 0.2; Mary River = 7.0 ± 0.6; Deception Bay = 6.6 ± 0.4). During the breeding season, all breeding Snowy Owls had a highly specialized diet almost entirely made of lemmings. Indeed, diet analyses from all three sites revealed that >95% of their prey were lemmings (Bylot Is. = 96%; Mary River = 100%; Deception Bay = 98%).

Tracked individuals from the breeding grounds exhibited extended breeding dispersal (average = 715 km, range = 18 – 2224; Therrien et al. 2014b, Robillard et al. 2018). During each winter for which we had tracked birds, around 80% of them remained at high latitudes (range of latitudes = 56°N – 80°N) despite some of them wintering south of the boreal forest (see Therrien et al. 2011, Robillard et al. 2018 for details). Overall, individuals tend to be more faithful to their wintering areas than breeding areas (Robillard et al. 2018).

Winter abundance south of the boreal forest varied annually both in regular and irregular areas. Not surprisingly, owl abundance was almost always higher in regular wintering areas than in irregular ones (Figure 1). Despite some peaks occuring simultaneously, the two areas didn't show much synchrony ($r = 0.20$, $t = 0.99$, $df = 23$, $p = 0.33$). In irregular wintering areas, periodic winter irruptions occurred roughly every 4 years and were mainly composed of juvenile individuals (Santonja et al. 2018). Body condition of all age and sex-classes is usually good (similar to breeding individuals) with a very low percentage (<2%) of individuals approaching the emaciation threshold (Curk et al. 2018).

Figure 1 - Winter abundance of snowy owl recorded on Christmas Bird Counts in regular and irregular areas.

Figura 1 - Abundância de coruja-das-neves no inverno, registada no censo *Christmas Bird Counts* em áreas de presença regular e irregular da espécie.



Discussion

The Snowy Owl has been referred to as an irruptive migrant for a long time (reviewed in Newton 2006). Until recently however, detailed empirical evidence was lacking to describe the full annual cycle of its movement ecology, in part because of the challenge to track this species. For the first time, our long-term study combined surveys from the breeding and wintering grounds as well as tracking of individuals, and now allows for a complete understanding of their annual cycle. Furthermore, it is expected that the improvements in technology combined with ongoing long-term studies will allow for similar description of behavior in other species (especially owls).

Indeed, it is likely that other owl species behave in a very similar way. For example, the Northern Hawk-owl (*Surnia ulula*) also seems to be raising large clutches when breeding conditions are good and its populations seem to be composed of a high proportion of juveniles when irrupting during winter (Cramp 1985). The Short-eared Owl *(Asio flammeus*) is also known for invading a site during the summer when breeding conditions are good and to irrupt during winter (Holt and Leasure 1993, Keyes 2011, Johnson et al. 2013, Johnson et al. 2017). The miniaturization in tracking devices is likely to allow researchers to track these species breeding in far apart regions over consecutive years in the near future.

On the other hand, the irruptive behavior observed in other owl species might be caused by a different combination of factors and life-history traits among species. In the Great Grey Owl (*Strix nebulosa*) for exam-

ple, it was suggested that irruptions occur when food sources are depleted and that reproduction has been very limited, resulting in most individuals irrupting during winter being adults in bad body condition (Graves et al. 2012). However, the limited empirical information available to date limits our ability to assess the phenomenon accurately (but see Duncan 1987 and Duncan 1992). More long-term monitoring combining breeding and wintering ground surveys in addition to individual tracking is thus needed to understand movement ecology in these species.

Even if some aspects of the behavioral ecology of the Snowy Owl still remain to be studied in detail (e.g. breeding pair fidelity, dispersal behavior of juveniles), our results provide empirical details of its irruptive nature over a complete annual period.

Acknowledgements

We thank all the field assistants that have helped us over the years, both in the Arctic breeding grounds and across the wintering areas. We are grateful to the community of Pond Inlet, the Hunters and Trappers Organization of Pond Inlet, the Joint Park Management Committee of Sirmilik National Park, the Parks Canada's staff in Pond Inlet, Iqaluit and Pangnirtung, the Union Québécoise de Réhabilitation des Oiseaux de Proie, First Air, the Baffinland Iron Mines Corporation and the Glencore Mine Raglan Corporation for their assistance. We also want to thank all ProjectSNOWstorm supporters and all volunteers involved with the Christmas Bird Counts. This study was funded in part by the International Polar Year program from the Department of Indian and Northern Affairs Canada, the Natural Sciences and Engineering Research Council of Canada, the Nunavut Wildlife Management Board, the Fond Québécois de Recherche sur la Nature et les Technologies (FQRNT), the network of Center of Excellence ArcticNet, the Garfield-Weston Foundation, the Centre d'Études Nordiques, Université Laval, Université du Québec à Rimouski, and Université de Moncton. Finally, this study could not have been conducted without the outstanding logistic support of the Polar Continental Shelf Program. This is Hawk Mountain Sanctuary contribution to conservation science number 312 and Project SNOWstorm contribution 004.

References

Bilodeau, F., Gauthier, G. & Berteaux, D. 2013. The effect of snow cover on lemming population cycles in the Canadian High Arctic. Oecologia 172: 1007-1016.

Buonaccorsi, J.P., Elkinton, J.S., Evans, S.R. & Liebhold, A.M. 2001. Measuring and testing for spatial synchrony. Ecology 82: 1668-1679.

Chang, A.M. & Wiebe, K.L. 2016. Body condition in snowy owls wintering on the prairies is greater in females and older individuals and may contribute to sex-biased mortality. Auk 133: 738-746.

Cramp, S. 1985. Handbook of the birds of Europe, the Middle East and North Africa, Vol. 4. Oxford University Press, Oxford.

Curk, T., McDonald, T., Zazelenchuk, D., Weidensaul, S., Brinker, D., Huy, S., Smith, N., Miller, T., Robillard, A., Gauthier, G., Lecomte, N., Therrien, J.F. 2018. Winter irruptive snowy owls in North America are not starving. Canadian Journal of Zoology 96: 553-558.

Duncan, J.R. 1987. Movement strategies, mortality, and behavior of radio-marked Great Gray Owls in southeastern Manitoba and northern Minnesota. In: Nero, R.W., Clark, R.J., Knapton, J. & Hamre,

R.H. (eds) Biology and conservation of northern forest owls. USDA Forest Service General Technical Report RM-142, Fort Collins, CO U.S.A, pp. 101-107

Duncan, J.R. 1987. Influence of prey abundance and snow cover on Great Gray Owl breeding dispersal. Ph.D. Thesis. University of Manitoba, Winnipeg, Canada.

Gilg, O., Sittler B., Sabard B., Hurstel A., Sane R., Delattre P. & Hanski I. 2006. Functional and numerical responses of four lemming predators in high arctic Greenland. Oikos 113: 193-216.

Graves, G.R., Newsome, S.D., Willard, D.E, Grosshuesch, D.A., Wurzel, W.W.& Fogel, M.L. 2012. Nutritional stress and body condition in the great gray owl (*Strix nebulosa*) during winter irruptive migrations. Canadian Journal of Zoology 90: 787-797.

Holt, D.W., Larson, M.D., Smith, N., Evans, D. & Parmalee, D.F. 2015. The snowy owl (*Bubo scandiacus*). In: Poole, A. (ed) The Birds of North America Online. Cornell Lab of Ornithology, Ithaca.

Holt, D.W. & Leasure, S.M.. 1993. Short-eared Owl (*Asio flammeus*). In: Poole, A. & Gill, F. (eds) The Birds of North America, No. 62. The Academy of Natural Sciences, Philadelphia, Pennsylvania; The American Ornithologists' Union, Washington, D.C., p. 22.

Johnson, D.H., Swengel, S.R. & Swengel, A.B. 2013. Short-eared Owl (*Asio flammeus*) occurrence at Buena Vista Grassland, Wisconsin, during 1955-2011. Journal of Raptor Research 47: 271-281.

Johnson, J.A., Booms, T.L., DeCicco, L.H. & Douglas, D.C. 2017. Seasonal movements of the Short-Eared Owl (*Asio flammeus*) in western North America as revealed by satellite telemetry. Journal of Raptor Research. 51: 115-128.

Keyes, K. 2011. Geographic and habitat fidelity in the Short-eared Owl. M.S. Thesis. McGill University, Montreal, Canada. 110 pp.

Krebs, C.J. 2011. Of lemmings and snowshoe hares: the ecology of northern Canada. Proceedings of the Royal Society B-Biological Sciences 278: 481-489.

National Audubon Society. 2010. The Christmas Bird Count historical results (Online). http://www.christmasbirdcount.org (accessed 20 August 2016).

Newton, I. 2006. Advances in the study of irruptive migration. Ardea 94: 433-460.

Newton, I. 2008. Irruptive migrations: owls, raptors and waterfowl. In: Newton, I. (ed) The Migration Ecology of Birds, Academic Press, London, pp.563-586.

Ostfeld, R. S. & Keesing, F. 2000. Pulsed resources and community dynamics of consumers in terrestrial ecosystems. Trends in Ecology & Evolution 15: 232-237.

Robillard, A., Therrien, J.F., Gauthier, G., Clark, K.M. & Bêty, J. 2016. Pulsed resources at tundra breeding sites affect winter irruptions at temperate latitudes of a top predator, the snowy owl. Oecologia, 181: 423-433.

Robillard, A., Gauthier, G., Therrien, J.F. & Bêty, J.. 2018. Wintering space use and site fidelity in a nomadic species, the snowy owl. Journal of Avian Biology 49: jav-01707.

Santonja, P., Mestre, I., Weidensaul, S., Brinker, D., Huy, S., Smith, N., McDonald, T., Blom, M., Weber, D., Gauthier, G., Lecomte,, N. & Therrien, J.F.. Under

review. Age composition of winter irruptive snowy owls in North America. Ibis 161: 211-215.

Steenhof, K., Bates, K. K., Fuller, M. R., Kochert, M. N., McKinley, J. O., & Lukacs, P. M. 2006. Effects of radiomarking on Prairie falcons: attachments failures provide insights about survival. Wildlife Society Bulletin 34: 116-126.

Therrien, J.F., Gauthier, G., & Bêty, J. 2011. An avian terrestrial predator of the Arctic relies on the marine ecosystem during winter. Journal of Avian Biology 42: 363-369.

Therrien, J.F., G. Gauthier, & Bêty, J. 2012. Survival and reproduction of adult snowy owls tracked by satellite. Journal of Wildlife Management 76: 1562-1567.

Therrien, J.F., Gauthier, G., Korpimäki, E.& Bêty, J. 2014a. Predation pressure by avian predators suggests summer limitation of small mammal populations in the Canadian Arctic. Ecology 95: 56–67.

Therrien, J.F., Gauthier, G., Pinaud, D. & Bêty, J. 2014b. Irruptive movements and breeding dispersal of snowy owls: a specialized predator exploiting a pulsed resource. Journal of Avian Biology 45: 536–544.

Therrien, J.F., Gauthier, G., Robillard, A., Lecomte, N. & Bêty, J. 2015. Écologie de la reproduction du harfang des neiges dans l'Arctique canadien. Naturaliste Canadien 139: 17-23.