

Latitudinal variation in snowshoe hare (*Lepus americanus*) body mass: a test of Bergmann's rule

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Abstract: The relationship between body size and latitude has been the focus of dozens of studies across many species. However, results of testing Bergmann's rule — that organisms in colder climates or at higher latitudes possess larger body sizes — have been inconsistent across studies. We investigated whether snowshoe hares (*Lepus americanus* Erxleben, 1777) follow Bergmann's rule by investigating differences in body mass using data from six published studies and from data of 755 individual hares captured from 10 populations across North America covering 26° of north latitude. We also explored alternative hypotheses related to variation in hare body mass, including winter severity, length of growing season, elevation, and snow depth. We found body mass of hares varied throughout their range, but the drivers of body mass differed based on geographic location. In northern populations, females followed Bergmann's rule, whereas males did not. In northern populations, male mass was related to mean snow depth. In contrast, in southern populations, body mass of both sexes was related to length of the growing season. These differences likely represent variation in the drivers of selection. Specifically, in the north, a large body size is beneficial to conserve heat because of low winter temperatures, whereas in the south, it is likely due to increased food supply associated with longer growing seasons.

Key words: snowshoe hare, *Lepus americanus*, latitudinal variation, energy expenditure, food supply, winter, snow depth, growing season.

Résumé : Le lien entre la taille du corps et la latitude a fait l'objet de dizaines d'études portant sur de nombreuses espèces. Les résultats des études visant à valider la règle de Bergmann, qui stipule que les organismes vivant en climat plus froid ou à plus haute altitude auraient des corps de plus grandes tailles, ne sont pas cohérents d'une étude à l'autre. Nous avons vérifié si les lièvres d'Amérique (*Lepus americanus* Erxleben, 1777) suivaient la règle de Bergmann en examinant les différences de masse corporelle dans des données de six études publiées et pour 755 lièvres capturés de 10 populations réparties à la grandeur de l'Amérique du Nord, sur un territoire couvrant 26° de latitude nord. Nous avons aussi examiné différentes hypothèses concernant les variations de la masse corporelle de lièvres, touchant notamment à la rigueur de l'hiver, la durée de la période végétative, l'altitude et l'épaisseur de la neige. Nous avons constaté que la masse corporelle des lièvres varie dans toute leur aire de répartition, mais que les facteurs qui l'influencent diffèrent selon l'endroit. Dans les populations nordiques, les femelles suivent la règle de Bergmann, mais non les mâles. Dans les populations nordiques, la masse des mâles est reliée à l'épaisseur moyenne de la neige, alors que dans les populations méridionales, la masse corporelle des deux sexes est reliée à la durée de la période végétative. Ces différences représentent vraisemblablement des variations des facteurs influant sur la sélection. Plus précisément, au nord, une grande taille du corps est utile parce qu'elle facilite la conservation de chaleur pour faire face aux

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faibles températures hivernales, alors que dans le sud, elle est probablement due à un meilleur approvisionnement en nourriture associé à des périodes végétatives plus longues. [Traduit par la Rédaction]

Mots-clés : lièvre d'Amérique, *Lepus americanus*, variation latitudinale, dépense énergétique, approvisionnement en nourriture, hiver, épaisseur de la neige, période végétative.

Introduction

Latitudinal variation in body size is a phenomenon common across many taxa (McNab 1971; Ashton et al. 2000; Meiri and Dayan 2003). In particular, Bergmann's rule states that, within a species or clade, body mass is greater in cold climates, which leads to latitudinal clines in body mass (Bergmann 1847). Individuals with a larger body size possess a smaller surface area to volume ratio, resulting in reduced rates of relative heat loss. This is advantageous for endotherms because it allows for survival at a lower critical temperature (Brown et al. 2004). Bergmann's rule has been supported within geographically distinct populations of mammals, (e.g., packrats, genus *Neotoma* Say and Ord, 1825; Brown and Lee 1969; elk, *Cervus elaphus* Linnaeus, 1758; Langvatn and Albon 1986; bobcat, *Lynx rufus* (Schreber, 1777); Wigginton and Dobson 1999) and birds (e.g., Singing Honeyeater, *Meliphaga virescens* Vieillot, 1817 = *Gavicalis virescens* (Vieillot, 1817); Wooller et al. 1985; Eurasian Sparrowhawk, *Accipiter nisus* (Linnaeus, 1758); Wyllie and Newton 1994; Cerulean Warbler, *Dendroica cerulea* (A. Wilson, 1810) = *Setophaga cerulea* (A. Wilson, 1810); Jones et al. 2005). However, Bergmann's rule has not been found in other species (e.g., coyote, *Canis latrans* Say, 1823; Thurber and Peterson 1991; Eurasian Blackcap, *Sylvia atricapilla* (Linnaeus, 1758); Telleria and Carbonell 1999; brown bear, *Ursus arctos* Linnaeus, 1758; Kojola and Laitala 2001). In a meta-analysis of birds and mammals, Meiri and Dayan (2003) found that 72% of bird species and 65% of mammal species conformed to Bergmann's rule.

However, factors that might be correlated with latitude, such as food availability, may override the importance of heat conservation in driving within-species geographic body size variation (Lindstedt and Boyce 1985; Millar and Hickling 1990). In New World deer (Cervidae), Geist (1987) found the largest individuals occurred in populations at middle latitudes where forage was available for the longest time period, with smaller bodied individuals occurring at the highest and lowest latitudes. Similarly, Erlinge (1987) found the European stoat or ermine (*Mustela erminea* Linnaeus, 1758) exhibited body size variation in relation to prey size and availability, rather than latitude. As such, patterns of body size in relation to food availability are likely indirectly correlated with environmental factors such as length of growing season, rainfall, or net primary productivity, which in turn influences forage and prey availability (McNab 2010; Huston and Wolverton 2011). In addition, research has suggested animals with larger surface area to volume ratios might not reduce heat loss as expected, and larger animals might be at a disadvantage in cold climates when resources are limited (McNab 1971), which has led to some small mammals reducing their body size in winter (Dehnel's phenomena; Speakman 1996; Lovegrove 2005). Bergmann's rule has also been criticized for being overly simplistic, and only considering energetic costs of larger body sizes, while ignoring the greater capacity for energy gains associated with larger size (Speakman 1996). Support for Bergmann's rule has been inconsistent and latitudinal gradients in body size may be driven by alternative mechanisms. However, understanding drivers of these relationships is complicated by differences in measurement techniques across studies.

Snowshoe hares (*Lepus americanus* Erxleben, 1777) are an ideal species to test Bergmann's rule because they have a broad geographic range that spans both a latitudinal gradient from 36°N to 68°N and a broad temperature gradient. Additionally, they do not hibernate and are nocturnal. Consequently, they experience the

coldest winter conditions. Previous research on morphometric differences in snowshoe hare populations suggested that hares were structurally larger in eastern North America, Alaska (USA), and northwestern Canada, and smallest in the Pacific Northwest (Nagorsen 1985). However, as this previous study relied on cranial measurements from shot or snared museum specimens, it was not an ideal test of Bergmann's rule because conformity to Bergmann's rule may be dependent on the size metric used (Meiri and Dayan 2003). We combine published body mass data from live-trapped hares from 6 sites across their geographic range with raw capture data from 10 sites (also from live-trapped hares) to assess whether snowshoe hares conform to Bergman's rule. As an alternative hypothesis, we also tested whether snowshoe hare body mass may be more strongly predicted by temperature (degree-days), length of growing season, elevation, or snow depth.

Materials and methods

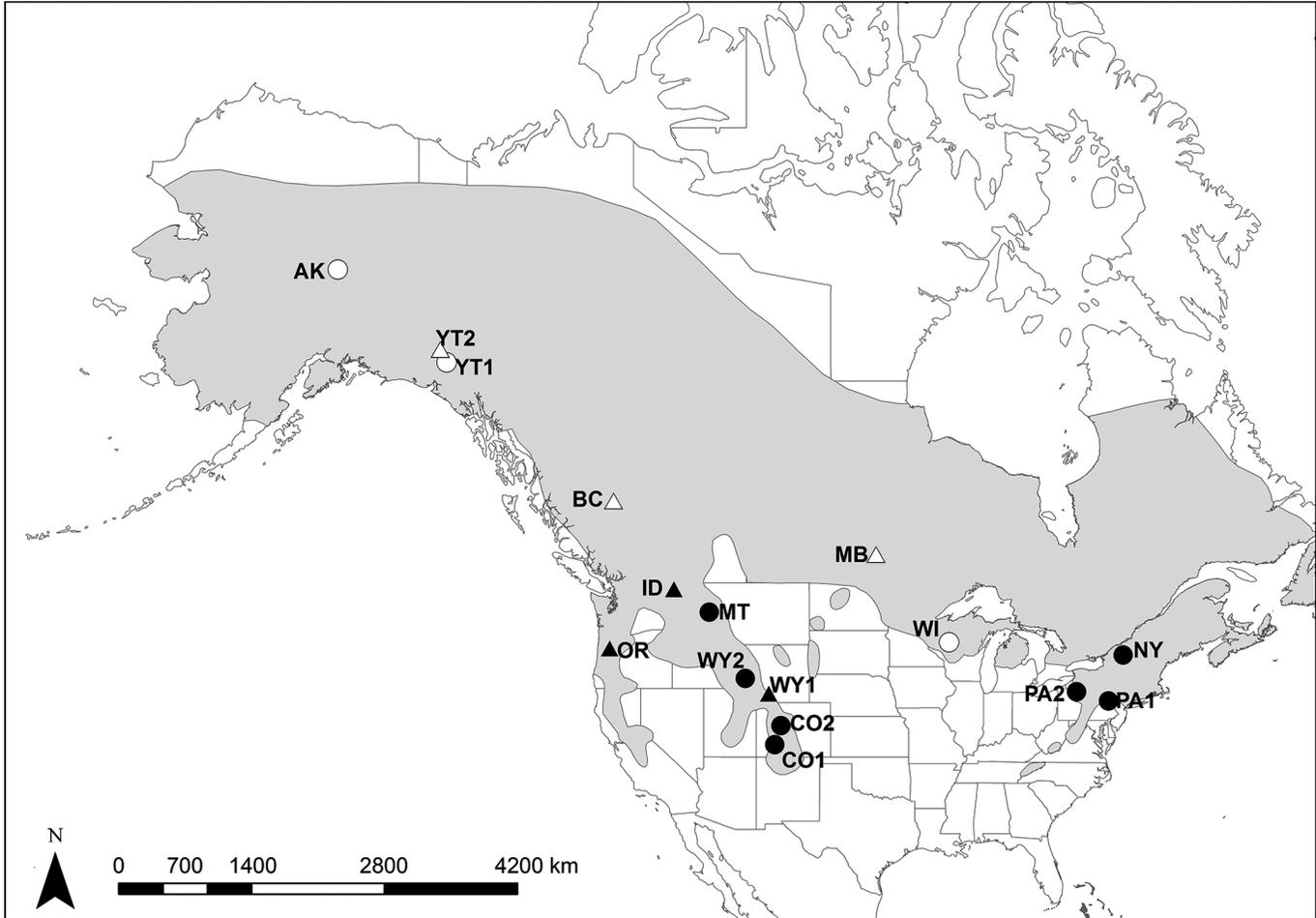
Published body mass data

Through a literature search using Google Scholar® in April 2017 with terms “snowshoe hare” or “varying hare” and “body weight” or “body mass” or “capture” or “trap”, we compiled winter body mass data across the geographic range of snowshoe hares. We limited our analysis to data collected on hares from December to March to exclude bias from pregnant females, and we excluded any studies in which male and female masses were pooled. Because postmortem treatment of carcasses could affect desiccation and changes in body morphometrics, we excluded studies where hares were shot or snared and not weighed immediately (including museum specimens). From this search, we used published data from populations in Wyoming (USA) (Lawrence 1955), Oregon (USA) (Black 1965), Idaho (USA) (Ellsworth et al. 2016), Manitoba (Canada) (Murray 2002), British Columbia (Canada) (Sullivan and Sullivan 1988), and the Yukon (Canada) (Trostel 1986).

Capture data

We compiled body mass data obtained on snowshoe hares captured across a range of latitudes from 10 different populations (Fig. 1; Table 1). Study areas included San Juan Mountains, Colorado (USA); Taylor Park, Colorado (USA); Long Pond, Pennsylvania (USA); Warren, Pennsylvania (USA); the southern portion of the Bridger-Teton National Forest, Wyoming (USA); Wanakena, New York (USA); Chequamegon National Forest, Medford District, Wisconsin (USA); Seeley-Swan Valley, Montana (USA); the Klauene region of the Yukon (Canada); and the Bonanza Creek Experimental Forest in Alaska (USA). Detailed descriptions of these study areas can be found in Ivan et al. (2014) (Colorado); Gigliotti et al. (2018) (Pennsylvania); Berg et al. (2012) (Wyoming); S.M. Cleveland, unpublished data (New York); Wilson et al. (2019) (Wisconsin); Mills et al. (2005) and Griffin and Mills (2007) (Montana); Krebs et al. (2001) (Yukon); and Kielland et al. (2010) (Alaska). For all populations, we trapped adult snowshoe hares during winter (December–March) and recorded sex and body mass (using a Pesola® spring scale). If a hare was caught multiple times in a given season, then we used measurements from only the first capture. For hares captured across multiple seasons, we averaged their initial capture mass across seasons. Capture and handling protocols were approved by The Pennsylvania State University (No. 43476), The University of Wisconsin-Madison (No. A005849), The University of Montana (No. AUP 010-07), Environment Yukon (No. 202), The University of Alaska Fairbanks (No. 135211-5), The State University

Fig. 1. Location of snowshoe hare (*Lepus americanus*) populations used in analyses, including published measurements (triangles) and raw capture data (circles), overlaid on the geographic range of the snowshoe hare (gray shading; NatureServe and IUCN 2012). Populations are separated into northern contiguous populations (white symbols) and southern extension populations (black symbols). Population abbreviations are found in Table 1.



of New York College of Environmental Science and Forestry (No. 150401), Colorado State University and Colorado Parks and Wildlife (No. 06-062A-03), and the U.S. Department of Agriculture, National Wildlife Research Center (QA-491).

Environmental data

We calculated degree-days, length of growing season, and mean daily snow depth (cm) for each study location (Table 1). We obtained daily minimum and maximum temperatures, as well as daily snow depths, from the National Oceanic and Atmospheric Administration's National Climate Data Center (now known as National Centers for Environmental Information; <https://www.ncdc.noaa.gov/>). We selected the closest weather station (<20 km) to each of the study areas in our analyses. To ensure that years in which each study was conducted was representative of the mean weather conditions of the area, we used data starting 5 years prior to the individual study period through the end of the data collection period. We calculated yearly degree-days for each location by summing the daily minimum temperatures <0 °C averaged across years to obtain an overall degree-day value (Mills et al. 2013). We calculated the length of the growing season for each location with the climdex.pcic package for the program R (Bronaugh 2015), which defines the growing season as the length of time between the first warm spell of the year (5 days with a mean temperature >5 °C) and the first cold spell of the year (5 days with a mean temperature <5 °C). We averaged the growing season length

across all years that data were collected for each study location. We calculated elevation for each location using a 30 m digital elevation model. We calculated mean daily snow depth for each location by averaging the daily snow depth measurements across all years of data collection. As a result, our snow depth metric can be interpreted as an index of seasonality in that it incorporated both the amount of snow during the winter and the number of days that had snow.

Analysis

A test of Bergmann's rule: body mass

For our analysis of Bergmann's rule, we regressed body mass, from both published literature and our capture-based data set, with latitude. We ran models for males and females separately because hares are known to exhibit sexual dimorphism (Whittaker and Thomas 1983; Nagorsen 1985), and because of different energetics between sexes (Ellsworth et al. 2016) resulting in different environmental factors influencing body size. Hare body mass and condition are associated with the phase of their population cycle, with the greatest mass and condition occurring during the peak of the cycle and the lowest mass and condition occurring during the late low phase (Keith and Windberg 1978; Kielland et al. 2010). The hare populations in the Yukon and Alaska exhibit 9- to 11-year population cycles (Krebs et al. 1995; Kielland et al. 2010), whereas those from Pennsylvania, New York, Wisconsin, Montana, Colorado,

Table 1. Summary of studies reporting snowshoe hare (*Lepus americanus*) body mass data used in our analyses.

Study citation	Location	Abbreviation	Latitude (°N)	Longitude (°W)	Elevation (m)	Degree-days (°C)	Growing season (days)	Mean daily snow depth (cm)	Cyclic phase	N
Published data										
Lawrence 1955	Wyoming	WY2	41	106	2640	-1635.4	164	1.03	NA	12
Black 1965	Oregon	OR	44	122	869	-152.22	305	0.05	NA	53
Ellsworth et al. 2016	Idaho	ID	48	116	825	-1054.5	143	12.32	NA	38
Murray 2002	Manitoba	MB	51	98	280	-2754.9	172	3.03	Low	22
Sullivan and Sullivan 1988	British Columbia	BC	53	122	960	-1665.2	187	8.62	Late increase, peak, decline	599
Trostel 1986	Yukon	YT2	61	138	817	-4334.4	124	5.98	NA	131
Raw capture data										
J.S.I., this study	Colorado	CO1	38	107	3429	-2654.26	140	30.9	NA	118
J.S.I., this study	Colorado	CO2	38.8	106.6	2903	-2992.1	160	26.9	NA	189
L.C.G. and D.R.D., this study	Pennsylvania	PA1	41	75	580	-939.8	221	2.23	NA	48
L.C.G. and D.R.D., this study	Pennsylvania	PA2	41.7	79	566	-910.5	224	2.03	NA	12
N.D.B. and E.M.G., this study	Wyoming	WY1	43	110	2877	-2058.7	162	19.3	NA	91
S.M.C. and H.B.U., this study	New York	NY	44	74	571	-1776.8	191	10.8	NA	6
J.N.P. and E.C.W., this study	Wisconsin	WI	45	91	454	-1851.2	205	8.32	NA	45
L.S.M., this study	Montana	MT	47	114	1225	-1480.8	184	13.89	NA	79
R.B., C.J.K., and M.J.S., this study	Yukon	YT1	60	138	781	-3366.1	133	6.14	Late increase, peak	122
K.K., this study	Alaska	AK	64	148	136	-4067.5	151	16.57	Late increase, peak	45

Note: NA indicates that the study did not mention the cyclic phase or that the population is not known to cycle. N is the sample size. Researchers associated with the raw capture data are as follows: J.S. Ivan (J.S.I.), L.C. Gigliotti (L.C.G.), D.R. Diefenbach (D.R.D.), N.D. Berg (N.D.B.), E.M. Gese (E.M.G.), S.M. Cleveland (S.M.C.), H.B. Underwood (H.B.U.), J.N. Pauli (J.N.P.), E.C. Wilson (E.C.W.), L.S. Mills (L.S.M.), R. Boonstra (R.B.), C.J. Krebs (C.J.K.), M.J. Sheriff (M.J.S.), and K. Kielland (K.K.).

Table 2. Model selection results for regressions of drivers of snowshoe hare (*Lepus americanus*) winter body mass.

Sex	Model	ΔAIC_c	$-2 \times \ln(L)$	Model		
				likelihood	w	k
Female	Elevation	0.00	209.25	1.00	0.43	2
	Snow depth	1.03	210.25	0.60	0.26	2
	Intercept only	2.45	213.72	0.29	0.12	1
	Latitude	3.26	212.53	0.19	0.08	2
	Growing season	4.06	213.33	0.13	0.06	2
Male	Degree-days	4.40	213.61	0.11	0.05	2
	Elevation	0.00	212.35	1.00	0.32	2
	Intercept only	0.69	215.04	0.71	0.22	1
	Snow depth	1.24	213.60	0.54	0.17	2
	Latitude	2.28	214.63	0.32	0.10	2
	Growing season	2.29	214.64	0.32	0.10	2
	Degree-days	2.67	215.02	0.26	0.08	2

Note: All locations were included, with data from Alaska and Yukon populations being restricted to hares measured during the high phases of the 10-year population cycle. AIC_c is Akaike's information criterion corrected for small sample size; $-2 \times \ln(L)$ is log-likelihood, where L is likelihood; w is Akaike model weight; k is the number of model parameters.

and Wyoming are non-cyclic or weakly cyclic (Keith et al. 1993; Hodges 2000; Murray 2000). Because we expected patterns conforming to Bergmann's rule to be most apparent during the times which hares are the largest, we ran models with data from the final year of the increase phase and peak year for the Yukon (2006) and Alaska (1999, 2008–2009). We were not able to standardize cyclic phase for data from the published literature.

We specified six a priori regression models to explore the relationship between snowshoe hare body mass and latitude, as well as alternative drivers of body mass. We considered a linear latitude model, a degree-day model, a growing season model, an elevation model, a snow depth model, and an intercept-only model. We ran all analyses using the lm function in the program R (R Core Team 2019). We compared models using Akaike's information criterion corrected for small sample size (AIC_c) (Burnham and Anderson 2002) and considered models within 2 AIC_c units of the top model to be competitive.

Locational differences in hare morphometrics

Because populations that project beyond the contiguous range of a species may encounter significantly different environmental forces, we also assessed the conformity to Bergmann's rule on geographic subsets of our data. Specifically, we separated out the populations into a contiguous northern group, demarcated by unbroken segments in the range map of the species (Fig. 1), and a southern extension group, demarcated by projecting segments in the range map of the species (Fig. 1). Based on this classification, we included Alaska, Yukon, British Columbia, Manitoba, and Wisconsin populations in the contiguous northern analysis, and Pennsylvania, New York, Colorado, Wyoming, Montana, Idaho, and Oregon populations in the southern extension analysis. These southern populations mostly coincide with southern projections along mountain ranges.

We also conducted our analysis of the southern populations without the Oregon population because this population, like other populations in the Cascades, experience reduced seasonality, mild winters, and live in areas that were historical glacial refugia (Nagorsen 1985; Cheng et al. 2014). The historic and current environmental conditions that these populations encounter differ from the other populations in our analysis; therefore, evolutionary forces acting upon this population may have resulted in selection for different characteristics. Hare populations in the Cascades have high genetic uniqueness compared with other hare populations (Cheng et al. 2014).

Fig. 2. Relationship between snowshoe hare (*Lepus americanus*) winter body mass and latitude for females (solid circles) and males (open squares) using published and raw capture body mass data. Locations are labeled using abbreviations found in Table 1 and represent high cyclic phases of Yukon and Alaska populations.

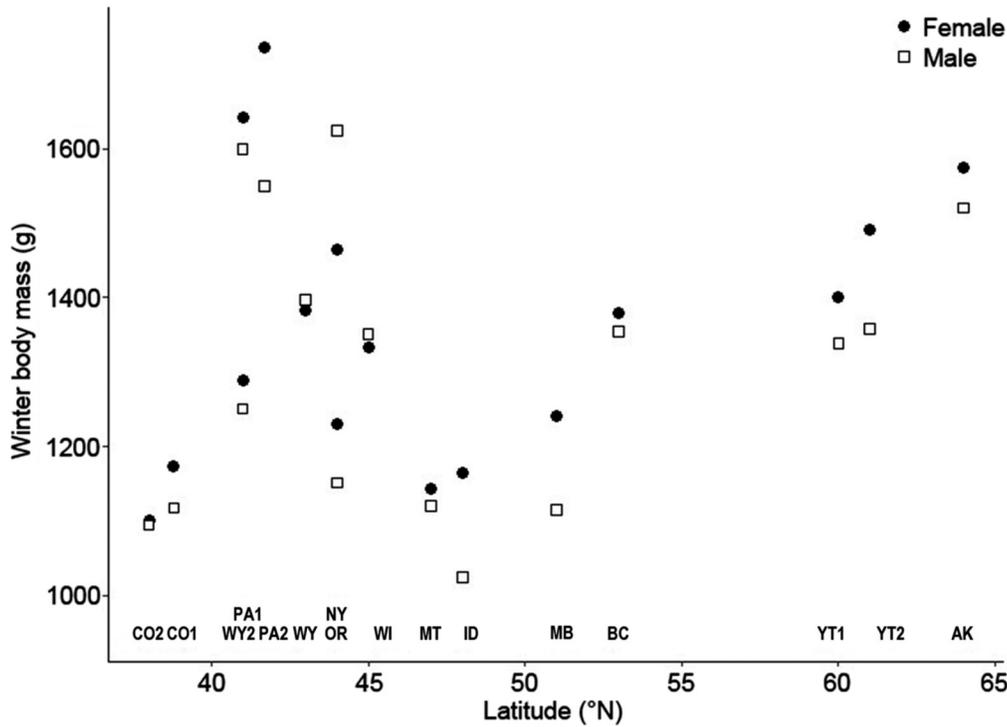


Table 3. Model selection results for regressions of drivers of snowshoe hare (*Lepus americanus*) winter body mass for northern contiguous populations, using data from high phases of the Alaska and Yukon populations.

Sex	Model	ΔAIC_c	$-2 \times \ln(L)$	Model likelihood	w	k
Female	Latitude	0.00	68.60	1.00	0.49	2
	Snow depth	1.30	69.90	0.52	0.25	2
	Degree-days	2.69	71.29	0.26	0.13	2
	Growing season	4.30	72.90	0.12	0.06	2
	Intercept only	4.53	75.13	0.10	0.05	1
	Elevation	6.25	74.85	0.04	0.02	2
Male	Snow depth	0.00	67.06	1.00	0.92	2
	Latitude	7.23	74.29	0.03	0.02	2
	Intercept only	7.24	76.30	0.03	0.02	1
	Degree-days	8.54	75.61	0.01	0.01	2
	Growing season	9.00	76.07	0.01	0.01	2
	Elevation	9.06	76.12	0.01	0.01	2

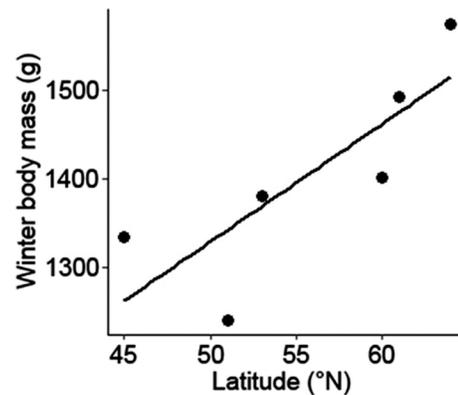
Note: AIC_c is Akaike's information criterion corrected for small sample size; $-2 \times \ln(L)$ is log-likelihood, where L is likelihood; w is Akaike model weight; k is the number of model parameters.

Results

A test of Bergmann's rule: body mass

Across all populations, hare winter body mass was not associated with latitude, and therefore did not follow Bergmann's rule (Table 2; Fig. 2). For females, the mean winter body mass (g) was best described by elevation or mean snow depth (Table 2). Female snowshoe hares were larger at lower elevations and in locations with shallower snow depths. For every 10 m increase in elevation, the body mass of females decreased by 0.87 g, and for every 1 cm increase in snow depth, the body mass of females decreased by 9 g. For males, the mean winter body mass was best described by elevation or mean snow depth, but the 85% confidence intervals of the snow depth parameter overlapped zero indicating that it was

Fig. 3. Relationship between female snowshoe hare (*Lepus americanus*) winter body mass and latitude for northern contiguous populations.



uninformative ($\beta = -6.25$; 85% CI = -14.57 to 2.02). Male snowshoe hares were larger at lower elevations, and for every 10 m increase in elevation, the body mass of males decreased by 0.72 g.

Northern contiguous populations

The mean body mass of females in the northern contiguous region was best described by latitude or mean snow depth (Table 3). Based on the latitude model, females in the northern contiguous region followed Bergmann's rule, with body mass increasing 13.3 g for every 1° increase in latitude (Fig. 3). Based on the snow depth model, female snowshoe hare body mass was positively associated with snow depth, with body mass increasing 19.5 g with each 1 cm increase in mean snow depth (Fig. 4). The mean body mass of males in the northern contiguous region was best described by mean snow depth (Table 3). Based on this model, male body mass was positively associated with mean snow depth,

Fig. 4. Relationship between female snowshoe hare (*Lepus americanus*) winter body mass and mean snow depth for northern contiguous populations.

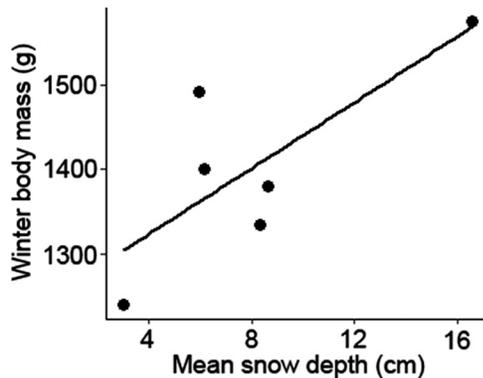
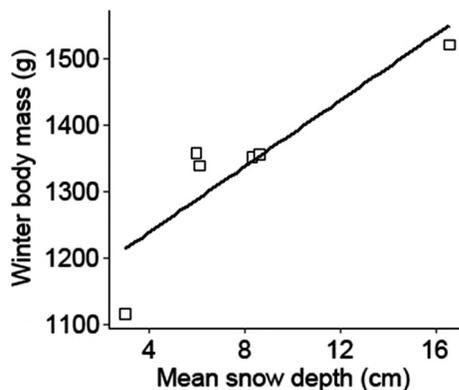


Fig. 5. Relationship between male snowshoe hare (*Lepus americanus*) winter body mass and mean snow depth for northern contiguous populations.



with body mass increasing 24.9 g with each 1 cm increase in mean snow depth (Fig. 5).

Southern extension populations

The mean winter body mass of both females and males in the southern extension region was best described by length of the growing season (Table 4). Based on this model, both female and male body mass was positively associated with growing season length, with body mass increasing 6.6 and 6.3 g, respectively, with each 1-day increase in growing season length (Fig. 6).

Discussion

Body mass of snowshoe hares only conformed to Bergmann's rule in certain portions of their range. Specifically, females in northern contiguous populations followed Bergmann's rule (Fig. 3) and also body mass increased with snow depth, whereas body mass of males in northern contiguous populations was only positively related to mean snow depth (Fig. 4). In the southern extension populations, the body mass of female and male hares increased with length of the growing season (Fig. 5).

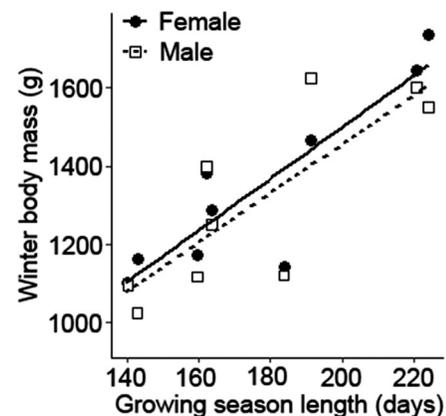
In northern contiguous populations, the conformity of females to Bergmann's rule can be explained by the harsh winters experienced by the northernmost populations. Maintaining a greater body mass is likely beneficial for two reasons: reduced relative heat loss because of a smaller surface area to volume ratio (James 1970) and enhanced fasting endurance (Lindstedt and Boyce 1985; Millar and Hickling 1990). Bergmann's rule was formulated based on the heat retention hypothesis and larger body masses have been found to be associated with increased absolute heat production and higher cooling resistance in a variety of species

Table 4. Model selection results for regressions of drivers of snowshoe hare (*Lepus americanus*) winter body mass for southern extension populations.

Sex	Model	ΔAIC_c	$-2 \times \ln(L)$	Model		
				likelihood	w	k
Female	Growing season	0.00	110.69	1.00	0.96	2
	Snow depth	8.00	118.67	0.02	0.02	2
	Elevation	9.73	120.42	0.01	0.01	2
	Degree-days	9.85	120.54	0.01	0.01	2
	Intercept only	11.68	124.37	0.00	0.00	1
	Latitude	13.59	124.27	0.00	0.00	2
Male	Growing season	0.00	115.25	1.00	0.89	2
	Snow depth	6.24	121.49	0.04	0.04	2
	Elevation	6.84	122.10	0.03	0.03	2
	Intercept only	7.74	124.99	0.02	0.02	1
	Degree-days	8.07	123.33	0.02	0.01	2
	Latitude	9.61	124.86	0.01	0.01	2

Note: AIC_c is Akaike's information criterion corrected for small sample size; $-2 \times \ln(L)$ is log-likelihood, where L is likelihood; w is Akaike model weight; k is the number of model parameters.

Fig. 6. Relationship between snowshoe hare (*Lepus americanus*) winter body mass and growing season length for females (solid circles and solid line) and males (open squares and broken line) for southern extension populations.



(Scholander et al. 1950; Gilgooly et al. 2001). In addition to other adaptations, such as lower metabolic rates and increased winter pelage insulation (Sheriff et al. 2009), a larger body mass potentially helps hares in the coldest parts of their range maintain a proper heat balance in winter. A relatively greater body mass also may enhance the ability of hares in the north to cope with a long winter of poor food availability by increasing their energy reserves. For example, moose (*Alces alces* (Linnaeus, 1758)) in Sweden have been found to follow Bergmann's rule in regard to body mass; this relationship is likely driven by fat reserves that help them survive the winter (Sand et al. 1995). However, we do not believe that this is the case with hares, as they have little if any fat accumulation in winter (Hodges et al. 2006) and cannot survive for more than a day without eating (Pease et al. 1979; Whittaker and Thomas 1983). Thus, we suggest that the greater body mass of female hares in the most northern populations is to reduce heat loss (sensu stricto Bergman's rule; Bergmann 1847).

We did not see the same relationship between body mass and latitude for male hares in the northern contiguous populations. This lack of support for Bergmann's rule for males might be a consequence of different energy demands of males compared with females (Ellsworth et al. 2016). In most mammalian species, females have higher energetic demands than males because of the large energetic requirements associated with gestation and lactation (Gittleman and Thompson 1988). Because snowshoe hares

breed in the late-winter months when temperatures are still low, maintaining a high winter body mass might be the most essential for female hares in populations that experience the highest thermal energy demands.

The body mass of males in the northern contiguous populations was positively related to snow depth. Higher body masses could be disadvantageous for hares in areas of deep snow because of increased foot-loading and associated energetic costs (Murray and Boutin 1991; Crête and Larivière 2003). However, as snow accumulates, hares have access to more vegetation during the winter because they are able to access taller shrubs and vegetation (Meslow and Keith 1971), which in turn could reduce overwinter mass loss and result in higher body masses in winter. In addition, males in northern populations with higher body masses may also have larger feet, which would reduce foot-loading and minimize the negative effects of larger body masses in areas with deeper snow. Females in northern contiguous populations might not follow the same pattern of higher body masses with deeper snow because their body mass might be more driven by reproductive energetic demands. Finally, because we calculated mean snow depth across the entire year, higher mean snow depths are also associated with longer time periods with snow on the ground, and thus lower winter food availability. As a result, it would be beneficial for hares in areas with more snow to have larger body masses to survive during longer times of reduced food availability (Hodges et al. 2006).

In the southern extension populations, hare body mass was related to the length of the growing season. Many of these southern populations experience milder winter conditions; therefore, heat conservation may not be as important of a driver of body mass as it is for more northern populations (Gigliotti et al. 2017). Hares in areas with longer growing seasons have more opportunity to gain mass over the summer, which in turn could result in higher body masses in winter (Lindstedt and Boyce 1985). Furthermore, they have less time to lose mass over the winter, given its shorter duration. Food availability has also been shown to drive latitudinal relationships with body size in other taxa (Geist 1987; Wolverton et al. 2009).

Our results are similar to those of Nagorsen (1985), who found that hares in eastern North America, Alaska, and northeastern Canada had larger cranial measurements than hares in other regions. Additional, in both studies, hares were smallest, either in cranial measurements or body mass, in the Pacific Northwest. The similarity of our results indicates that body mass and cranial measurements are likely correlated and that the same general patterns between size and latitude can be found regardless of the size metric used.

Conclusions

Body mass of snowshoe hares varies across their distributional range, but they only conform to Bergman's rule in the central and northern extent of the range of the species. In contrast, the body mass of hares in southern extension populations is driven by the length of the growing season. Thus, the selective forces driving these patterns vary: in the north, the size and mass of hares may be driven by their need to conserve heat and energy during a long and cold winter; whereas in the south, the size and mass of hares may be driven by increased food availability. For species that have extensive geographic ranges, such as snowshoe hares, it appears important to understand local factors that govern site-specific adaptations, rather than attempting to fit an all-encompassing general taxonomic explanation.

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