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Note

Another mention of Meadow Vole (*Microtus pennsylvanicus*) found in pellets of Snowy Owl (*Bubo scandiacus*) in northern Ungava Peninsula, Canada

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Abstract

The examination of raptor pellets can be used to evaluate Arctic biodiversity. We found the remains of Meadow Vole (Microtus pennsylvanicus) and Ungava Collared Lemming (Dicrostonyx hudsonius) in pellets from Snowy Owl (Bubo scandiacus) nesting in the northern part of the Ungava Peninsula. We differentiated the two species by visual identification and geometric morphometric analysis of molar shape. The results of our study combined with historical data suggest that most commonly used range maps of Meadow Vole should be revised.

Key words: Ungava Peninsula; Meadow Vole; Microtus pennsylvanicus; Ungava Collared Lemming; Dicrostonyx hudsonius; morphological identification

L'étude des pelotes de rejection de rapaces est utile pour évaluer la biodiversité arctique. Des restes de Campagnol de Prairie (Microtus pennsylvanicus) et de Lemming à Collier d'Ungava (Dicrostonyx hudsonius) dans des pelotes de rejections de Harfang (Bubo scandiacus) nichant à l'extrême nord de la péninsule d'Ungava. Les deux espèces sont séparées par identification visuelle et par l'analyse morphométrique des molaires. Les résultats de cette étude combinés aux données historiques suggèrent que les cartes de distribution les plus communément utilisées pour le Campagnol de Prairie devraient être révisées.

Mots clefs: Péninsule d'Ungava; Microtus pennsylvanicus; Dicrostonyx hudsonius; identification morphologique

The northern part of the Ungava Peninsula, Canada, is remarkable for its low rodent diversity, with some distribution maps (Hall 1981; Tamarin et al. 1985; Shenbrot and Krasnov 2005; Wilson et al. 2017) indicating the presence of only the endemic Ungava Collared Lemming (Dicrostonyx hudsonius). This low diversity is peculiar at this latitude, where additional rodent species are generally documented (e.g., North America: Hall [1981] and Feldhamer et al. [2003]; Eurasia: Ognev [1948]). However, a few records of another small rodent, Meadow Vole (Microtus pennsylvanicus), from the northern end of the Ungava Peninsula have not been included in general range maps by some (e.g., Hall 1981; Feldhamer et al. 2003; Shenbrot and Krasnov 2005; Cassola 2016; Wilson et al. 2017). Three records are in the Canadian Museum of Nature (CMN): two juvenile males stored in alcohol collected before 1934 from Salliut (formerly Sugluk) on the southwest side of Hudson Strait (CMNMA 12572 and 12573), and a male study skin (CMNMA 31130) collected from the same area in 1954. Banfield's (1974: 212) range map for the species covers the entire peninsula and the 1954 record is mentioned in Desrosier et al. (2002) and compiled in the CMN database, as well as in the Global Biodiversity Information Facility database (Khidas and Torgersen 2021). Additional specimens were collected in 2013 by Robillard et al. (2013, 2017) from Deception Bay, 60 km east of Salliut Inlet. More recently, five additional specimens of Meadow Vole were snap-trapped by Fortin and Caron (2015) along with five Northern Bog Lemming (Synaptomys

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borealis) in the northern portion of the Ungava Peninsula near the Raglan Mine. Despite these previous records, the northern part of the Ungava Peninsula has not generally been included in widely used distribution maps of Meadow Vole (e.g., Hall 1981; Feldhamer et al. 2003; Shenbrot and Krasnov 2005; Cassola 2016; Wilson et al. 2017; but see Banfield 1974).

We visually examined the teeth of small mammals collected from regurgitated pellets from Snowy Owl (*Bubo scandiacus*) nests near Salluit, northern Quebec, Canada (Figure 1), in July 2013 (see Robillard *et al.* 2013, 2017 for details) and used geometric morphometrics to differentiate and distinguish rodent species. Unlike traditional morphometrics, landmarkbased geometric morphometric analyses use generalized procrustes analysis (GPA), which removes the effects of size, position, and orientation. Thus, only shape parameters remain, with a minimum loss of information (Adams *et al.* 2004).

The regurgitated pellets of undigested material from birds of prey are commonly used to assess the diversity of small to medium sized animals around the world (e.g., Chaline et al. 1974; Ba et al. 2000; Meek et al. 2012; McDonald et al. 2014; Heisler et al. 2016; Linchamps et al. 2021). Cranial and dental remains in pellets can be confidently identified to the species level, hence determining prey diversity in the environment of a predator (Chaline et al. 1974; Andrews 1990). The circumpolar Snowy Owl is a key predator in the Arctic tundra ecosystem. Its summer diet includes a diversity of small to medium sized animals, such as birds and hares, but generally consists mainly of rodents (e.g., Watson 1957; Gilg et al. 2006; Therrien et al. 2014; Robillard et al. 2017; Royer et al. 2019).

In July 2013, 12 Snowy Owls were captured near Salluit, Ungava Peninsula (Figure 1) and equipped with global positioning system tracking transmitters (Robillard *et al.* 2013). The transmitters were pro-

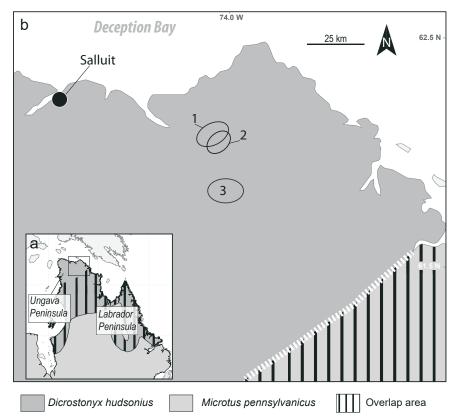


FIGURE 1. Distribution of Ungava Collared Lemming (*Dicrostonyx hudsonius*) and Meadow Vole (*Microtus pennsylvanicus*) according to Hall (1981). The black square (in a) indicates the Ragalan Mine sector from which all pellets were obtained. Specific movement ranges of the three Snowy Owl (*Bubo scandiacus*) that captured Meadow Voles are shown as ovals in b. The areas where Robillard *et al.* (2017) collected blood samples are within the owl home ranges. The dotted line indicates the erroneous northern limit of Meadow Vole (Hall 1981). Map created using the "rnaturalearth" package v.0.2.0 in R (R Core Team 2020).

grammed to communicate position every 4.5 days. Summer tracking showed that owls' movements were limited to their nesting areas. Regurgitated pellets—10 sets from 10 different nests—were collected from Snowy Owl nests a few days after the owls were captured and released (Table 1). Each pellet was dried and analysed to assess prey items from undigested materials (bones and teeth) at the Biogéosciences laboratory in Dijon, France.

Based on current distribution maps (e.g., Hall 1981; Feldhamer *et al.* 2003; Shenbrot and Krasnov 2005; Wilson *et al.* 2017; but see Banfield 1974), five rodent species can be expected throughout the entire Ungava Peninsula: Ungava Collared Lemming, Meadow Vole, Southern Red-backed Vole (*Myodes gapperi*), Northern Bog Lemming, and Eastern Heather Vole (*Phenacomys ungava*), with Ungava Collared Lemming the only species in the northern part of the peninsula. Rock Vole (*Microtus chrotorrhinus*) is mentioned at the very southern limits of the Ungava Peninsula by Desrosiers *et al.* (2002).

We identified rodent species from the owl pellets based on the morphology of the lower and upper molars following Guilday (1982), Semken and Wallace (2002), Lupien (2002), and Fauteux *et al.* (2014). Ungava Collared Lemming molars lack cementum in the re-entrant angles, unlike the four other genera (see Meadow Vole and Ungava Collared Lemming in Figure 2). The first lower molar has seven

triangles on the occlusal surface, in contrast with Microtus spp. with five or six closed triangles (Figure 2), P. ungava with five closed asymmetrical triangles, M. gapperi with four closed triangles on the occlusal surface, and Synaptomys spp. with only two closed triangles on the internal side. The most reliable criterion for separating the two Microtus species is the presence of an additional small "button-shaped" element at the posterior part of the second upper molar for Meadow Vole, which is always absent in M. chrotorrhinus (Tamarin 1985; Semken and Wallace 2002). The occlusal pattern of the third upper molar can also be a distinguishing feature, as M. chrotorrhinus always has a complex posterior loop, which is rare in Meadow Vole (Guilday 1982; Semken and Wallace 2002). One last criterion is the number of closed triangles on the lower second molar: M. chrotorrhinus has two while Meadow Vole has four.

To support this descriptive, visual identification, geometric morphometric analysis was used on the first lower molars following the protocol of Navarro et al. (2018) and Montuire et al. (2019). All teeth were first photographed using a macro objective lens (MP-E 65 mm f/2.8 on a Canon EOS6D mark II camera, Canon, Inc., Tokyo, Japan) and saved in jpg format at a resolution of 72 dots per inch. Outlines were then extracted from pictures using ImageJ v.1.52a (free software with a Public Domain License available on GitHub; Schneider et al. 2012). Two-dimensional

TABLE 1. Counts of Ungava Collared Lemming (*Dicrostonyx hudsonius*) and Meadow Vole (*Microtus pennsylvanicus*) remains found in 10 sets of Snowy Owl (*Bubo scandiacus*) pellets from Ungava Peninsula, Quebec, Canada.

Owl no.	Collection date	Rodent species	MNI*	No. left mandibles	No. right mandibles	No. skulls
2	8 July 2013	Dicrostonyx hudsonius	3	3	2	3
3	9 July 2013	D. hudsonius	17	14	17	6
		Microtus pennsylvanicus	4	4	0	2
4	4 July 2013	D. hudsonius	12	12	12	9
		M. pennsylvanicus	2	2	1	0
5	8 July 2013	D. hudsonius	1	1	1	0
6	14 July 2013	D. hudsonius	14	10	14	5
8	13 July 2013	D. hudsonius	8	8	7	6
		M. pennsylvanicus	2	1	2	1
9	_	D. hudsonius	5	5	4	2
		M. pennsylvanicus	2	1	2	2
10	13 July 2013	D. hudsonius	2	2	2	2
11	July2013	D. hudsonius	3	3	1	2
Total			75			
Dicrostonyx			65 (86.7%)			
Microtus			10 (13.3%)			

^{*}MNI = minimum no. individuals contained in the pellet, calculated for each pellet based on counts of the maxillary and left or right mandible for each species.

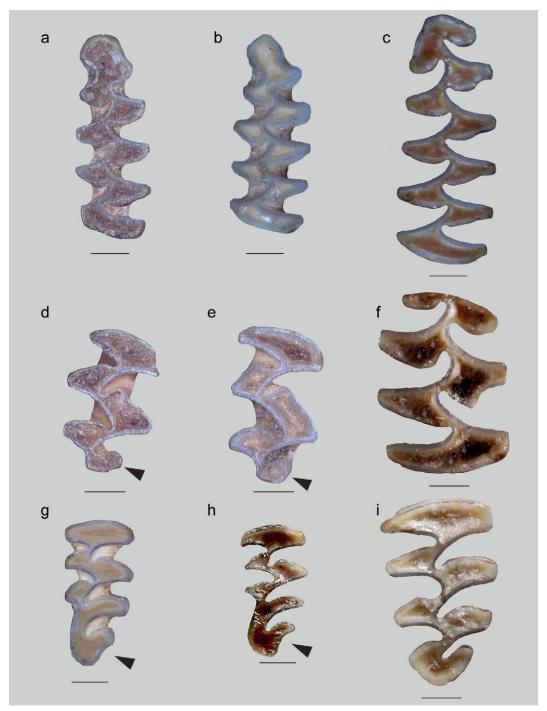


FIGURE 2. Characteristics of rodent teeth collected from Snowy Owl (*Bubo scandiacus*) pellets from Ungava Peninsula, Quebec. a and b. First lower molar of Meadow Vole (*Microtus pennsylvanicus*). c. First lower molar of Ungava Collared Lemming (*Dicrostonyx hudsonius*). d and e. Second upper molar of Meadow Vole. f. Second upper molar of Ungava Collared Lemming. g and h. Third upper molar of Meadow Vole. i. Third upper molar of Ungava Collared Lemming. Black arrows indicate the diagnostic supplementary "button shape" element in second upper molar of Meadow Vole, and the simplicity of the loop of the third upper molar of Meadow Vole. Scale bar: 1 mm. Photos: Louis Arbez.

landmark placement is automated by first standardizing the orientation of the molar by manually marking four landmarks (white circles in Figure 3a) enabling the automatic detection of 14 additional landmarks defined as extreme tips of salient and re-entrant triangles and loop tips (Navarro *et al.* 2018). GPA and principal component analyses (PCA) were performed in R version 4.0.3 (R Core Team 2020) using the "geomorph" package, version 3.2.0 (Adams *et al.* 2019). Tooth length was estimated using the Euclidean distance between landmarks 1 and 13 (Figure 3a,b).

The minimum number of individual (MNI) rodents was calculated for each pellet based on the most numerous skeletal component (i.e., left and right mandible or teeth). For example, a pellet with two left mandibles and five right mandibles has an MNI of 5.

Nine of the 10 sets of owl pellets contained small vertebrate remains that did not show a high degree of digestion and in which teeth were found (Figure 2). A total of 75 individual rodents were identified to the species level, including 65 Ungava Collared Lemmings (86.6% of the MNI) and 10 voles (*Microtus* spp.; 13.3% of the MNI; Table 1). All vole second upper molars possessed a supplementary "button shaped" element at the anterior part, no third upper molar exhibited a complex posterior loop morphology, and all second lower molars had four closed

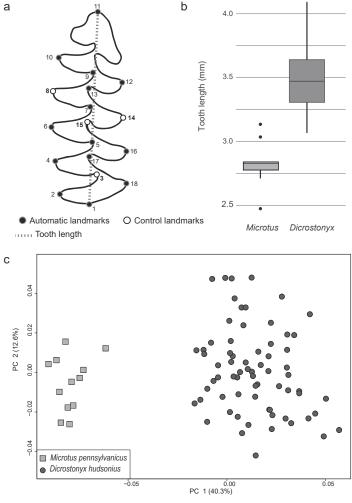


FIGURE 3. a. Landmarks for lemming (*Dicrostonyx* spp.) and vole (*Microtus* spp.) first lower molar (m1). White circles indicate manually applied landmarks, black circles are automatically detected landmarks, dotted line shows tooth length. b. Boxplot of m1 length of Meadow Vole (*Microtus pennsylvanicus*) and Ungava Collared Lemming (*Dicrostonyx hudsonius*). c. Principal component analysis (PC 1 and PC 2 planes) of Meadow Vole (*Microtus pennsylvanicus*) and Ungava Collared Lemming (*Dicrostonyx hudsonius*) m1, including percentage of shape variation explained by each PC.

triangles, indicating that they were all Meadow Voles. These two species were the only rodent remains in the owl pellets and no juvenile lemmings or voles were found.

PCA (Figure 3c) showed that the morphological distribution of the specimens from the owl pellets was not uniform (PC 1: 40.3%; PC 2: 12.6%), but fell into two homogeneous groups; this confirms the presence of two species. These two distinct groups can be identified along the PC 1 axis, one attributed to Ungava Collared Lemming on the positive side and the other to a vole species, confidently identified as Meadow Vole, on the negative side. This difference is also shown by tooth length: Ungava Collared Lemmings have longer teeth than Meadow Voles (Figure 3b). Variability of Meadow Vole tooth length (range 2.4–3.2 mm) is commonly found among adults in other populations (e.g., Wallace 2006).

The distribution range maps for North American rodents generated by Hall (1981) are widely used in many studies (e.g., Barnosky 1990; Feldhamer et al. 2003; Spaeth 2009; Jackson and Cook 2020). According to Hall (1981), Ungava Collared Lemming is the only lemming species inhabiting the Ungava Peninsula. Meadow Vole is widespread across North America; it occupies humid grassland, marsh, and riparian areas (Tamarin 1985) and is one of the most common Microtus species in subarctic taiga and tundra areas in Alaska and northern Canada (Tamarin 1985). Meadow Vole is also widespread in the south and centre of the Labrador Peninsula and its distribution is thought to be limited northward by the Ungava trough (Tamarin 1985). However, few occurrences of this species have been reported beyond this limit: two specimens in the Canadian Museum of Nature collected before 1934 (CMNMA 12572 and 12573), another individual collected near Salluit in 1954 (CMNMA 31130), and five more specimens snap-trapped by Fortin and Caron (2015). Robillard et al. (2013) also mentioned the presence of carcasses of Meadow Voles in Snowy Owl nests. We analysed the owl pellets collected in such nests and report once again the presence of Meadow Vole in the region. Several individuals (at least 10 of various sizes) were detected in Snowy Owl pellets, suggesting that the species is part of the owl's food web, although nearly 90% of the rodent individuals in the owl pellets were Ungava Collared Lemmings.

Will the abundance of Meadow Voles in the Ungava Peninsula increase with climate change? The species' presence has been known for some time (two specimens were found in 1934) and more specimens have been found since 2013, although few animals have been collected. In both our study and the one by Fortin and Carron (2015), Meadow

Voles represented approximately 10% of the identified individuals. The Labrador Peninsula is currently experiencing the effects of climate change with the southern part of Ungava Peninsula getting dryer because of a decrease in precipitation and an increase in summer temperatures (Furgal et al. 2002; Barrette et al. 2020). These changes will most likely impact marshes and meadows, habitats sought preferentially by Meadow Voles, and could disadvantage the vole. Continuous field monitoring will increase understanding of how climate change could affect the dynamics of the Meadow Vole–Ungava Collared Lemming community in the area.

In conclusion, our results suggest that the current widely used range maps for rodents should always be interpreted with caution and the one for Meadow Vole should be revised to include the northern tip of the Labrador Peninsula, namely the Ungava Peninsula.

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Author Contributions

Conceptualization: L.A., J.-F.T., A.R., and S.M.; Methodology: L.A., J.-F.T., A.R., and S.M.; Formal Analysis: L.A., J.-F.T., A.R., and S.M.; Data Curation: L.A., J.-F.T., A.R., and S.M.; Writing – Original Draft: L.A., J.-F.T., A.R., and S.M.; Visualization: L.A., J.-F.T., A.R., and S.M.

Literature Cited

Adams, D., M. Collyer, A. Kaliontzopoulou, and E. Baken. 2019. Geomorph: software for geometric morphometric analyses. R package version 3.2.0.

Adams, D.C., F.J. Rohlf, and D.E. Slice. 2004. Geometric morphometrics: ten years of progress following the 'revolution'. Italian Journal of Zoology 71: 5–16. https://doi. org/10.1080/11250000409356545

Andrews, P. 1990. Owls, Caves, and Fossils: Predation, Preservation and Accumulation of Small Mammal Bones in Caves, with an Analysis of the Pleistocene Cave Faunas from Westbury-Sub-Mendip, Somerset, U.K. Natural History Museum, British Museum, London, United Kingdom.

Ba, K., L. Granjon, R. Hutterer, et J.M. Duplantier. 2000. Les micromammifères du Djoudj (Delta du Sénégal) par l'analyse du régime alimentaire de la chouette effraie, *Tyto alba*. Bonner Zoologische Beiträge 49: 31–38.

Banfield, A.W.F. 1974. The Mammals of Canada. University of Toronto Press, Toronto, Ontario, Canada.

Barnosky, A.D. 1990. Evolution of dental traits since latest Pleistocene in meadow voles (*Microtus pennsylvanicus*) from Virginia. Paleobiology 16: 370–383. https://doi.org/10.1017/S0094837300010071

- Barrette, C., R. Brown, R. Way, A. Mailhot, E.P. Diaconescu, P. Grenier, D. Chaumont, D. Dumont, C. Sévigny, S. Howell, and S. Senneville. 2020. Nunavik and Nunatsiavut regional climate information update. Pages 57–114 in Nunavik and Nunatsiavut: from Science to Policy: an Integrated Regional Impact Study (IRIS) of Climate Change and Modernization, Second Edition. Edited by P. Ropars, M. Allard, and M. Lemay. ArcticNet Inc., Québec, Quebec, Canada.
- Cassola, F. 2016. Microtus pennsylvanicus (errata version published in 2017). IUCN Red List of Threatened Species 2016: e.T13452A115114123. https://doi.org/10. 2305/iucn.uk.2016-3.rlts.t13452a22347596.en
- Chaline, J., H. Baudvin, D. Jammot, et M.C. Saint-Girons. 1974. Les Proies des Rapaces. Doin, Paris, France.
- Desrosiers, N., R. Morin, et J. Jutras. 2002. Atlas des Micromammifères du Québec. Société de la faune et des parcs du Québec, Fondation de la faune du Québec, Québec, Quebec, Canada.
- Fauteux, D., G. Lupien, F. Fabianek, J. Gagnon, M. Séguy, and L. Imbeau. 2014. An illustrated key to the mandibles of small mammals of eastern Canada. Canadian Field-Naturalist 128: 25–37. https://doi.org/10.22621/cfn.v128i1.1546
- Feldhamer, G.A., B.C. Thompson, and J.A. Chapman. 2003. Wild Mammals of North America: Biology, Management, and Conservation. Second Edition. Johns Hopkins University Press, Baltimore, Maryland, USA.
- Fortin, C., et B. Caron. 2015. Aire de répartition du campagnol-lemming boréal au Québec: mentions les plus nordiques. Le Naturaliste canadien 139: 42–47. https://doi. org/10.7202/1030820ar
- Furgal, C., D. Martin, and P. Gosselin. 2002. Climate change and health in Nunavik and Labrador: lessons from Inuit Knowledge. Pages 266–300 in The Earth is Faster Now: Indigenous Observations of Arctic Environmental Change. Edited by I.Krupnik and D. Jolly. Arctic Research Consortium of the United States, Arctic Studies Centre, Smithsonian Institution, Washington, DC, USA.
- Gilg, O., B. Sittler, B. Sabard, A. Hurstel, R. Sané, P. Delattre, and I. Hanski. 2006. Functional and numerical responses of four lemming predators in high arctic Greenland. Oikos 113: 193–216. https://doi.org/10.1111/ j.2006.0030-1299.14125.x
- Guilday, J.E. 1982. Dental variation in *Microtus xanthog-nathus*, *M. chrotorrhinus*, and *M. pennsylvanicus* (Rodentia, Mammalia). Annals of Carnegie Museum 51: 211–230.
- Hall, E.R. 1981. The Mammals of North America. John Wiley, New York, New York, USA.
- Heisler, L.M., C.M. Somers, and R.G. Poulin. 2016. Owl pellets: a more effective alternative to conventional trapping for broad-scale studies of small mammal communities. Methods in Ecology and Evolution 7: 96–103. https://doi.org/10.1111/2041-210X.12454
- Jackson, D.J., and J.A. Cook. 2020. A precarious future for distinctive peripheral populations of meadow voles (*Mi-crotus pennsylvanicus*). Journal of Mammalogy 101: 36– 51. https://doi.org/10.1093/jmammal/gyz196
- Khidas, K., and J. Torgersen. 2021. Occurrence: Micro-

- tus pennsylvanicus (Ord, 1815). Canadian Museum of Nature mammal collection. Canadian Museum of Nature, Ottawa, Ontario, Canada. Accessed 15 June 2021. https://www.gbif.org/occurrence/1804068870.
- Linchamps, P., E. Stoetzel, R. Hanon, and C. Denys. 2021. Neotaphonomic study of two *Tyto alba* assemblages from Botswana: palaeoecological implications. Journal of Archaeological Science: Reports 38: 103085. https://doi.org/10.1016/j.jasrep.2021.103085
- Lupien, G. 2002. Recueil Photographique des Caractéristiques Morphologiques Servant à l'Identification des Micromammifères du Québec, Vol. II: Rongeurs. Société de la faune et des parcs du Québec, Jonquière, Quebec, Canada.
- McDonald, K., S. Burnett, and W. Robinson. 2014. Utility of owl pellets for monitoring threatened mammal communities: an Australian case study. Wildlife Research 40: 685–697. https://doi.org/10.1071/wr13041
- Meek, W.R., P.J. Burman, T.H. Sparks, M. Nowakowski, and N.J. Burman. 2012. The use of Barn Owl (*Tyto alba*) pellets to assess population change in small mammals. Bird Study 59: 166–174. https://doi.org/10.1080/0063657.2012.656076
- Montuire, S., A. Royer, A. Lemanik, O. Gilg, N. Sokolova, A. Sokolov, E. Desclaux, A. Nadachowski, and N. Navarro. 2019. Molar shape differentiation during range expansions of the collared lemming (*Dicrostonyx torquatus*) related to past climate changes. Quaternary Science Reviews 221: 105886. https://doi.org/10.1016/j.quascirev.2019.105886
- Navarro, N., S. Montuire, R. Laffont, E. Steimetz, C. Onofrei, and A. Royer. 2018. Identifying past remains of morphologically similar vole species using molar shapes. Quaternary 1: 20. https://doi.org/10.3390/quat1030020
- **Ognev, S.I.** 1948. Mammals of the U.S.S.R. and Adjacent Countries. Volume V, Rodents. Israel Program for Scientific Translation, Jerusalem, Israel.
- R Core Team. 2020. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Robillard, A., G. Gauthier, J.F. Therrien, et J. Bêty. 2013. Étude des mouvements et de la nidification du harfang des neiges au Nunavik. Rapport d'activités présenté au Service Environnement Mine Glencore Xstrata Nickel, Raglan. Université Laval Hawk Mountain Sanctuary, et Université du Québec à Rimouski, Quebec, Canada. Accessed 18 February 2022. https://www.cen.ulaval.ca/bylot/document/rapport_snow_2013.pdf.
- Robillard, A., G. Gauthier, J.F. Therrien, G. Fitzgerald, J.F. Provencher, and J. Bêty. 2017. Variability in stable isotopes of snowy owl feathers and contribution of marine resources to their winter diet. Journal of Avian Biology 48: 759–769. https://doi.org/10.1111/jav.01257
- Royer, A., S. Montuire, O. Gilg, and V. Laroulandie. 2019. A taphonomic investigation of small vertebrate accumulations produced by the snowy owl (*Bubo scandiacus*) and its implications for fossil studies. Palaeogeography, Palaeoclimatology, Palaeoecology 514: 189–205. https://doi.org/10.1016/j.palaeo.2018.10.018
- Schneider, C.A., W.S. Rasband, and K.W. Eliceiri. 2012.NIH Image to ImageJ: 25 years of image analysis. Na-

- ture Methods 9: 671–675. https://doi.org/10.1038/nmeth. 2089
- Semken, Jr., H.A., and S.C. Wallace. 2002. Key to Arvicoline ("Microtine" rodents) and Arvicoline-like lower first molars recovered from Late Wisconsinan and Holocene archaeological and palaeontological sites in eastern North America. Journal of Archaeological Science 29: 23–31. https://doi.org/10.1006/jasc.2001.0680
- Shenbrot, G.I., and B.R. Krasnov. 2005. Atlas of the Geographic Distribution of the Arvicoline Rodents of the World (Rodentia, Muridae: Arvicolinae). Pensoft, Sofia, Bulgaria.
- Spaeth, P.A. 2009. Morphological convergence and coexistence in three sympatric North American species of *Microtus* (Rodentia: Arvicolinae). Journal of Biogeography 36: 350–361. https://doi.org/10.1111/j.1365-2699. 2008.02015.x
- Tamarin, R.H. 1985. Biology of New World Microtus. Special publication 8. American Society of Mammalogists, Pittsburg, Pennsylvania, USA.
- Therrien, J.F., G. Gauthier, A. Robillard, N. Lecomte, et J. Bêty. 2014. Écologie de la reproduction du harfang

- des neiges dans l'Arctique canadien. Le Naturaliste canadien 139: 17–23. https://doi.org/10.7202/1027666ar
- Wallace, S.C. 2006. Differentiating Microtus xanthognathus and Microtus pennsylvanicus lower first molars using discriminant analysis of landmark data. Journal of Mammalogy 87: 1261–1269. https://doi.org/10.1644/05mamm-a-209r3.1
- Watson, A. 1957. The behaviour, breeding, and food ecology of the snowy owl *Nyctea scandiaca*. Ibis 99: 419–462. https://doi.org/10.1111/j.1474-919X.1957.tb01959.x
- Wilken, E.B., D. Gauthier, I. Marshall, K. Lawton, and H. Hirvonen. 1996. A perspective on Canada's ecosystems: an overview of the terrestrial and marine ecozones. Canadian Council on Ecological Areas, Ottawa, Ontario, Canada.
- Wilson, D.E., T.E. Lacher, and R.A. Mittermeier. 2017. Handbook of the Mammals of the World, Volume 7. Lynx Edicions, Barcelona, Spain.

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