The complex effects of geography, ambient temperature, and North Atlantic Oscillation on the body size of Arctic hares in Greenland

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Greenland is one of the coldest areas on earth that are inhabited by animals. In this study, we sought to examine the effect of several environmental factors on skull size of Arctic hares (Lepus arcticus). We measured 263 skulls of Arctic hares, collected in Greenland between 1906 and 1971. We employed two full models: one that includes latitude, longitude, and seasonal surface temperature during collection year and a second that includes the two spatial axes and the North Atlantic Oscillation (NAO) index during collection year. We found complex relationships between the examined parameters and hare skull size, which resemble the trends reported by Post & Forchhammer (2002) between the NAO index and the population dynamics of caribou and musk oxen in Greenland. Our two models provided a similar picture of opposite trends in skull size across Greenland, as reflected by the two- or three-way interactions (between latitude, longitude, and temperature in the first model, and latitude, longitude, and NAO in the second model). This complex picture, in which during both summer and winter the pattern of change in skull size toward north-east Greenland is an inverse of that observed in its south-west, is illustrated in Figure 3. The first and second models explained c. 31% and c. 25%, respectively, of the variation in skull size in both winter and summer. We discuss several possible mechanisms that could affect skull size in such an opposite way across Greenland.


INTRODUCTION

Geographic and temporal changes in body size of animals are common and have been attributed to geographical location being related to many factors, including ambient temperature (Smith et al., 1998) and other climate factors, predation (Gosler et al., 1995), food availability (Yom-Tov, Yom-Tov & Baagøe, 2003; Yom-Tov, Kvam & Wiig, 2011), and habitat fragmentation (Schmidt & Jensen, 2003). The effect of climate is especially influential in extreme environments (Hansen et al., 2013), where ecosystems are simpler than in temperate or tropical region and abiotic factors are often more important than biotic ones. This was already indicated by Darwin (1859: 69), who, while ignoring the effect of predation, stated 'when we reach the Arctic regions, or snow-capped summits, or absolute deserts, the struggle for life is almost exclusively with the elements’. In this study, we examined the effect of several environmental factors on skull size of Arctic hares (Lepus arcticus, Ross, 1819).

The Arctic hare is a medium-sized herbivore distributed widely across the tundra regions of Greenland and the northernmost parts of Canada (MacDonald & Barrett, 1993; Best & Henry, 1994). In Greenland, it occurs on the ice-free coastal regions at elevations below
900 m a.s.l., along the western, northern, and north-eastern shores, but not along the south-eastern coast or in the vast frozen centre (Best & Henry, 1994; Fig. 1). Arctic hares do not hibernate in winter, give birth from late May to July, and grow fast, and by the end of the short summer, the young are nearly as large as their parents (Best & Henry, 1994). Little information exists on their longevity, but anecdotal evidence suggests a lifespan of 3–5 years (http://animaldiversity.ummz.umich.edu/site/accounts/information/Lepus_arcticus.html).

Baker et al. (1978), who studied geographic variation in skull size of the Arctic hare in eastern Canada and Greenland, found that hare skull size declines from the polar region southwards, as predicted by Bergmann’s rule (Bermann 1847). A Bergmannian trend in body size was also reported for hares in Israel (Yom-Tov, 1967) and New Zealand (Flux, 1967). However, Baker et al. (1978) noted some unexplained inconsistencies in the observed north-south cline, namely, changes that do not fit a Bergmannian cline.

Greenland is the world’s largest island (2,166,086 km²), lying between latitudes 59 and 83°N and longitudes 11 and 74°W. Hence, most of Greenland lies north of the Arctic Circle (at 66.6°N; Fig. 1). Over three quarters of Greenland is covered by an ice sheet, and most wildlife live on its southern, western, and

Figure 1. Locations (dots in the map) of Arctic hares from Greenland in our sample. The distribution area of hares in Greenland is marked by the grey area.
north-eastern shores. In Greenland, ambient temperatures during winter (December–February) vary greatly along the latitudinal scale in comparison with those in summer (June–August). For example, the mean difference between the winter mean monthly temperatures at 61 and 69°N is 8.0 °C, while in summer, it is only 0.65 °C (data from http://www.cru.uea.ac.uk/cru/data/greenland). Due to the extensive ice sheet in the centre of Greenland, the surface temperature is generally highest in the coastal areas (Fig. 2a).

Latitude and longitude do not affect organisms directly, but rather as proxies for global trends that may affect body size, such as the decrease in ambient temperature toward the Polar regions and the south-north trend of increase in day length during summer. Climate may vary also longitudinally: for example, in Greenland, the north-east region is generally colder than the north-west region.

Several climate parameters may affect body size indirectly through their effect on net primary

Figure 2. (a) Mean surface temperature averaged for winter (December–January–February) and summer (June–July–August) in Greenland over the period of 110 years (1901–2010). (b) Correlation coefficient between mean surface temperature and North Atlantic Oscillation averaged for winter (December–January–February) and summer (June–July–August) in Greenland over the period of 65 years (1948–2013). These maps were generated based on NCEP reanalysis tool and data provided by Earth System Research Laboratory, NOAA (http://www.esrl.noaa.gov/psd/data/). (c) The mean annual frequency of rain on snow events in Greenland during winter and summer. These maps were generated by the algorithm and data in Rennert et al. (2009). The maps are only for the purpose of illustration, as the data used here are not completely overlapping in time with the skull data used in the analysis.
productivity (NPP) and thus on food availability (Yom-Tov & Yom-Tov, 2005). For example, several authors have contended that the positive relationship between body size and latitude is a product of food availability (Rosenzweig, 1968), the length of the growing season (Geist, 1987), a response to interaction between moisture and temperature (James, 1970), and precipitation (Yom-Tov & Nix, 1986). Body size may reflect the conditions that prevailed during an organism’s birth year, while environmental conditions affect body size almost continuously throughout life. Harsh conditions operate to select those individuals that are best adapted to them, thus determining which size cohorts survive.

The effect of temperature on body size was described in Bergmann’s rule, which states that body size of homeotherms is negatively related to ambient temperature: a higher body surface-to-volume ratio in warm areas enables effective heat dissipation and a lower surface-to-volume ratio reduces heat loss in cold areas. In the cold climate that prevails at high latitudes, animals whose surface area is relatively small (large body size is associated with relatively small surface area) lose less heat. The reverse is true in a warm climate, where animals face the problem of heat dissipation, and the larger the surface area, the quicker such dissipation occurs. Bergmann’s rule predicts that a large body size is advantageous during cold periods (Yom-Tov & Yom-Tov, 2006; Yom-Tov et al., 2006).

Conversely, small-bodied animals may satisfy their energetic demands with smaller amounts of food, and, under harsh conditions, when food is scarce, they may survive better. This was demonstrated, for example, by Ochocinska & Taylor (2003), who suggested that food scarcity in winter is a major factor selecting for smaller body size in shrews and in other animals facing harsh conditions. Similarly, Tornberg et al. (2014) have shown that small male goshawks breeding in rabbit-poor habitats demonstrate a better body condition than do larger males.

The North Atlantic Oscillation (NAO) is a climatic index in the North-Atlantic Ocean of fluctuations in the difference in sea-level pressure between the Icelandic Low and the Azores High. NAO predicts the weather, including ambient temperature, precipitation, and winds, throughout the North-Atlantic region. A positive NAO index implies relatively strong westerly winds across the mid-latitudes of the Atlantic to Europe, resulting in cool, wet summers and mild, wet winters in Europe and to cold and dry winters in Greenland. In contrast, when the NAO is negative, European winters will be cold, while Greenland will have milder winter temperatures. It has been shown that the NAO index is related to changes in ecological ecosystems and animal biology (reviewed by Mysterud et al., 2003), and its ecological responses include changes in timing of reproduction, population dynamics, abundance, spatial distribution, and interspecific relationships such as competition and predator–prey relationships (reviewed by Ottersen et al., 2004). Further, Post & Forchhammer (2002: Fig. 1a) have shown that, in Greenland, the direction of the correlation between the NAO winter index and average winter temperature changes in relation to latitude and longitude from a positive correlation on the east coast to a negative correlation on the west coast (Fig. 2b). These relationships are reflected in synchronization and spatial dichotomy of the population dynamics of caribou and musk oxen populations across Greenland (Forchhammer et al., 2002; Post & Forchhammer, 2002).

Herbivores living in Arctic regions may also be affected by a peculiar phenomenon called rain-on-snow (ROS) events, when ambient temperature drops below zero after rain, and a layer of ice forms above the ground. Warm winters may result in a high likelihood of the occurrence of ROS events, reducing food availability catastrophically by forming a thick ice layer on the ground, trapping the short-growing vegetation and suppressing food accessibility (Hansen et al., 2013). Such events have caused mass mortality among several species of Arctic herbivores by affecting food availability (Aanes, Sæther & Ørterrit, 2000; Hansen et al., 2013). Rennert et al. (2009: Fig. 3) modelled the frequency of ROS events across the Arctic and found that in Greenland they occur below latitude 68°N at a frequency of about two per winter.

Climate patterns in Greenland do not change linearly along its latitudinal range and, as noted above, its north-east region is colder than the north-west one (Post & Forchhammer, 2002). We therefore hypothesized that if climate both directly and indirectly affects skull size (and by implication body size) of animals, then the skull size of hares during collection (death) year will reflect Greenland’s climate, and will vary non-linearly from south to north and differ between west and east. This climate pattern may explain the inconsistencies in the north-south cline of the skull size of the Arctic hare in Greenland observed by Baker et al. (1978). In order to test this prediction, we examined the effects of sex, latitude, longitude, and winter and summer seasonal ambient temperature, as well as summer and winter NAO during collection year, on the skull size of Arctic hares collected in Greenland during the 20th century.

MATERIAL AND METHODS

Skulls of 263 Arctic hares L. arcticus (94 females, 108 males, and 61 unsexed specimens) from Greenland (Fig. 1) were measured at the Zoological Museum of Copenhagen, the Smithsonian Institution in Washington, Oslo Natural History Museum, the American Museum of Natural History in New York, Museum of Comparative Zoology, Harvard University,
and University of Michigan Museum of Zoology. Only skulls of adults were measured and were defined as
such by their teeth and the fusion of the cranial bones (Morris, 1972). Most of the specimens were collected
during the period 1906–1971. Collection effort had not been uniform throughout the studied period; during
the 66 years for which we have data, for 7 years, there was only one specimen each, and for the rest,
sample size varied between 2 and 24. For each skull, we noted (from its label or museum catalogue) its sex,
locality (latitude and longitude), and date of collection (Supporting Information, Table S1). Hares collected
between 1 January and 30 June in a particular year were assigned to the previous year because Arctic
hares give birth between May and July. Using digital calipers, four measurements were taken from each
skull to an accuracy of 0.01 mm: greatest length (GTL) of the skull, condylobasal length (CBL), zygomatic
breadth (ZB), and the length of the mandible (M). Our skull data are relatively evenly distributed across latitude
and longitude in Greenland (Fig. 1).

Climatological data were taken from the database of the National Oceanic and Atmospheric Administration
(NOAA, http://www.esrl.noaa.gov). These data were downloaded from the NOAA-CIRES 20th Century
Reanalysis Version 2 Data (http://www.esrl.noaa.gov/psd/data/gridded/). From these data, we assigned a
winter and summer surface temperature to each skull measurement according to year and coordinates of col-
lection. Both summer and winter temperatures may affect body and skull size (Yom-Tov et al., 2003, 2011). Month of collection was added as a random effect. All calculations were performed in JMP
11 (SAS Inc.).

RESULTS

We measured four skull size parameters, which ranged from 90.3 to 113.9 mm for GTL, from 79.4 to 100.8 mm
for CBL, from 46.1 to 55.3 mm for ZB, and from 63.4 to 90.0 mm for M. The PCA clumped the four morpho-
logical measurements into a single factor (PC1), which accounted for 86.2% of the variance (eigenvalue = 3.4;
Supporting Information, Table S2). Preliminary exam-
ination indicated that skull size and body size were closely linked ($R^2 = 0.3409, F_{(1,22)} = 0.0027, n = 24$) and
that skull size (PC1) of males and females did not differ significantly from one another (t$_{184} = 0.8946,
P = 0.3722$), as also found by Baker et al. (1978). Therefore, we did not include gender in further analy-
yses (see below).

We used latitude, longitude, seasonal temperature, and NAO as our independent variables. The correlation
between latitude, longitude, and seasonal temperature ranged from 0.56 to 0.49, which implies that no more
than 31.5% of the variance in one variable is explained by the others. Further, variance inflation factor (VIF)
for the independent variables ranged from 1.0 to 3.1, considerably lower values than those expected from
the high collinearity cut-off (VIF > 10). We explored two full models: one that comprised spatial axes and
surface temperature (Table 1) and a second that comprises spatial axes and NAO (Table 2). We chose sepa-
rate analyses because the correlation between NAO and surface temperature, ranging in Greenland from
−0.8 to 0.2, is spatially dependent (Fig. 2b; Post & Forchhammer, 2002). In other words, NAO and surface
temperature are not interchangeable and might not contain the same information.

In the first model (Table 1), which includes surface temperature, the total effect (i.e. the total contribution
to the variance of y from all terms that involve x) was highest for latitude in both winter (0.73) and summer
(0.88). The total effect of longitude was higher in summer (0.81) than in winter (0.45). Temperature showed
a rather similar total effect for both winter (0.57) and summer (0.69). Both winter and summer models
accounted for ~25% of the variance in skull size. The total effect of the month of capture on skull size was
negligible (< 0.0001) for both summer and winter. Sex also had a negligible effect (total effect of 0.006 and
0.007 during summer and winter, respectively), and none of its interactions with the other independent
variables were significant. Therefore, sex was excluded from the models presented in Table 1.
The change in skull size in Greenland is complex, as reflected by the strong significant interaction between latitude, longitude, and temperature (Table 1). This interaction can be clearly viewed in Figure 3a by comparing the pattern of change in skull size across gradients. Any one of two contrasting faces in this cube plot shows an opposite image of the other. To better illustrate these patterns, we calculated changes in GTL from the model-predicted PC1 values. PC1 and GTL were tightly correlated (\(R^2 = 0.938\), \(F(1,269) = 4124.4\), \(P < 0.0001\)), and GTL was estimated using the equation, \(GTL = 2.21 \times PC1 + 101.14\). During summer in eastern Greenland (longitude \(\sim 20^\circ\)), skull size increases with temperature at the low latitudes (\(\sim 70^\circ\); 0.8 mm in GTL/1 °C) but decreases at high latitudes (\(\sim 80^\circ\); −3.1 mm in GTL/1 °C). Our model showed an increase of 2.2 mm in GTL/1° latitude at the low end of summer surface temperature (\(\sim 13^\circ\) C) but a decrease of 1.3 mm in GTL/1° latitude at the high end of summer surface temperature (2 °C). In contrast, in western Greenland (longitude \(\sim 70^\circ\)), skull size decreases with temperature at the low latitudes (−60°; −2.8 mm in GTL/1 °C) but increases at high latitudes (−80°; 0.8 mm in GTL/1 °C) (Fig. 3a; Supporting Information, Fig. S1). GTL decreased in 1.7 mm/1° latitude at the low end of summer surface temperature (−13 °C) but increased by 1.1 mm/1° latitude at the high end of summer surface temperatures (2 °C). In other words, the pattern of change in skull size toward the north-east Greenland is an inverse of that observed for the south-west.

In winter, the pattern of change in skull size across Greenland is more complex (Fig. 3b; Supporting Information, Fig. S1b). We detected significant interactions in winter between latitude and longitude, latitude and temperature, and longitude and temperature, but not a three-way interaction with all three variables (Table 1). During winter in eastern Greenland (longitude \(\sim 20^\circ\)), skull size largely decreased with rise in temperature (−0.2 mm in GTL/1 °C at latitude 70° and −0.1 mm/1 °C at latitude 80°) and slightly changed with latitude (−0.2 mm in GTL/1 °C at latitude 70° and 0.1 mm/1 °C at latitude 80°), being the smallest in the far north in warm winters (Fig. 3). In
contrast, in western Greenland (longitude ~70°), skull size increased with temperature at the low latitudes (~60°; 1.5 mm in GTL/1 °C) but decreased at higher latitudes (~80°; −0.3 mm in GTL/1 °C). The GTL size of hares increased by 2.5 mm/1° latitude at the low end of winter surface temperature (~28 °C) but decreased by 0.6 mm/1° latitude at the high end of winter surface temperature (2 °C) (Fig. 3b; Supporting Information, Fig. S2).

In the second model, the NAO index replaced surface temperature. Skull size significantly increased with latitude in both seasons and decreased with the rise in NAO during winter. However, this model also detected significant interactions between location and NAO. In winter, we detected a significant three-way interaction (Table 2). In east Greenland, the change in latitude and NAO had little effect on skull size. However, in western Greenland at low latitudes, skull size increased with the rise in NAO, and at high latitudes, it decreased with the rise in NAO. In summer, we detected a significant two-way interaction between latitude and NAO (Table 2). In both eastern and western Greenland, with the rise in NAO, skull size increased at low latitudes and decreased at high latitudes. Both models accounted for a rather similar level in variation (~25%), as both involve surface temperature (~31%; Tables 1 and 2).

Finally, in order to evaluate non-linearity trends in our models, we recalculated both models for summer and winter, but expressing ambient temperature and NAO as quadratic terms. Both models accounted for a rather similar amount of variance, as with the linear terms above (winter temperature: $R^2 = 0.342$; summer temperature: $R^2 = 0.353$; winter NAO: $R^2 = 0.301$; summer NAO: $R^2 = 0.293$); therefore, we did not use these models further.

**DISCUSSION**

Overall, our two models show that skull size of the Arctic hare during their year of death in Greenland is affected by a variety of geographic (latitude and longitude) and climate factors (winter and summer temperature and the NAO index). Both models explain a similar proportion of the variation in skull size (~31 and 25% for the first model and second model, respectively), with little difference between winter and summer in each of the models. In the first model, the three-way interaction between temperature, longitude, and latitude had highly significant ($P < 0.0001$) effect on skull size during summer, and a nearly significant ($P = 0.0585$) effect during winter; while in the second model, the three-way interaction between NAO, longitude, and latitude had a significant ($P = 0.0482$) effect on skull size during winter, but not during summer.
However, we found the most interesting result to be the fact that both models provided a similar picture of opposite trends in body size across Greenland, as reflected by the two- or three-way interactions (between latitude, longitude, and temperature in the first model, and between latitude, longitude, and NAO in the second model). This complex picture, in which during both summer and winter the pattern of change in skull size toward north-east Greenland is an inverse of that observed in its south-west, is given in Figure 3.

We suggest that these opposite patterns are probably, and at least partly, a reflection of the inverse relationships between the NAO index and ambient temperature that occur across Greenland, where the correlation between NAO and surface temperature, ranging in Greenland from −0.8 to 0.2, is spatially dependent (Post & Forchhammer, 2002; Fig. 2b). Post and Forchhammer found that the long-term population dynamics of caribou (Rangifer tarandus) and musk oxen (Ovis moschatus) is spatially synchronized across Greenland, apparently due to a similar dichotomy in the relationship between winter NAO and temperature from east to west. The three-way interactions that have been found between longitude, latitude, and ambient temperature (or NAO) in both winter and summer indicate complex relationships between these factors and may explain the inconsistencies in the Bergmannian trend in the Arctic hares’ skull size observed by Baker et al. (1978).

The NAO index represents fluctuations in the difference in sea-level pressure between the Icelandic Low and the Azores High. It is related to many climatological parameters, including winds, ambient temperature, relative humidity, and precipitation throughout the North Atlantic region and, in turn, also NPP and food availability (Mysterud et al., 2003). Due to lack of long-term data on most of the above-mentioned climatic factors, in this study, we used only one climate parameter, namely, seasonal temperature. However, any of the other climate factors may affect skull size. This may be why our models explain less than a third of the variation in skull size. In both models, latitude had a much stronger effect on skull size than longitude. Contrary to our expectation, we found that our second model (which included the NAO index and its interactions with longitude and latitude) explained a slightly smaller proportion of the variation in skull size than the first model, which included only surface temperature and its interactions. We have no satisfactory explanation for this finding.

In addition to the effects of temperature and NAO, ROS events may also play an important role in determining body size. Although we do not have data on ROS events for the years of sampling, we noticed that during winter, when severe ROS events are most likely to occur, the distribution of such events across Greenland is far from random (Fig. 2c). Long-term measurements of the conditions favouring severe ROS show that such events are most likely to occur in south-west and north-east Greenland. Severe ROS events are not likely to occur in north-west Greenland (Fig. 2e). The contrasting climatic pattern of ROS events might also fit the pattern of change in hare skull size across Greenland, but this requires a further examination when the appropriate data will become available.

How might the above climatic variables affect the skull size of Arctic hares? Below we provide several possible explanations.

At low latitudes, skull size was positively related to ambient temperature, contrary to Bergmann’s rule. In contrast, at high latitudes (at ~75°N during winter and 70°N in summer), the direction of the relationship changed, and skull size was negatively related to temperature, as predicted by Bergmann’s rule. It should be noted that our hare sample from eastern Greenland does not include any hare collected below 70°N, as this species does not inhabit most of the eastern Greenland coast south of that latitude (Fig. 1). We suggest that the positive relationship between temperature and skull size observed at low latitudes in Greenland is due to two factors: first, in the Arctic and particularly during winter, an increase in ambient temperature decreases energy expenditure, enabling energy to be converted to an increase in skull size; second, during summer, higher temperatures enhance plant primary productivity (NPP) and, in turn, food availability to the hares. However, above a certain threshold north of the Arctic Circle (66.5°N), the direction of the relationship changed. We suggest that the reason for the change is that at high latitudes in Greenland, NPP is limited mainly by two factors, temperature and precipitation. In Greenland, at latitudes above 70°N, annual precipitation is generally less than 400 mm due to limited evaporation of the cold sea water, and when it coincides with high temperatures, precipitation is less likely to form and reach the local plants, thus reducing potential NPP and food availability. This may explain the trend of negative relationship between skull size and summer temperature in northern Greenland. The fact that the change in the direction of the trends in skull size is located between 70 and 75°N may indicate that additional climatic factors, such as cloudiness, affect these trends (see below).

In this study, we examined the effects of several environmental factors that had prevailed during the year of death, namely, latitude, longitude, seasonal ambient temperature, and the NAO index on skull size of the Arctic hare. Together, these factors explained, at the most, 33% of the variation of skull size. We do not know which factors are responsible for the rest of the variation and suggest that it is probably determined by a combination of genetic and environmental factors.
Lack of adequate long-term data prevented us from including in this study other environmental factors. We suggest that future work will examine the effects of other specific factors such as cloudiness. In the high Arctic, the combination of a short-growing season, low temperature, and low light severely constrains the diversity and productivity of terrestrial ecosystems (Wal van der & Hessen, 2009; Devasthale et al., 2012). One of these factors, low light, depends to some extent on cloud type. Ice clouds scatter sunlight, which increases diffused radiation, which, in turn, greatly increases photosynthesis. The importance of scattered light for photosynthesis was demonstrated by Lianhong et al. (2003), who reported that after major volcanic eruptions (such as Pinatubo in 1991 and El Chichon in 1982) plant productivity increased at the mid and high latitudes due to increased multiple scattering and diffused radiation by aerosols (Lianhong et al., 2003). In the 2 years following Mount Pinatubo’s eruption (in 1991), the increase in diffused radiation alone enhanced noontime photosynthesis of deciduous forests by 23% in 1992 and 8% in 1993 under cloudless conditions. We suggest that the increase in ice clouds and the related increase in diffused light merit more attention as a possible key positive effect on plant productivity and thus on body size of homeotherms at northern latitudes.

Finally, we are aware that although we provided only a partial explanation to the body size trends of hares in Greenland, we identify a good model system for future testing. We think that this model provides a significant contribution to the understanding of the relationship between trends in body size of the Arctic hare in Greenland. The Arctic is the most affected region by global warming, and this phenomenon has an enormous effect on the wildlife in the Arctic, including Greenland. It is imperative that we understand how changes in climate are affecting the local wildlife. Here, we bring a case where it is clear that our understanding of the effect of climate on morphology and survival is lacking at best. In other words, we understand very little of the complex climate effects in Greenland, the largest landmass in the Arctic zone. Hence, bringing this message to the scientific community that is interested in the Arctic region is important.

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REFERENCES


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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher’s website:

Figure S1. Surface plot of predicted skull size in PC1 units as a function of latitude and mean summer temperature (ºC) at the extreme east (a; 18º) and west (b; 73º) of Greenland.

Figure S2. Surface plot of predicted skull size in PC1 units as a function of latitude and mean winter temperature (ºC) at the extreme east (a; 18º) and west (b; 73º) of Greenland.