


# Improving diet assessment of Arctic terrestrial predators with the size of rodent mandibles

E. Schmidt<sup>1</sup> , D. Fauteux<sup>1,2</sup>, J.-F. Therrien<sup>3</sup>, G. Gauthier<sup>2</sup> & Y. Seyer<sup>2</sup>

<sup>1</sup> Canadian Museum of Nature, Ottawa, ON, Canada

<sup>2</sup> Department of Biology, Centre d'Études Nordiques, Université Laval, Québec, QC, Canada

<sup>3</sup> Acopian Center for Conservation Learning, Hawk Mountain Sanctuary, Orwigsburg, PA, USA

## Keywords

small mammals; morphology; trophic interactions; regurgitation pellets; diet; predation; Arctic; rodent mandibles.

## Correspondence

Elliott Schmidt, Canadian Museum of Nature, P.O. Box 3443, Ottawa, ON, Canada K1P 6P4.  
Email: eschmidt@nature.ca

Editor: Andrew Kitchener  
Associate Editor: Abby Drake

Received 27 March 2019; revised 30 September 2019; accepted 5 December 2019

doi:10.1111/jzo.12756

## Abstract

Predator–prey interactions can control population fluctuations of several terrestrial vertebrates and energy fluxes in food webs. Quantifying these interactions typically requires the number of prey consumed by predators to be known, but prey size is often ignored. We hypothesized that rodent mandibles, which are routinely found in predatory bird pellets and mammalian scats, could be used to accurately determine prey size and thus estimate biomass consumed by Arctic predators. We used 1863 lemmings and voles from museum and field specimens collected across the North American Arctic to relate three measurements of the dentary bone and one on the molar tooththrow with individual body mass. When species and location of specimens are known, our results suggest that the body mass of small rodents can be estimated with high precision using the dentary bone measurements (average  $R^2$  ranging from 0.73 to 0.81), especially for lemmings and *Microtus* voles. Body mass can also be estimated with reasonable precision using the dentary bone measurements even when species or location was unknown ( $0.71 \leq R^2 \leq 0.80$ ). Equations to convert mandible size to body mass are provided for site- and species-specific estimations. Geographic variations in the relationship between mandible size and body mass were found, suggesting potential effects of genetic isolation or interactions with the immediate environment on size. Using mandible measurements in prey remains allows more precise estimation of biomass consumed by predators, which is essential to quantify energy fluxes within ecosystems and examine resource partitioning among Arctic predators.

## Introduction

Predator–prey interactions play a key role in simple trophic systems such as the Arctic tundra (Hanski *et al.*, 2001; Myers, 2018). Strong top-down effects are well-documented in Arctic ecosystems even though primary productivity is low and was initially thought to be insufficient to support a large predator guild (Oksanen & Oksanen, 2000; Gilg, Hanski & Sittler, 2003; Legagneux *et al.*, 2012). Seasonal migrations of Arctic species such as owls, jaegers and foxes create a dynamic meta-ecosystem involving tundra, temperate, tropical and marine habitats (Gravel *et al.*, 2010; Therrien, Gauthier & Bêty, 2011; Tarroux *et al.*, 2012). These migrants and their movements create energy fluxes among ecosystems, adding or subtracting nutrients through food consumption, defecations and mortalities and thus affecting nutrient cycles globally (Bauer & Hoye, 2014). Recent studies suggested that these ecosystem fluxes are key to understand the functioning of food webs (Barnes *et al.*, 2018). Quantifying consumed biomass within food webs is critical to identifying and quantifying energy

fluxes (Cohen, Jonsson & Carpenter, 2003; Reuman & Cohen, 2005).

At the local scale, determining diets of avian or mammalian predators reveals functional aspects of food webs such as how prey are shared among consumers (Hartman & Brandt, 2018) and niche breadth (Hayward & Garton, 1988; Wien, Anthony & Forsman, 2014). In the Arctic, a large number of predators mainly prey on small rodents (i.e. lemmings and voles) and typically only one or two rodent species are present at any given site (Wilson, Krebs & Sinclair, 1999; Schmidt *et al.*, 2012). Competition among predators would therefore favour resource partitioning, for instance according to body mass (or size). Obtaining the body mass of prey consumed is challenging, but bones found in regurgitated pellets of predatory birds or in scats of mustelids and foxes may yield valuable information about the size and mass of prey consumed. Counting and identifying prey remains in pellets or scats has been done in the past to assess the diet of avian and mammalian predators (Maser & Brodie, 1966; Redpath *et al.*, 2001; Buidin, Rochepault & Savard, 2007). Identification keys using skull parts or

mandibles can be used to determine the species consumed (Carraway, 1995; Glass & Thies, 1997; Naughton, 2012; Fau-teux *et al.*, 2014). Mandibles are particularly useful because of their high resistance to gastric degradation. When converting predator diets, based on proportions, into biomass consumed, averages of prey body mass have often been used, ignoring individual variation due for instance to sex or age of prey (Marti, 1976; Collopy, 1983). However, taking into account variability in prey size within species and even within individuals of the same species can improve estimates of biomass consumed.

In this study, we analysed the relationship between the size of mandibles and the body mass of six species of lemmings and voles found across the North American Arctic. We hypothesized that in small rodents, the size of mandibles is closely related to body mass because voles and lemmings rarely live more than a few months due to high mortality rate (i.e. negligible senescence or degradation of the bones) and seasonal variation in fat is low due to their year-long activity (i.e. body mass is mostly related to size of skeleton, not fat mass; Batzli & Esseks, 1992). Since jawbones can be broken or degraded in pellets and scats, we took four different measurements of mandibles and determined whether one or several of them could provide a flexible tool to estimate body mass. We examined whether body mass could still be estimated reliably when mandibles cannot be identified to species, and thus, an overall relationship based on mixed species is used. We also examined whether geographical differences were a large source of variation in those relationships within species. Equations to convert size of mandibles to body mass are provided for each of these situations. Our results will allow refined estimations of small rodent body mass based on prey remains, which is important for studies of energy fluxes within and between food webs or of resource partitioning among arctic predators.

## Materials and methods

### Study area and species

Our study was based on six species of small rodents found in the North American continental Arctic and the Arctic Archipelago (Fig. 1). These species are prey to a vast spectrum of Arctic predators, including predatory birds (e.g. snowy owls, *Bubo scandiacus*; rough-legged hawks, *Buteo lagopus*; long-tailed jaegers, *Stercorarius longicaudus*) and mammalian carnivores (e.g. Arctic foxes, *Vulpes lagopus*; red foxes, *Vulpes vulpes*; ermines, *Mustela erminea*). We used specimens stored in the Canadian Museum of Nature's natural history collection and specimens collected on Bylot Island, Nunavut, during recent field studies. They were collected between 1950 and 2010 in Yukon, Nunavut, Northwest Territories and Alaska (Fig. 1).

The collared lemming (*Dicrostonyx groenlandicus*) is the most widespread small rodent of the North American Arctic and can be found from Alaska all the way to Greenland (maximum length and body mass: 162 mm and 118 g; Naughton, 2012). The brown lemming (*Lemmus trimucronatus*) is also

common in both the continental Arctic and the Archipelago but is absent in the northernmost islands (maximum length and mass: 170 mm and 105 g; Naughton, 2012; this study). These two lemming species are the only rodents of the Canadian Arctic Archipelago. The Ungava lemming (*Dicrostonyx hudsonius*) is found in the eastern continental part of the Canadian Arctic (maximum length and mass: 167 mm and 112 g; Naughton, 2012). The meadow vole (*Microtus pennsylvanicus*) is the most widespread species of voles in North America but is only found in continental Arctic, as are all the voles (maximum length and mass: 195 mm and 83 g; Reich, 1981, Naughton, 2012). The tundra vole (*Microtus oeconomus*) and northern red-backed vole (*Myodes rutilus*) are both found in western continental Arctic (maximum length and mass: 187 mm and 69 g and 166 mm and 35 g, respectively; Naughton, 2012).

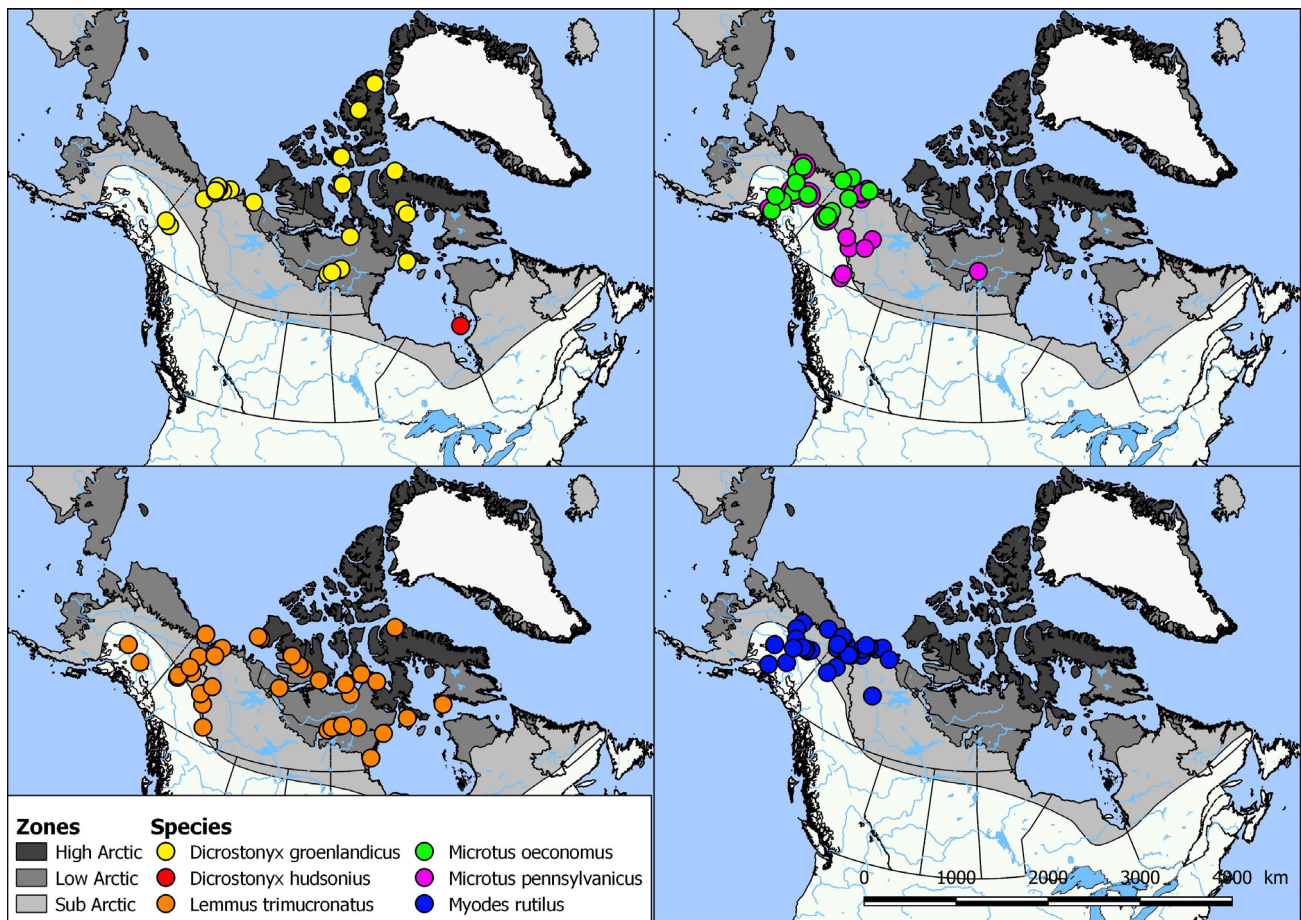
### Mandible size and other measurements

Sample sizes for mandible measurements varied among species: collared lemmings ( $n = 423$ ), brown lemmings ( $n = 523$ ), Ungava lemmings ( $n = 63$ ), meadow voles ( $n = 254$ ), tundra voles ( $n = 297$ ) and northern red-backed voles ( $n = 303$ ). Only specimens for which the body mass was recorded by the collector were selected. We also excluded females noted as pregnant to avoid positive mass bias for females. Indeed, including pregnant females would have penalized the precision for males when estimating their body mass from a general equation developed for all lemmings. Callipers (CD-S15CT, Mitutoyo, Toronto, ON, Canada,) were used to take three dentary bone and one molar tooththrow measurements ( $\pm 0.1$  mm; Fig. 2) on each individual: molar tooththrow socket (MT), ramus–molar tooththrow (RMT), condylo-incisor (CI) and angulo-incisor (AI; Fig. 2). These measurements were selected on the basis of their general availability on mandibles found in pellets of avian predators (Y. Seyer, pers. obs.). In addition, location of capture, and sex were known in most cases.

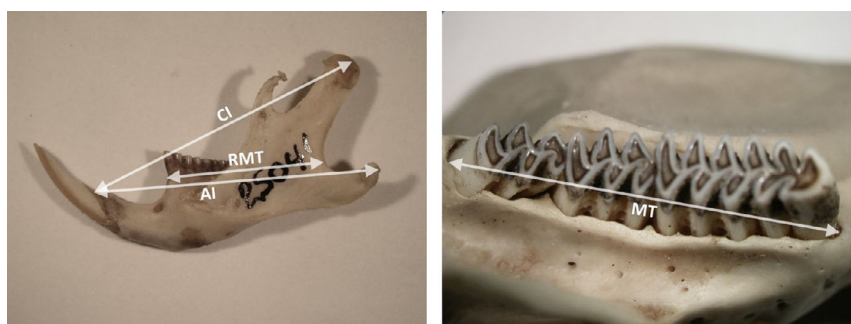
### Statistical analyses

Because growth rate declines with age, we assumed a non-linear relationship between body mass and mandible size. We used generalized linear models with the gamma distribution and a log link to model these relationships. Model fit was assessed visually by plotting studentized residuals against theoretical quantiles and plotting the fitted curve to data points.

We first considered a situation where mandibles were not identified to species. We ran a single model per mandible measurement on our whole data set ( $n = 1863$ ) and report a single goodness-of-fit value ( $R^2$ ) along with the equation and the coefficients to convert mandible values to body mass ( $n_{\text{model}} = 4$ ). Considering that the vast Canadian Arctic Archipelago only has lemmings, we also report equations for situations when only lemmings are present ( $n_{\text{model}} = 4$ ). For the situation where species were identified, we ran one model per species per mandible part ( $n_{\text{model}} = 24$ ). The equations used in these models and the estimated coefficients are provided as tools to convert mandible size to body mass.



**Figure 1** Locations where the specimens used in the relationships between body mass and mandibular measurements were originally collected. Each map shows the distribution of specimens per genus. Upper left: *Dicrostonyx* spp.; upper right: *Microtus* spp.; lower left: *Lemmus trimucronatus*; lower right; *Myodes rutilus*.



**Figure 2** Measurements taken on lemming and vole mandibles. AI, angulo-incisor distance; CI, condylo-incisor distance; RMT, ramus-molar tooththrow distance; MT, molar tooththrow socket length (the measurement is based on the socket, not the teeth).

We tested the effects of two factors that could affect the relationships between body mass and mandibular measurements. First, we examined the effects of location (i.e. territories and state) to determine whether populations from different regions showed differences in their relationship between body

mass and mandible size. We also tested whether this relationship was different between males and females because of sexual dimorphism and body mass of females could be more variable due to pregnancy. The Ungava lemming was excluded from this analysis because our samples only came from the



Belcher Islands, Nunavut, and our sample size was too small to test for an effect of sex. To determine how much variability in the relationship between body mass and mandible size was caused by location or sex, we included them as fixed effects in our generalized linear models. Model selection was conducted on eight candidate models per mandibular measurement with the second-order Akaike's information criterion (AICc). The candidate set included a null model, a model with the mandibular measurement only, and six models with the mandibular measurement and/or sex, location and an interaction between the mandibular measurement and sex or site. The selected top model was the one with the highest support (next model had a  $\Delta\text{AICc} \geq 2$ ) or with the least number of parameters ( $K$ ) among those with a  $\Delta\text{AICc} < 2$ . Because our analyses revealed site-specific relationships between body mass and mandible size for some species (see below), we also ran one model per species per location per mandible part ( $n_{\text{model}} = 48$ ).

## Results

### Relationship between body mass and mandible size

Moderate-to-strong relationships were found between body mass of all small mammal species pooled and mandible size (Fig. 3). The relationship was strongest when using the three dentary bone measurements: CI ( $R^2 = 0.80$ ), RMT ( $R^2 = 0.79$ ) and AI ( $R^2 = 0.77$ ). In contrast, the relationship was weaker when using the tooth measurement MT ( $R^2 = 0.61$ ). Complete equations are presented in Table S1A. Results were similar when using lemmings only ( $R^2 \geq 0.71$ ; Table S1A).

For species-specific analyses, all rodents showed significant (based on 95% confidence interval of slope parameters) relationships between body mass and all four mandibular measurements (Table 1). The strongest relationships were found between mass and CI or AI length in collared and brown lemmings ( $R^2 \geq 0.84$ ) and also tundra and meadow voles ( $R^2 \geq 0.76$ ). Ungava lemmings and northern red-backed voles showed the weakest relationships between mass and CI or AI length ( $R^2$  ranging from 0.57 to 0.72).

The relationship between body mass and RMT was relatively strong for collared and brown lemmings as well as tundra and meadow voles ( $R^2 \geq 0.73$ ), but weak for Ungava lemmings and northern red-backed voles ( $R^2 \leq 0.55$ ). Body mass was weakly related to MT in all small mammal species (Table 1). Equations derived from each model for each species and mandible measurement are presented in Table 1.

### Effects of location and sex

Since MT was weakly related to body mass, we excluded this measurement and focused on the three dentary bone ones for the following results. In general, the most parsimonious models for all dentary bone measurements and species included an effect of location and sex was included in some situations (Table S1B). In collared lemmings, females had lower body mass than males for similar AI and the same effect was found in brown lemmings for RMT but only at large values (i.e.

significant RMT and sex interaction; Table S2B). In meadow voles, however, females were heavier than males for similar CI.

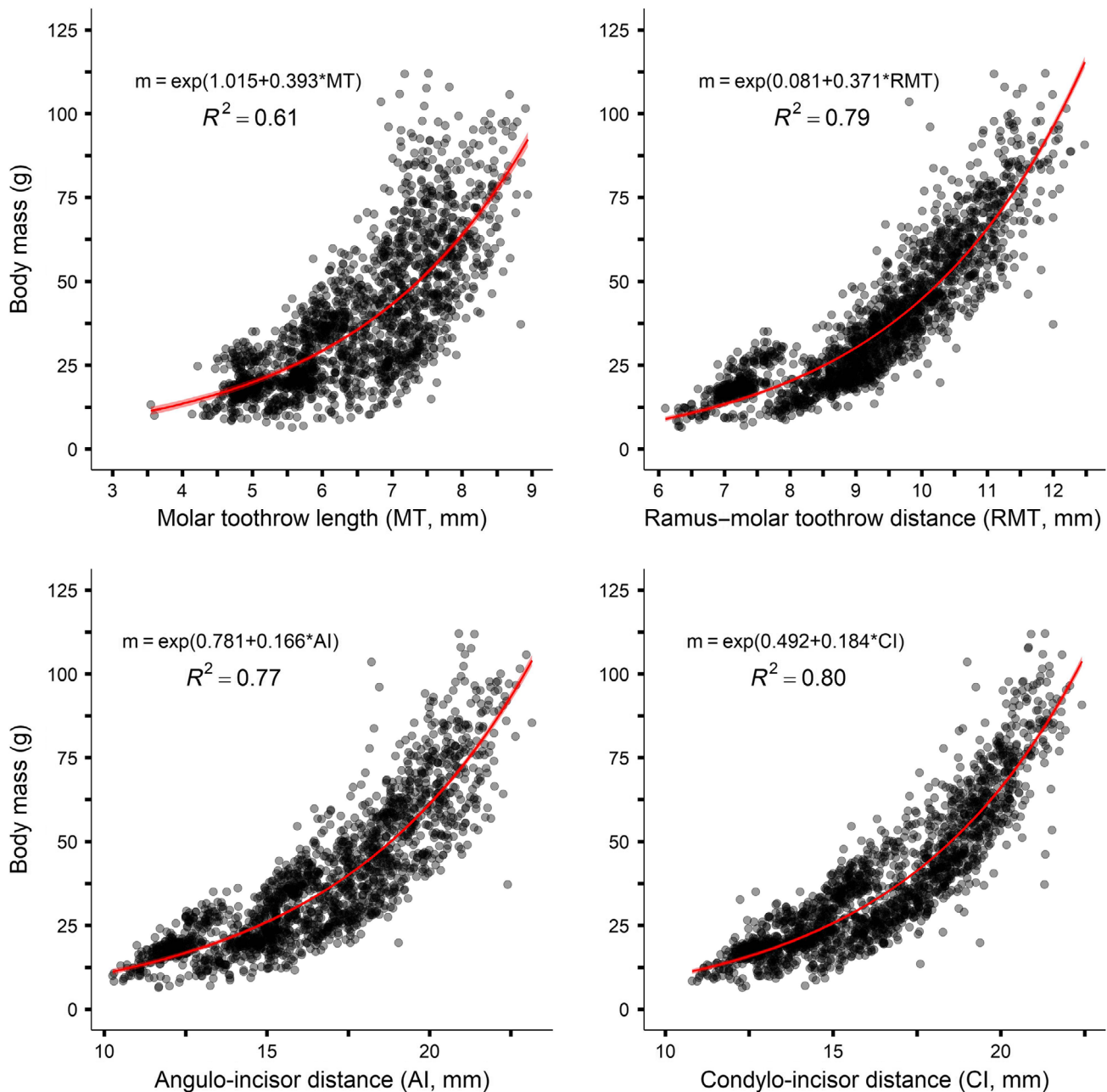
Collared and brown lemmings from Yukon and Alaska generally had larger body mass for similar CI and AI values compared with individuals from Nunavut and Northwest Territories (Fig. 4). Brown lemmings from Yukon and Alaska were also the heaviest for equivalent RMT distances, followed by Nunavut specimens. In tundra voles, individuals generally had larger body masses in Yukon than in other regions with equivalent RMT, CI and AI at small body sizes, but not at large body size (Fig. 5; Table S2B). In Alaska, tundra voles with large CI generally had higher body mass than those from other regions. In meadow voles, individuals from Alaska with short RMT and AI were slightly heavier than at the other sites (Fig. 6). For northern red-backed voles, small-sized individuals from Yukon and Northwest Territories generally had larger body masses compared to those from Alaska with similar CI, AI and RMT, whereas large individuals from the Northwest Territories tended to be lighter (Fig. 7).

Location and species-specific equations derived from the top models to convert mandible size to body mass are presented in Table S3B.

## Discussion

Our results demonstrate that estimates of body mass of consumed rodent prey can be obtained from the size of their mandible with relatively high precision, especially for lemmings and *Microtus* voles. However, our results also show that the individual variability can still be quite high, especially at large mandible sizes due to factors such as sex, site and potentially reproductive condition that we could not consider here. We found that the longest mandibular measurements, being here CI and AI measurements (Fig. 2), offered the most precise estimates. However, considering that bones can be damaged during gastric degradation, it is encouraging that the RMT measurement was also highly reliable in most cases. According to a related study conducted on Bylot Island, Nunavut (Y. Seyer, G. Gauthier, D. Fauteux, and J.-F. Therrien, unpublished data), the RMT length could be measured on most mandibles collected from pellets of rough-legged hawks (97%,  $n = 169$ ), long-tailed jaegers (81%,  $n = 315$ ) and snowy owls (83%,  $n = 317$ ), compared with the CI (respectively, 75%, 70% and 70%) and AI (respectively, 28%, 46% and 50%). Although molar tooththrows have been reported to grow continually during the life span of small mammals (Lidicker & MacLean, 1969), it was a poor proxy for body mass indicating high inter-individual variability in its growth. This relatively low reliability was also observed in other small rodents in temperate forests (Pagels & Blem, 1984). Molar tooththrow length is not recommended as being used as a proxy for indicating individual body mass, therefore will no longer be discussed.

Models pooling all species for individuals where species cannot be identified or location is unknown performed relatively well. When focusing specifically on the Canadian Arctic Archipelago, where only lemmings are present, we found that the angulo-incisor distance was the best proxy for body mass



**Figure 3** Relationship between body mass ( $m$ ) and four mandibular measurements of six Arctic small rodents pooled together. The curve was fitted with a non-linear model using the gamma distribution and a log link. The resulting equations are shown with their associated  $R^2$ .

compared with the other measurements, owing to a similar relationship in both lemming species. However, applying equations based on pooled species across the Arctic must be done with care because the relationship between body mass and dentary bone size differed between several species, as shown by the different coefficients obtained in the species-specific equations of Table 1. Failing to identify the species may lead to biased estimations of body mass in some situations. For instance, body mass of red-backed voles would be

underestimated due to their generally higher body mass for a similar size compared with lemmings, whereas body mass for lemmings would be overestimated. Therefore, we suggest that identification keys should be used to identify skull parts to determine the species that each mandible found belongs to. In Appendix S1, we present an illustrated identification key to mandibles of *Dicrostonyx*, *Lemmus*, *Microtus* and *Myodes* based on characteristics used in the literature to differentiate them (Naughton, 2012; Cadieux, Fauteux & Gauthier, 2015).

**Table 1** Relationships between body mass (m) and four mandibular measurements in six small arctic rodent species

Species	Measurement	Equation	95% c.i.	R <sup>2</sup>	n
<i>Dicrostonyx groenlandicus</i>	MT	$m = \exp(-1.070 + 0.700*MT)$	[0.650, 0.751]	0.61	488
	RMT	$m = \exp(-0.566 + 0.441*RMT)$	[0.422, 0.460]	0.79	478
	AI	$m = \exp(-0.924 + 0.262*AI)$	[0.252, 0.272]	0.85	473
	CI	$m = \exp(-1.248 + 0.273*CI)$	[0.262, 0.284]	0.84	506
<i>Dicrostonyx hudsonius</i>	MT	$m = \exp(0.270 + 0.556*MT)$	[0.390, 0.720]	0.40	63
	RMT	$m = \exp(1.090 + 0.287*RMT)$	[0.218, 0.355]	0.55	63
	AI	$m = \exp(0.352 + 0.196*AI)$	[0.151, 0.241]	0.57	63
	CI	$m = \exp(-0.126 + 0.215*CI)$	[0.169, 0.260]	0.60	63
<i>Lemmus trimucronatus</i>	MT	$m = \exp(-1.740 + 0.723*MT)$	[0.683, 0.762]	0.72	492
	RMT	$m = \exp(-0.993 + 0.473*RMT)$	[0.453, 0.493]	0.81	521
	AI	$m = \exp(-0.930 + 0.246*AI)$	[0.236, 0.255]	0.85	486
	CI	$m = \exp(-1.148 + 0.272*CI)$	[0.261, 0.282]	0.85	489
<i>Microtus oeconomus</i>	MT	$m = \exp(-1.240 + 0.802*MT)$	[0.719, 0.885]	0.57	293
	RMT	$m = \exp(-1.585 + 0.531*RMT)$	[0.495, 0.565]	0.76	296
	AI	$m = \exp(-1.279 + 0.302*AI)$	[0.284, 0.320]	0.79	289
	CI	$m = \exp(-1.459 + 0.321*CI)$	[0.301, 0.341]	0.82	271
<i>Microtus pennsylvanicus</i>	MT	$m = \exp(-2.060 + 0.913*MT)$	[0.813, 1.014]	0.58	250
	RMT	$m = \exp(-2.007 + 0.589*RMT)$	[0.545, 0.632]	0.73	253
	AI	$m = \exp(-2.029 + 0.354*AI)$	[0.330, 0.378]	0.78	239
	CI	$m = \exp(-2.000 + 0.356*CI)$	[0.328, 0.385]	0.76	237
<i>Myodes rutilus</i>	MT	$m = \exp(0.511 + 0.506*MT)$	[0.372, 0.638]	0.21	298
	RMT	$m = \exp(-1.654 + 0.639*RMT)$	[0.585, 0.692]	0.65	303
	AI	$m = \exp(-0.756 + 0.303*AI)$	[0.281, 0.326]	0.72	294
	CI	$m = \exp(-0.870 + 0.298*CI)$	[0.272, 0.323]	0.66	292

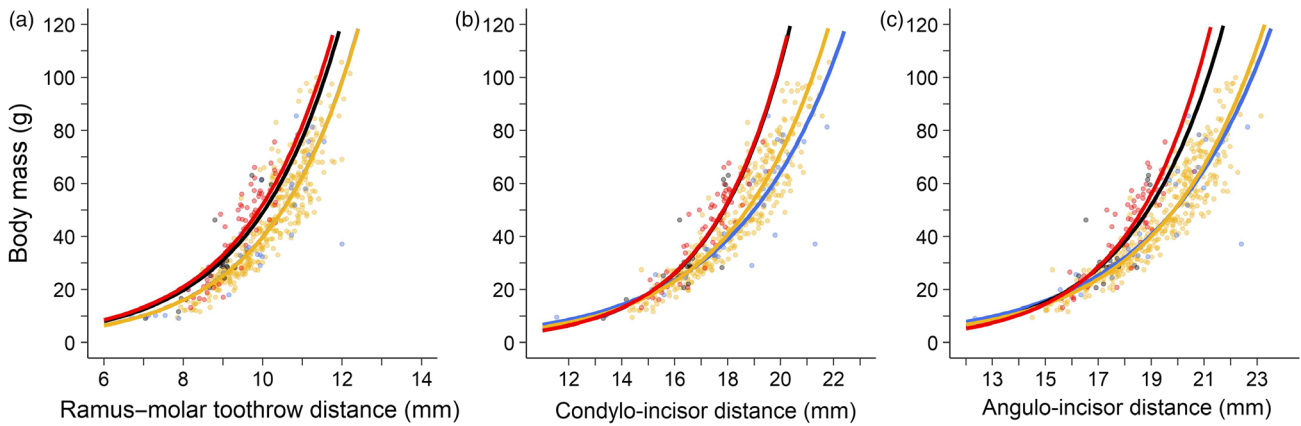
Mandibular measurements are the molar tooththrow socket length (MT), the ramus–molar tooththrow distance (RMT), the angulo-incisor distance (AI) and the condylo-incisor distance (CI).

Equations for each relationship are shown along with the 95% confidence intervals of the slope parameter (c.i.) and the R<sup>2</sup>.

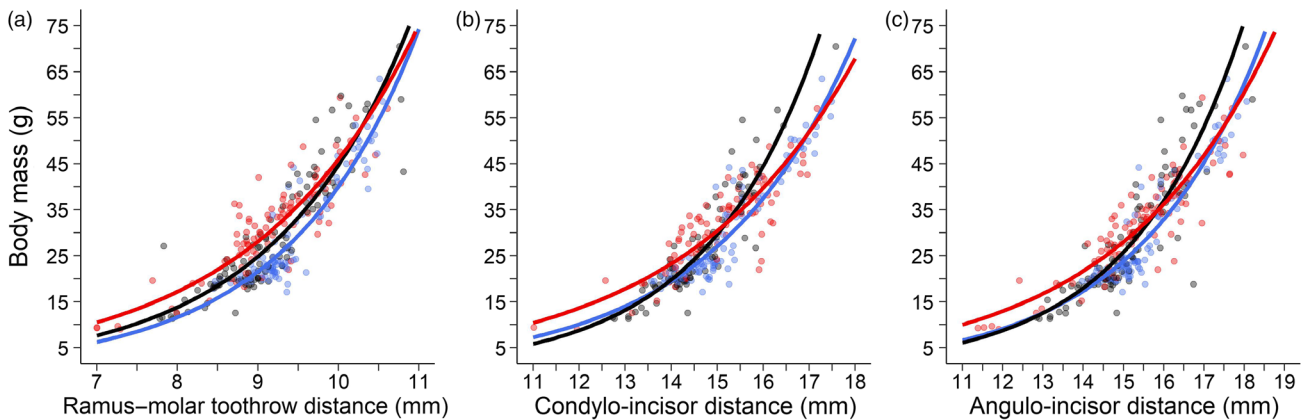
Relationship between body mass and mandible size often varied among locations, which suggests potential genetic differentiation or local environmental effects, or an interaction between both through epigenetics on body growth. Yukon and Alaska populations of brown lemmings were generally of higher body mass for similar mandible size compared with lemmings from elsewhere. This may be related to higher primary productivity in that region (boreal and subarctic vs. low and high Arctic), but more studies are needed to clarify this. It is important to note that for all the species covered, especially voles, we did not cover their entire geographical distribution. However, by focusing on voles captured in their northernmost distribution, we have reduced the amount of latitudinal differentiation potentially caused by the increasing productivity in boreal and temperate biomes (Hansen & Boonstra, 2000). The average body mass of small rodents has been shown to be dependent on the phase of the population fluctuation (e.g. peak vs. low abundance years), which is a factor that we could not control because Museum specimens are rarely associated with information on population dynamics (Krebs, 1964; Gilg, 2002; Fauteux, Gauthier & Berteaux, 2015). However, the higher body mass observed in years of high abundance is often found in parallel with high survival compared to low abundance years (Agrell *et al.*, 1992; Wilson *et al.*, 1999), which suggests that the average body mass of the population is increased by the presence of a higher proportion of old individuals and not because of a different relationship between mass and size.

For most species and mandible measurements, relationships between body mass and mandible size did not differ between sexes, which are not surprising due to the exclusion of known pregnant females from our analyses and the general lack of sexual dimorphism in body size in Arctic lemmings and voles (Naughton, 2012). However, in both lemming species there was a tendency for males to be heavier than females of similar size, especially in larger individuals. This sexual dimorphism may be underlined by a competitive mechanism where males reach higher mass of muscles and reproductive organs than females, which confer them a dominant status when competing for females, especially in older individuals (Huck, Banks & Wang, 1986; Schmidt *et al.*, 2012).

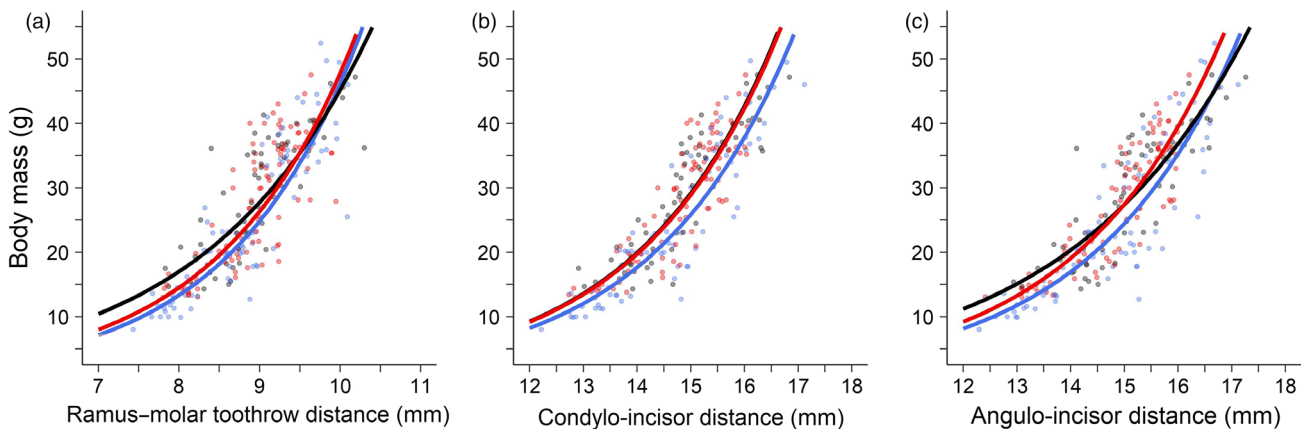
Several studies conducted outside the Arctic have shown that bone remains in regurgitation pellets are useful to assess the diet of predators with high precision. However, care must be taken due to the potential overrepresentation of mammals compared with birds (Hamilton & Neill, 1981; Simmons, Avery & Avery, 1991; Redpath *et al.*, 2001). Estimating biomass consumed using averaged body mass of prey species (e.g. Petty, 1999; Marchesi, Paolo & Sergio, 2002; Balčiauskienė *et al.*, 2006) may hide important information on a predator diet and may cause over- or underestimation of total biomass consumed per species. Resource partitioning among predators may occur not only on the basis of species consumed, but also on the basis of prey size within the same species. Goszczyński (1977) reported that birds of prey fed in a higher proportion on large common voles (*Microtus arvalis*) than mustelids and foxes in agricultural



**Figure 4** Relationship between body mass and the ramus–molar tooththrow (a), condylar–incisor (b) and angulo–incisor (c) distance for brown lemmings in Yukon (red), Nunavut (yellow), Alaska (black) and Northwest Territories (blue). The curve was fitted with a non-linear model using the gamma distribution and a log link.

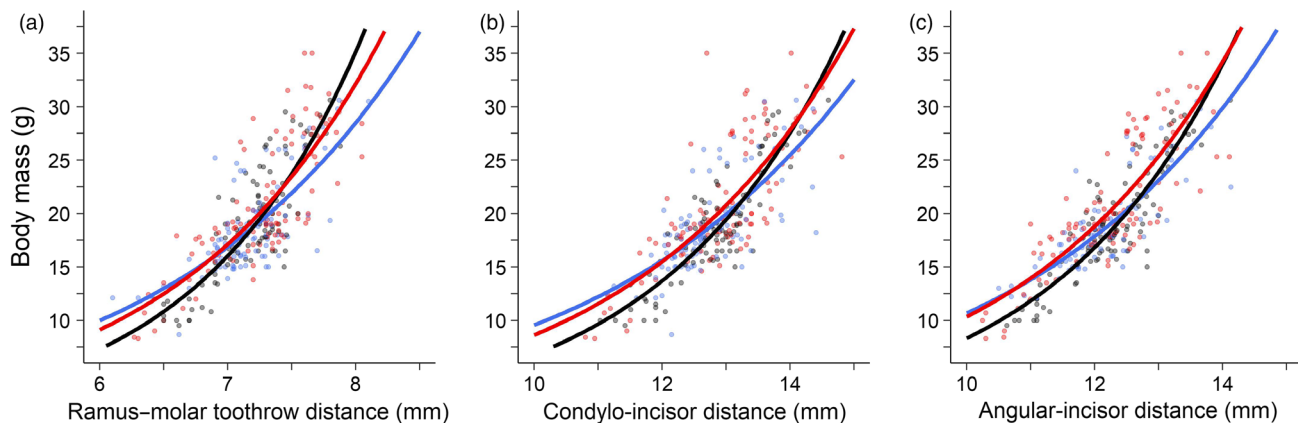


**Figure 5** Relationship between body mass and the ramus–molar tooththrow (a), condylar–incisor (b) and angulo–incisor (c) distances for tundra voles in Yukon (red), Alaska (black) and Northwest Territories (blue). The curve was fitted with a non-linear model using the gamma distribution and a log link.



**Figure 6** Relationship between body mass and the ramus–molar tooththrow (a), condylar–incisor (b) and angulo–incisor (c) distances for meadow voles in Yukon (red), Alaska (black) and Northwest Territories (blue). The curve was fitted with a non-linear model using the gamma distribution and a log link.





**Figure 7** Relationship between body mass and the ramus–molar tooththrow (a), condylar–incisor (b) and angular–incisor (c) distances for northern red-backed voles in Yukon (red), Alaska (black) and Northwest Territories (blue). The curve was fitted with a non-linear model using the gamma distribution and a log link.

habitats of western Poland, owing to the inaccessibility of young voles remaining in burrows. Similarly, Ashmole (1968) suggested that tropical terns achieved sympatry due to ecological segregation based on the body size of fish and squids that they eat. Determining prey species as well as prey mass can provide a better understanding of exchanges in biomass within food webs and quantifying energy fluxes (Legagneux *et al.*, 2012; Barnes *et al.*, 2018).

In conclusion, we provide equations to estimate body mass of several arctic small rodents based on mandible size for situations where species and location are known or not. When available and undamaged, the AI or CI distances will lead to the most precise estimates of body mass, but when unavailable, the RMT distance can also be used with high confidence in most cases. Using species-specific relationships will also improve body mass estimation. Because of geographical variations, we recommend establishing equations for populations not considered in this work. Precision of mass estimates is also affected by seasonal variations and frequency of pregnancy. Limiting sampling to a single season should eliminate the first issue but one must accept some inherent problems inherent to using mandibles, which currently does not allow identification of sex of the consumed prey. Thus, maximizing sample size is the main solution for these issues. Estimating the body mass of rodent prey from measurements of mandibles found in pellets allows a precise quantification of resource partitioning among predators and how biomass is transferred across trophic levels in food webs. This is especially important in situations where many large (e.g. foxes, owls, hawks and gulls) and small predators (e.g. jaegers and ermines) share only a few, often one or two, main prey species, as often is the case in the Arctic food web.

## Acknowledgements

We thank Annabelle Boudreault for her work with the specimens at the Canadian Museum of Nature. Collection of specimens on Bylot Island relied on the logistic assistance of the Polar Continental Shelf Program (Natural Resources Canada).

The research was funded by Polar Knowledge Canada, the Natural Sciences and Engineering Research Council of Canada (Discovery Grants and Frontiers to Discovery programmes), the Northern Student Training Program of Indigenous and Northern Affairs Canada, and the Canadian Network of Centres of Excellence ArcticNet.

## References

- Agrell, J., Erlinge, S., Nelson, J. & Sandell, M. (1992). Body weight and population dynamics: cyclic demography in a noncyclic population of the field vole (*Microtus agrestis*). *Can. J. Zool.* **70**, 494–501.
- Ashmole, P.N. (1968). Body size, prey size, and ecological segregation in five sympatric tropical terns (Aves: Laridae). *Syst. Biol.* **17**, 292–304.
- Balčiauskienė, L., Jovaišas, A., Naruševičius, V., Petraška, A. & Skuja, S. (2006). Diet of Tawny owl (*Strix aluco*) and Long-eared owl (*Asio otus*) in Lithuania as found from pellets. *Acta Zool. Lituanica* **16**, 37–45.
- Barnes, A.D., Jochum, M., Lefcheck, J.S., Eisenhauer, N., Scherber, C., O'Connor, M.I., de Ruiter, P. & Brose, U. (2018). Energy flux: the link between multitrophic biodiversity and ecosystem functioning. *Trends Ecol Evol* **33**, 186–197.
- Batzli, G.O. & Esseks, E. (1992). Body fat as an indicator of nutritional condition for the brown lemming. *J. Mammal.* **73**, 431–439.
- Bauer, S. & Hoye, B.J. (2014). Migratory animals couple biodiversity and ecosystem functioning worldwide. *Science* **344**, 1242552.
- Buidin, C., Rochepault, Y. & Savard, J.P.L. (2007). Régime alimentaire de la Nyctale de Tengmalm en Minganie durant la nidification. *Naturaliste Can.* **131**, 28–33.
- Cadieux, M.-C., Fauteux, D. & Gauthier, G. (2015). *Technical manual for sampling small mammals in the Arctic – version 1*. Centre d'Études Nordiques. Québec: Université Laval.



- Carraway, L.N. (1995). *A key to recent Soricidae of western United States and Canada based primarily on dentaries*. Lawrence: Museum of Natural History, The University of Kansas.
- Cohen, J.E., Jonsson, T. & Carpenter, S.R. (2003). Ecological community description using the food web, species abundance, and body size. *Proc. Natl Acad. Sci.* **100**, 1781–1786.
- Collopy, M.W. (1983). A comparison of direct observations and collections of prey remains in determining the diet of golden eagles. *J. Wildl. Manage.* **47**, 360–368.
- Fauteux, D., Lupien, G., Fabianek, F., Gagnon, J., Séguy, M. & Imbeau, L. (2014). An illustrated key to the mandibles of small mammals of eastern Canada. *Can. Field-Nat.* **128**, 25.
- Fauteux, D., Gauthier, G. & Berteaux, D. (2015). Seasonal demography of a cyclic lemming population in the Canadian Arctic. *J. Anim. Ecol.* **84**, 1412–1422.
- Gilg, O. (2002). The summer decline of the collared lemming, *Dicrostonyx groenlandicus*, in high arctic Greenland. *Oikos* **99**, 499–510.
- Gilg, O., Hanski, I. & Sittler, B. (2003). Cyclic dynamics in a simple vertebrate predator-prey community. *Science* **302**, 866–868.
- Glass, B.P. & Thies, M.L. (1997). *A key to the skulls of North American mammals*, 3rd edn. Huntsville, Texas: Sam Houston State University.
- Goszczyński, J. (1977). Connections between predatory birds and mammals and their prey. *Acta. Theriol.* **22**, 399–430.
- Gravel, D., Guichard, F., Loreau, M. & Mouquet, N. (2010). Source and sink dynamics in meta-ecosystems. *Ecology* **91**, 2172–2184.
- Hamilton, K.L. & Neill, R.L. (1981). Food habits and bioenergetics of a pair of Barn owls and owlets. *Am. Midl. Nat.* **106**, 1–9.
- Hansen, T.F. & Boonstra, R. (2000). The best in all possible worlds? A quantitative genetic study of geographic variation in the meadow vole, *Microtus pennsylvanicus*. *Oikos* **89**, 81–94.
- Hanski, I., Henttonen, H., Korpimäki, E., Oksanen, L. & Turchin, P. (2001). Small-rodent dynamics and predation. *Ecology* **82**, 1505–1520.
- Hartman, K.J. & Brandt, S.B. (2018). Trophic resource partitioning, diets, and growth of sympatric estuarine predators. *Trans. Am. Fish. Soc.* **124**, 520–537.
- Hayward, G.D. & Garton, E.O. (1988). Resource partitioning among forest owls in the River of No Return Wilderness, Idaho. *Oecologia* **75**, 253–265.
- Huck, U.W., Banks, E.M. & Wang, S.-C. (1986). Behavioral and physiological correlates of aggressive dominance in male brown lemmings (*Lemmus sibiricus*). *Aggress. Behav.* **12**, 139–148.
- Krebs, C.J. (1964). The lemming cycle at Baker Lake, Northwest Territories, during 1959–1962. *Arctic*. **15**, 1–104.
- Legagneux, P., Gauthier, G., Berteaux, D., Bêty, J., Cadieux, M.-C., Bilodeau, F., Bolduc, E., McKinnon, L., Tarroux, A., Therrien, J.-F., Morissette, L. & Krebs, C.J. (2012). Disentangling trophic relationships in a High Arctic tundra ecosystem through food web modeling. *Ecology* **93**, 1707–1716.
- Lidicker, W.Z. & MacLean, S.F. (1969). A method for estimating age in the California vole, *Microtus californicus*. *Am. Midl. Nat.* **82**, 450–470.
- Marchesi, L., Paolo, P. & Sergio, F. (2002). Biases associated with diet study methods in the Eurasian eagle-owl. *J. Raptor Res.* **36**, 11–16.
- Marti, C.D. (1976). A review of prey selection by the Long-Eared Owl. *Condor* **78**, 331–336.
- Maser, C. & Brodie, E.D. (1966). A study of owl pellet contents from Linn, Benton and Polk Counties, Oregon. *Murrelet* **47**, 9–14.
- Myers, J.H. (2018). Population cycles: generalities, exceptions and remaining mysteries. *Proc. R. Soc. B: Biol. Sci.* **285**, 20172841.
- Naughton, D. (2012). *The natural history of Canadian mammals*. Toronto: University of Toronto Press.
- Oksanen, L. & Oksanen, T. (2000). The logic and realism of the hypothesis of exploitation ecosystems. *Am. Nat.* **155**, 703–723.
- Pagels, J.F. & Blem, C.R. (1984). Prediction of body weights of small mammals from skull measurements. *Acta. Theriol.* **29**, 367–387.
- Petty, S.J. (1999). Diet of tawny owls (*Strix aluco*) in relation to field vole (*Microtus agrestis*) abundance in a conifer forest in northern England. *J. Zool.* **248**, 451–465.
- Redpath, S.M., Clarke, R., Madders, M. & Thirgood, S.J. (2001). Assessing raptor diet: comparing pellets, prey remains, and observational data at hen harrier nests. *Condor* **103**, 184–188.
- Reich, L.M. (1981). *Microtus pennsylvanicus*. *Mamm. Species* **159**, 1–8.
- Reuman, D.C. & Cohen, J.E. (2005). Estimating relative energy fluxes using the food web, species, abundance, and body size. *Adv. Ecol. Res.* **36**, 137–182.
- Schmidt, N.M., Ims, R.A., Høye, T.T., Gilg, O., Hansen, L.H., Hansen, J., Lund, M., Fuglei, E., Forchhammer, M.C. & Sittler, B. (2012). Response of an arctic predator guild to collapsing lemming cycles. *Proc. R. Soc. B: Biol. Sci.* **279**, 4417–4422.
- Simmons, R.E., Avery, D.M. & Avery, G. (1991). Biases in diets determined from pellets and remains: correction factors for a mammal and bird-eating raptor. *J. Raptor Res.* **25**, 63–67.
- Tarroux, A., Bêty, J., Gauthier, G. & Berteaux, D. (2012). The marine side of a terrestrial carnivore: intra-population variation in use of allochthonous resources by arctic foxes. *PLoS One* **7**, e42427.
- Therrien, J.-F., Gauthier, G. & Bêty, J. (2011). An avian terrestrial predator of the Arctic relies on the marine ecosystem during winter. *J. Avian Biol.* **42**, 363–369.
- Wiens, J.D., Anthony, R.G. & Forsman, E.D. (2014). Competitive interactions and resource partitioning between

northern spotted owls and barred owls in western Oregon.

*Wildl. Monogr.* **185**, 1–50.

Wilson, D.J., Krebs, C.J. & Sinclair, A.R.E. (1999). Limitation of collared lemming populations during a population cycle.

*Oikos* **87**, 382–398.

## Supporting Information

Additional Supporting Information may be found in the online version of this article:

**Figure S1.** Labial side of the left mandible of *M. oeconomus* (A), *M. pennsylvanicus* (B), *M. rutilus* (C), *L. trimucronatus* (D) and *D. groenlandicus* (E), showing the coronoid process (cor) condylar process (con) and the angular process (ang). *D. hudsonius* is not shown due to its resemblance with *D. groenlandicus*. Arrows numbered as 1 indicate the notches (dotted polygons) between each process, whereas the arrow numbered as 2 indicate posterior extension of the condylar process. Orientation of pictures: anterior, left; posterior, right; labial, top; lingual, bottom.

**Figure S2.** Occlusal patterns of mandibular molar tooththrows of *M. oeconomus* (A), *M. pennsylvanicus* (B), *M. rutilus* (C), *L. trimucronatus* (D) and *D. groenlandicus* (E). *D. hudsonius* is not shown due to its resemblance with *D. groenlandicus*. Closed triangles of m1 are numbered on each picture (1–7). Orientation of pictures: anterior, right; posterior, left; labial, top; lingual, bottom.

**Table S1A.** Relationships between body mass (m) and four mandibular measurements of six small arctic rodents for the North American continental Arctic (voles and lemmings species pooled), and of lemmings of the Arctic Archipelago only (two species pooled). Mandibular measurements are the molar tooththrow socket length (MT), the ramus–molar tooththrow

distance (RMT), the angulo-incisor distance (AI) and the condylo-incisor distance (CI). Equations for each relationship are shown along with the 95% confidence intervals (c.i.) of the slope parameter and the  $R^2$ .

**Table S2A.** Model selection for the relationship between body mass and mandible size of six small arctic rodents considering sex and location as covariates. Only models with  $\Delta\text{AICc} < 4$  and the following one are shown. Dentary bone measurements are the ramus–molar tooththrow distance (RMT), the angulo-incisor distance (AI) and the condylo-incisor distance (CI). The selected model for each analysis is underlined.

**Table S2B.** Effects of location and sex on the relationship between body mass and three mandibular measurements of six small arctic rodents. Covariates with no information (-) were not included in the most parsimonious model that was selected (Appendix B, Table S1B). In these analyses, males were used as the reference factor for the sex effect and Alaska was used as the reference factor for comparisons with Nunavut (NU), Yukon (YU) and Northwest Territories (NWT). The slope parameters along with their 95% c.i. are shown. Coefficients and their respective 95% c.i. are indicated in bold when the c.i. excludes 0.

**Table S2C.** Region-specific relationships between body mass (m) and three dentary bone measurements for five rodent species. Dentary bone measurements are the ramus–molar tooththrow distance (RMT), the angulo-incisor distance (AI) and the condylo-incisor distance (CI). Regions are Yukon (YU), Northwest Territories (NWT), Nunavut (NU) and Alaska (AL). Equations for each relationship are shown along with the 95% confidence interval (c.i.) of the slope parameter and the  $R^2$ .

**Appendix S1.** Illustrated key to mandibles of Arctic small rodents.