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Harsh climate selects for small body size among Iceland's Arctic foxes

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We studied the effect of the two environmental indices, the sub-polar gyre (SPG), and winter and summer North Atlantic Oscillation (NAO), together with mean annual winter and summer temperatures and geographic location on mandible size and body mass of Arctic foxes in Iceland (6345 and 2732 specimens, respectively) during the year of their death. We predicted that when favorable conditions prevailed, large specimens would be selected for, and vice versa.

Body size and body mass were significantly affected by the environmental parameters (i.e. SPG, NAO, ambient temperature and cloud cover) prevailing during the year of death. The effect of environmental conditions on body size was much stronger in the less productive region of eastern Iceland, apparently because in areas where food availability is meager, even a small difference in climate may tilt the balance from food sufficiency to food shortage. Western Iceland comprises only a quarter of the total surface area of the country, but its productive seashores are twice as long as those of all the rest of the country combined. It is interesting to note that the effect of the SPG, a marine phenomenon in the oceans surrounding Iceland, is reflected in the condition of the foxes more than the other climatic variables we used in this study, which are largely land-related. Because Arctic foxes in Iceland feed largely on marine birds and invertebrates, the SPG seems to encompass more accurate information regarding the direct ocean forces that affect food availability to the foxes.

In many birds and mammals, the environmental conditions experienced during their growth period affect food availability and energy expenditure, and ultimately adult body size, as well as a range of other life-history components (Geist 1987, Read and Gaskin 1990, Ulijaszek et al. 1998, Lindstrom 1999). These conditions include prey availability (Yom-Tov et al. 2006, 2010, 2011) and other biotic factors that affect food availability, such as prey population density (Pettorelli et al. 2002, Mysterud et al. 2003, Zedrosser et al. 2006). They also include specific climate variables such as ambient temperature (reviewed by Madsen and Shine 2000, Yom-Tov et al. 2011) and snow conditions (Stenseth et al. 2004).

Since it is difficult to determine precisely which of the many environmental conditions (temperature, precipitation, humidity, etc.) affects body size, researchers have used various indices as proxies that incorporate several climate factors (Hersteinsson et al. 2009, Nilsen et al. 2009). In the North Atlantic region, the North Atlantic Oscillation (NAO) and the sub-polar gyre (SPG) constitute such large-scale environmental indices. NAO is a climatic phenomenon in the North Atlantic Ocean of fluctuations in the difference in sea-level pressure between the Icelandic Low and the Azores High, and is responsible for much of the variability of weather in the North Atlantic region. NAO variation thus reflects weather, including ambient temperature, precipitation, wind speed and direction, as well as the intensity, number, and track of storms throughout the North Atlantic region. Positive NAO leads to 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 cold, dry winters in Greenland. In contrast, when the NAO is negative, European winters are cold, while Greenland experiences milder winter temperatures. The relationship between NAO and temperature in Iceland resembles that for Greenland, but is weaker and diminishes from west to east (Hurrell and van Loon 1997, Hanna et al. 2004).

The sub-polar gyre (SPG) is an ocean current carrying warm, subtropical waters into the north-eastern Atlantic, circulating northward and westward in a counterclockwise motion near Iceland and the southern tip of Greenland. The current loses heat to the atmosphere as it moves north, where it meets cold Arctic currents, thus affecting the climate of the entire North Atlantic region (<www.nasa.gov/vision/earth/environment/North_Atlantic.html>). When the SPG index is high, the temperature and salinity of waters flowing from the south across the Greenland–Scotland ridge on both sides of Iceland are relatively low, and vice versa for a low

†Deceased

index. This is because the relative contribution to the northeast Atlantic Ocean of the warmer, more saline, subtropical gyre is reduced when the SPG is high (Hátún et al. 2005). The surface waters lose heat to the atmosphere, bringing the region milder temperatures, depending on the strength of the SPG. The mixing of cold, Arctic-originated water with the warm current also influences the phytoplankton cycle, and thus the entire food chain that depends on it (Harrison 1991). Currently, only a few aspects of the marine food web have been studied in direct relation to the SPG, with the exception of its effect on the spawning and feeding distribution of the redfish *Sebastes mentella* in the Irminger Sea (Pedchenko 2005). During the past four decades the SPG has weakened, thus affecting the climate of the northern Atlantic region (Böning et al. 2006).

It has been shown that the North Atlantic thermohaline circulation (THC) is tightly linked to the SPG (Hátún et al. 2005). Hence, variability in the SPG index affects the mixing of cold, Arctic-originated water with the warm current, and influences the phytoplankton cycle and thus the food chains that depend on it (Harrison 1991). In spite of its significant effect on current regimes in the North Atlantic Ocean, as well as on the atmosphere above it, the ecological effects of SPG, as far as we are aware, have rarely been studied and are poorly understood.

In a previous article (Hersteinsson et al. 2009) we have shown that both body size at birth year and abundance of the Arctic fox *Vulpes lagopus* in Iceland are related to ambient temperature as well as to the NAO and SPG. The Arctic fox is the only native terrestrial carnivore occurring in Iceland, where it is found throughout the island (a stray individual of the polar bear *Ursus maritimus* may also occur there occasionally on an ice floe).

The diet of the western Icelandic Arctic fox population depends largely on seabirds, which nest in abundance on the cliffs (Gardarsson 1995). In contrast, in most of eastern Iceland, the foxes switch their diet in spring from ptarmigans *Lagopus mutus*, snow buntings *Plectrophenax nivalis*, and caches from the previous summer and carcasses, to migrant birds (geese, waders, and passerines) (Hersteinsson and Macdonald 1996).

While body size reflects the conditions that prevailed during an organism's birth year, 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 survives. According to the traditional explanation of Bergman's rule (Blackburn et al. 1999), large size of homeotherms is selected for under cold temperatures because of their relatively low rate of heat loss and high ability to reserve fat. Thus, Bergmann's rule predicts that large body size is advantageous during cold periods (Yom-Tov and Yom-Tov 2006, Yom-Tov et al. 2006). On the other hand, 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 and 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. Tornberg et al. (2014) have shown that small male goshawks breeding in rabbit-poor habitats demonstrate a better body condition than do larger males. Animals facing the harsh conditions may thus show a reduction in size, as occurred under the harsh El Nino conditions, in which the Galapagos marine iguana *Amblyrhynchus cristatus* reduced its body size (Wikelski and Thom 2000). Thus, according to this latter hypothesis, during harsh conditions average body size will be smaller than during good years.

In this study we sought to examine the relationship between mean annual body size and condition during the year of death, and mean annual environmental conditions or their indices (namely, ambient summer and winter temperatures, precipitation, and cloud cover, the SPG, and summer and winter NAO) in the Icelandic Arctic fox. These climatic factors may affect fox body size characteristics either directly through their effect on heat conservation, or indirectly through their effect on food availability. We predicted that, in Iceland, in a severely cold year or in a year when food resources are scarce (i.e. minimal fish stock and drop in breeding seabirds) only small-size foxes, which require less energy for long-term maintenance, would survive. We also predicted that such small-size foxes would display better body condition. In contrast, when the climate is mild and food is abundant, a larger body size would be favoured because such individuals are better competitors for breeding territories and resources. We expect that at the population level (i.e. the mean of a morphological variable) the difference in size and conditions between poor and abundant years will be apparent, and can be accounted for by climate conditions. In other words, in this study we predicted that annual mean of body size and condition would reflect the climate or resources available to the foxes in the year they were killed. Furthermore, in areas where food availability is meager, a small difference in climate might tilt the balance from food sufficiency to food shortage. Thus, in eastern Iceland, where poor conditions exist in comparison to the western region, the effect of climate on body size would be more profound. Arctic foxes are active year round; they do not go into torpor nor deposit large amounts of fat. Consequently, they are limited by the duration they can tolerate food shortage or the severe conditions that preclude successful foraging. Many studies have shown that when food is abundant, adult Arctic foxes experience higher survival rates, have higher pregnancy rates, and larger litters (reviewed by Audet et al. 2002). In other words, climatic conditions might favour either larger or smaller individuals through selective pressure on survival.

Material and methods

The present study is based on Arctic fox carcasses that were voluntarily supplied by fox-hunters between 1979–2005, who also provided specific information on the date and region of collection for every individual (Fig. 1). Between 1979 and 1985 hunters brought in mainly mandibles, while mostly whole carcasses were supplied from 1986 to 2005. There was no specific hunting season; foxes were killed throughout the year in both regions. In total, we obtained 3390 individuals from eastern Iceland, which were killed mostly during summer (52.0%) and spring (24.4%). However, more than 600 (18.1%) were killed in winter, while the least number (4.5%) were killed during autumn. A nearly similar distribu-

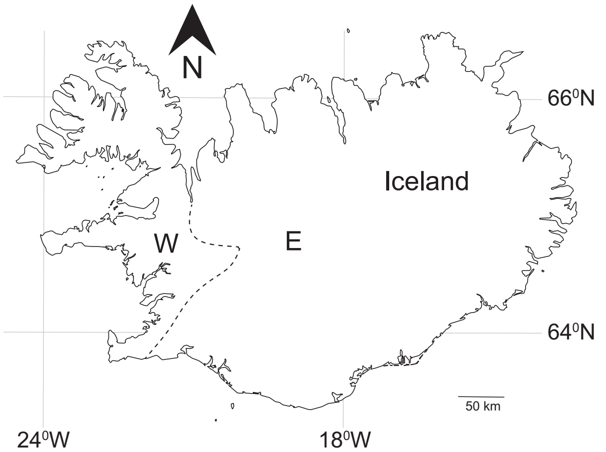

Figure 1. A map of Iceland showing the division (dotted line) into western and eastern regions.

tion across seasons was observed in the sample of 2940 foxes killed in western Iceland (55.1, 26.0, 14.0, and 4.8% for summer, spring, winter, and autumn, respectively). For the purpose of this study we made a simple division of the country into areas where a) productive coasts are an important part of the habitat, and b) inland habitat dominates.

We measured the length of 6322 mandibles, weighed the body mass of 3377, and determined rump fat thickness (RFT; Prestrud and Nilssen 1992) for 3512 Arctic foxes. Digital calipers were used for measuring the left mandible to an accuracy of 0.1 mm. In cases where this was not possible the right mandible was used. Carcasses were weighed to an accuracy of 100 g. Carcasses of foxes that had clearly lost much blood were not weighed. Body mass of individual foxes may vary considerably due to many factors, including time of latest meal and defecation, state of pregnancy and lactation in females, seasonal fat accumulation, and time of year. Accordingly, body mass is a less accurate measure for body size than the mandibles, whose size does not vary on a daily basis. We determined the age of all foxes by X-raying the canine teeth and counting the annual cementum lines of canine roots (Hersteinsson et al. 2009). We evaluated fox body condition by measuring rump fat thickness (RFT; Prestrud and Nilssen 1992) using sliding callipers to an accuracy of 1mm. Because larger individuals had a larger deposit of rump fat ($r_{2700} = 0.539$, $p < 0.0001$), we controlled for body mass using regression residuals.

We examined the effect of SPG index, NAO, temperature, precipitation, and cloud cover during the year of death on mandible length, body mass, and RFT variation of the Arctic fox in Iceland. We defined the following independent variables (data provided in Supplementary material Appendix 1, Table A1).

1) The sub-polar gyre index – we used data of the SPG Index (extracted from Fig. 2b in Hátún et al. 2005).

2) Mean annual summer (June, July and August) and winter (December, January and February) North Atlantic Oscillation (NAO) – monthly NAO data were obtained from the Climate Research Unit database at the Univ. of East Anglia (<www.cru.uea.ac.uk/cru/data/nao.htm>).

3) Mean annual summer (June, July and August) and winter (December, January and February) temperature – mean annual temperature in Iceland increased by 0.76°C between 1960–2000 ($r^2 = 0.137$, $F_{1,43} = 6.8$, $p = 0.0122$; $Y = 0.019 \times \text{Year} - 34.284$), and mean August temperature increased by 1.24°C during the same period ($r^2 = 0.251$, $F_{1,43} = 14.4$, $p = 0.0005$; $Y = 0.032 \times \text{Year} - 53.581$). Monthly mean temperature data from 16 weather stations across Iceland (Akureyri, Dalatangi, Eyrarbakki, Fagurhólsmýri, Hella, Höfní Hornafirði, Hveravellir, Keflavíkurflugvöllur, Kirkjubæjarklaustur, Kvígindisdalur, Lambavatn, Reykhólar, Reykjavík, Stórhöfði, Stykkishólmur, Vík í Mýrdal) were obtained from the Icelandic Meteorological Office (<www.vedur.is/vedurfar/yfirlit/medaltalstoflur/Manadargildi.html>) and used for calculating means per sector.

4) Mean annual summer (June, July and August) and winter (December, January and February) precipitation (mm) and cloud cover (oktas). Cloud cover is expressed in fractions of one-eight of the sky that are covered by clouds, ranging from completely clear sky (0 oktas) to complete overcast (8 oktas). Monthly means were obtained from the Icelandic Meteorological Office (<http://en.vedur.is/Medaltalstoflur-txt/Manadargildi.html>) and means per sector were calculated as for temperature.

5) Sector – the Arctic fox occurs throughout Iceland. Western Iceland has a far higher length of seashores per surface area than the northern, eastern, and southern seashores combined (excluding exposed sandy shores devoid of macroscopic life; Ingólfsson 1975, Fig. 1). Although western Iceland comprises only a quarter of the total surface area of the country, its productive seashores are twice as long as those of all the rest of the country (3884 versus 1985 km). The difference in the surface area of productive seashores (tidal range) is even greater in western Iceland, i.e. 205 km² (0.98% of the surface area) versus 21 km² (0.026% of surface area) in the rest of the country (Ingólfsson 1975). Of the three most populous Alcids that form fox prey the common guillemot *Uria aalge*, Brünnich's guillemot *U. lomvia*, and the razorbill *Alca torda* nesting on mainland Iceland 91, 97, and 93%, respectively nest in the cliffs of western Iceland (Gardarsson 1995). Thus, for the purpose of this study we made a simple division of the country into areas where a) productive coasts are an important part of the habitat, and b) inland habitat dominates. The country was thus divided into western Iceland, and the rest of the country (hereafter eastern Iceland), based on county borders in order to correspond to the subdivision of foxhunting statistics. With an average dispersal distance of only about 25 km for both sexes in coastal habitats (Angerbjörn et al. 2004) and about double that in inland habitats (Hersteinsson unpubl.), our division of the samples into two major regions (west and east) is reasonable (Fig. 1).

To access the level of multicollinearity between our nine independent variables we examined the correlation coefficients between all possible pairwises, and calculated the variance inflation factor (VIF) for each variable. VIF measures the inflation in the regression coefficient due to multicollinearity. $VIF = 0$ indicates no correlation, $1 < VIF < 5$ moderate correlation, and $VIF > 5$ high correlation.

Arctic foxes grow until the age of 8–9 months, after which growth is insignificant (Hersteinsson unpubl.). In this study we used only specimens older than 10 months. We

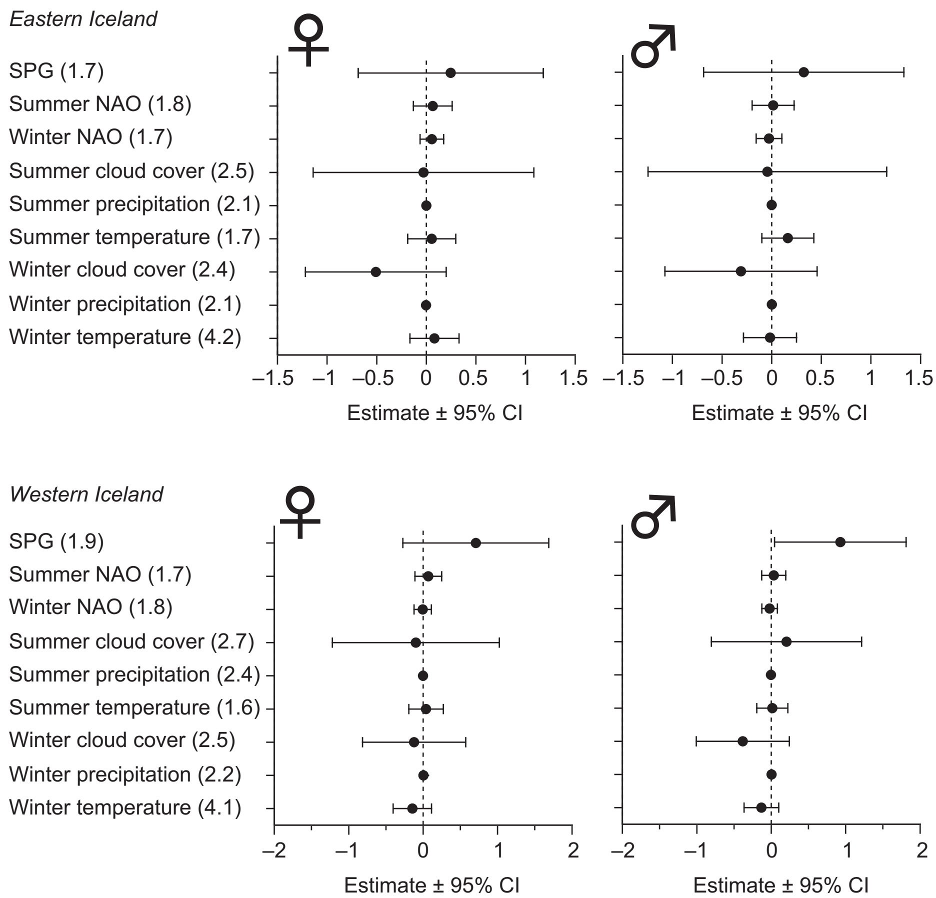

Figure 2. Effect estimate (± 95% CI) of nine climatic variables on body weight of female and male Arctic foxes in eastern and western Iceland. Dotted line denote the null hypothesis of no effect. The variance inflation factor (VIF) is presented in parentheses.

did not use years for which sample size was smaller than 10 specimens; thus the samples we used in this study spanned the years 1979–2005.

We examined the effects of SPG index, summer and winter NAO index, mean annual summer and winter temperature, precipitation and cloud cover in the year of death, and sector on fox mean annual mandible length, mean annual body mass, and mean annual RFT by fitting a general linear model (GLM) using JMP (ver. 11, SAS), and selected the best model (i.e. subset of predictors) using the Akaike's information criterion (AIC; Burnham and Anderson 2001). This approach weighs all the possible subsets (i.e. models) by the amount of variance explained and model complexity (i.e. the number of explanatory variables; K). When $n/K < 40$ the AIC values were corrected for small sample size (AIC_c) using the equation in Burnham and Anderson (2001). Level of support for an AIC_c value was evaluated by ΔAIC_c (i.e. $AIC_c = AIC_i - AIC_{min}$; Burnham and Anderson 2001). Models with ΔAIC_c values of 0–2 provided similar support (Burnham and Anderson 2001). We examined all 314 possible subsets.

Results

The pairwise correlation between independent climatic variables ranged from –0.41 to 0.55; thus each variable accounted for no more than 25% of the variance in any of the other variables (Supplementary material Appendix 1, Table A2). The mean pairwise correlation between independent climatic variables was 0.106 ± 0.272. VIF was below 3 in all variables except for mean winter temperature, which reached a value of 4.2 (Fig. 2), a level indicating low to moderate multicollinearity.

Age significantly correlated with body weight ($r_{1886} = -0.107$, $p < 0.0001$), mandible size ($r_{3386} = 0.038$, $p = 0.028$), and RFT ($r_{1915} = -0.048$, $p = 0.035$) in males. In females, only body weight ($r_{1492} = -0.075$, $p = 0.004$) significantly correlated with age (mandible size: $r_{2934} = 0.004$, $p = 0.813$, and RFT: $r_{1600} = -0.009$, $p = 0.728$). However, the effect of age (i.e. r^2) was negligible accounting for less than 1% of the variation in body weight, mandible size, and RFT. Therefore, we did not control for age in any of the analyses below.

Analysis using the full models showed that only males in western Iceland significantly increased their body mass in response to the increase in SPG (Fig. 2; $F_{1,23} = 4.9$, $p = 0.043$). Increase in mandible size in both males and females as a function of increase in SPG was only observed in eastern Iceland (Fig. 3; females: $F_{1,24} = 16.6$, $p < 0.001$, males: $F_{1,24} = 46.0$, $p < 0.001$). None of the full models (divided by sex and region) revealed any climatic variables that significantly affected RFT, controlled for body mass. Next, we present the most supported subset models.

Body mass – in eastern Iceland, the two supported models ($\Delta AIC_c \leq 2$) showed significant climatic affects on female body mass. The first model was composed of mean cloud cover during winter ($r^2 = 0.167$, $AIC_c = 7.5$, $F_{1,24} = 4.6$, $p = 0.042$, Table 1). An increase in winter cloud cover reduces female body mass ($\beta = -0.447$, Fig. 4). The second significant model was that of mean cloud cover during winter ($AIC_c = 8.2$, $F_{1,24} = 4.8$, $p = 0.040$) and mean summer temperature ($F_{1,24} = 3.4$, $p = 0.077$, Table 1). Mean summer temperature was the only significant factor affecting body mass of males in eastern Iceland ($r^2 = 0.228$, $AIC_c = 8.92$, $F_{1,24} = 6.8$, $p = 0.016$, Table 1). Male body mass increased with summer temperature ($\beta = 0.195$). The next supported model for males was that of SPG ($AIC_c = 9.47$), but this association was insignificant (verging on significance; $F_{1,24} = 4.2$, $p = 0.052$). The other two supported models comprised mean summer temperature and mean winter cloud cover for the first model, and mean summer temperature and mean summer cloud cover for the second model. However, only mean summer temperature showed a significant effect in these two models ($p \leq 0.016$).

On western Iceland, none of the supported models for females (mean winter cloud cover, mean winter temperature, and SPG) were significant. However, for males we detected two equally supported models. The first model was that of winter mean temperature and SPG ($AIC_c = 3.5$, $F_{1,23} = 9.7$, $p = 0.005$ and $F_{1,23} = 14.1$, $p = 0.001$, respectively). The second model comprised mean winter temperature, mean winter cloud cover, and SPG ($AIC_c = 5.0$) but only SPG had a significant effect ($F_{1,23} = 8.4$, $p = 0.011$, Table 1).

Mandible size – in eastern Iceland, SPG was the only supported variable that significantly affected mandible size in females ($\beta = 2.56$, $r^2 = 0.418$, $AIC_c = 43.8$, $F_{1,24} = 16.6$, $p = 0.0005$, Table 1, Fig. 4). In the other two supported models (SPG and mean summer cloud cover, and SPG and mean winter NAO) only SPG was significant ($p = 0.0003$). For eastern-Iceland males, we detected a combined significant model ($AIC_c = 30.4$, $r^2 = 0.726$), comprising of SPG ($\beta = 3.68$, $F_{1,24} = 57.7$, $p < 0.0001$) and mean winter NAO ($\beta = 0.17$, $F_{1,24} = 8.3$, $p = 0.009$). The other two supported models comprised of SPG, mean winter NAO, and mean winter and summer temperatures, but only SPG and mean winter NAO were significant in these two models (Table 1). The role of SPG diminished towards western Iceland. In western-Iceland males the effect of SPG was apparent but not significant ($\beta = 1.49$, $R^2 = 0.135$, $AIC_c = 55.0$, $F_{1,24} = 3.6$, $p = 0.071$), while in western-Iceland females we did not detect any significant effects.

Rump fat thickness (RFT) – in eastern Iceland, the only supported model ($AIC_c = 2.6$) for females was that of mean summer temperature ($F_{1,13} = 5.0$, $p = 0.044$; Table 1). In males, we found a single supported model comprising of two variables ($AIC_c = 0.7$, $r^2 = 0.671$): mean winter NAO ($\beta = -0.125$, $F_{1,11} = 11.5$, $p = 0.008$) and SPG ($\beta = -0.858$,

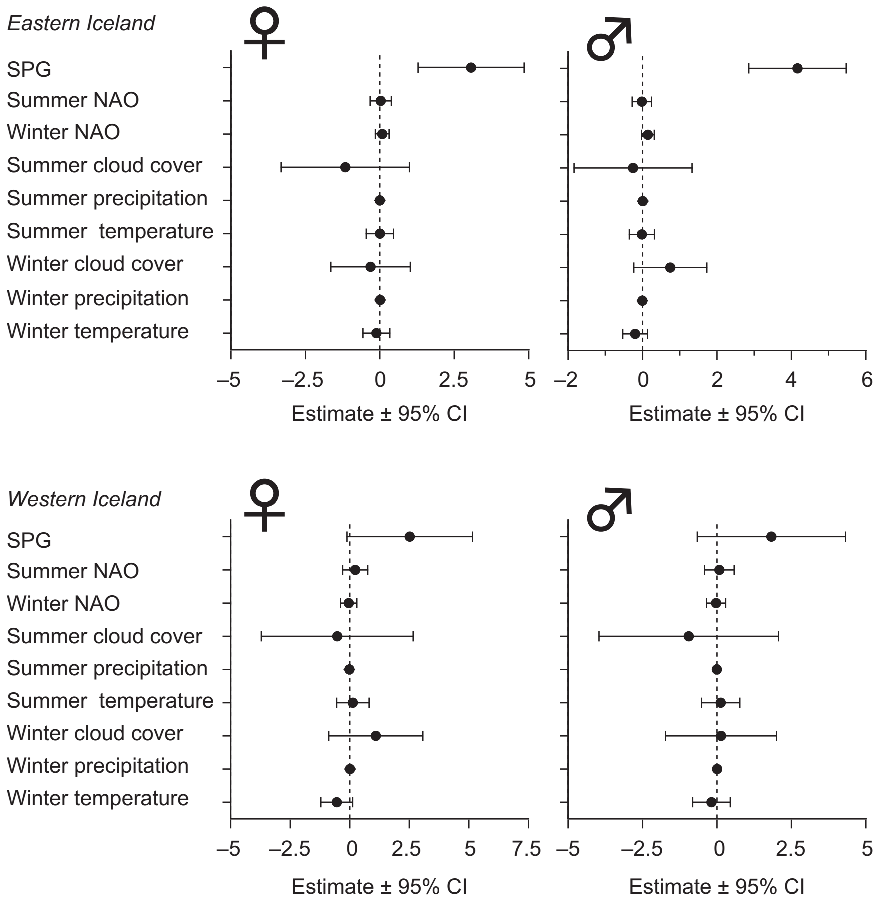

Figure 3. Effect estimate (± 95% CI) of nine climatic variables on mandible size of female and male Arctic foxes in eastern and western Iceland. Dotted line denote the null hypothesis of no effect.

Table 1. The most supported ($\Delta AIC_c \leq 2.0$) and significant climatic models affecting mandible, body weight, and RFT of male and female Arctic foxes in eastern and western Iceland. Upward arrow indicates positive association and downward arrow indicates inverse association. Climatic variables lacking an arrow have no significant effect. Model R^2 is denoted in parentheses. WinCC – mean winter cloud cover, SumCC – mean summer cloud cover, SumT – mean summer temperature, WinT – mean winter temperature, WinNAO – mean winter North Atlantic Oscilation, WinP – mean winter precipitation, and SPG – sub-polar gyre.

Variable	East ♀	East ♂	West ♀	West ♂
Mandible size	SPG↑ (0.418) SPG↑ + WinNAO (0.461) SPG↑ + SumCC (0.456)	SPG↑ + WinNAO↑ (0.726) SPG↑ + WinNAO↑ + WinT (0.747) SPG↑ + WinNAO↑ + SumT (0.744)		
Body weight	WinCC↓ (0.167) WinCC↓ + SumT (0.280)	SPG (0.167) SumT↑ (0.228) SumT↑ + SPG (0.291) SumT↑ + WinCC (0.291)		SPG↑ + WinT↓ (0.462) SPG↑ + WinT + WinCC (0.499)
Rump fat (RFT)	SumT↓ (0.296)	SPG↓ + WinNAO↓ (0.671)		WinCC↑ (0.384) WinCC↑ + WinNAO (0.474)

$F_{1,11} = 12.6$, $p = 0.006$). Not a single supported model was found for western-Iceland females. Mean winter cloud cover was the only significant effect in the two supported models for western-Iceland males (Table 1). The best model was that of mean winter cloud cover ($\beta = 0.414$, $r^2 = 0.384$, $AIC_c = -3.1$, $F_{1,12} = 7.5$, $p = 0.018$); while the second best model ($AIC_c = -1.97$) was that of mean winter cloud cover ($\beta = 0.498$, $F_{1,11} = 9.9$, $p = 0.009$) and mean winter NAO ($\beta = 0.05$, $F_{1,11} = 1.9$, $p = 0.198$), but the latter effect was not significant.

Discussion

As predicted, our findings indicate that the environmental conditions which had prevailed during the year of death were strongly related to both body size (as represented by mandible length), body mass and rump fat thickness (controlled for body mass). The findings also differ according to the method used to analyze the data: the full models, which include all nine environmental variables, selected SPG as the only significant variable for both females and males in eastern Iceland, and for males in western Iceland. AIC models, on the other hand, revealed that multiple variables were significantly related to the three dependent variables. SPG is included in four out of the eight models (Table 1), emphasizing the importance of this variable.

SPG is a proxy for a variety of climatic processes that may affect both ocean and atmospheric conditions in marine and terrestrial habitats around and in Iceland. However, at the present state of knowledge, the mechanisms by which SPG operates on climate are little understood and we can only speculate. Seabirds are a key ingredient in the diet of Arctic foxes, and SPG, through its effects on water temperature and salinity, may affect the entire food chain in the North Sea, on which the Arctic fox depends. For example, SPG effect on plankton density may lead to a higher abundance of fish and other seabird prey species. SPG may also influence conditions in the wintering grounds for many migrant bird species which nest in Iceland, and thus have a further effect on the Arctic fox's body size and abundance. SPG also affects atmospheric conditions that, in turn, affect net primary productivity in Iceland, and thus indirectly affect food availability of the terrestrial food web (i.e. land birds) to Arctic foxes. When the SPG index is high, the temperature and salinity of waters flowing from the south on both sides of Iceland are relatively low, and vice versa for a low index. The surface waters lose heat to the atmosphere, bringing the region milder temperatures, depending on the strength of the SPG. Hence, high SPG is related to warm air temperatures, which affect primary productivity, thus explaining the positive relationship between SPG and body size and mass of the Arctic foxes.

The effects of climate parameters on body size and mass were not uniform throughout Iceland or between the sexes, and varied in relation to region and sex. In general, foxes in eastern Iceland were more affected by the variation in climate parameters than those in the west (R^2 ranged 0.167–0.726 and 0.384–0.462 in eastern and western Iceland, respectively; Table 1). We suggest that the stronger effect of environmental conditions in the east in comparison with the west may be explained by the variation in food availability between the two regions. The diet of the western-Iceland Arctic fox population depends largely on seabirds throughout the year, while they also scavenge for mussel shells, crustaceans, and beached seal carcasses in winter. Hence, the foxes there enjoy the favorable food conditions that prevail in western Iceland. Western Iceland also has a far higher proportion of productive seashores than northern, eastern, and southern Iceland combined (Ingólfsson 1975, Fig. 1).

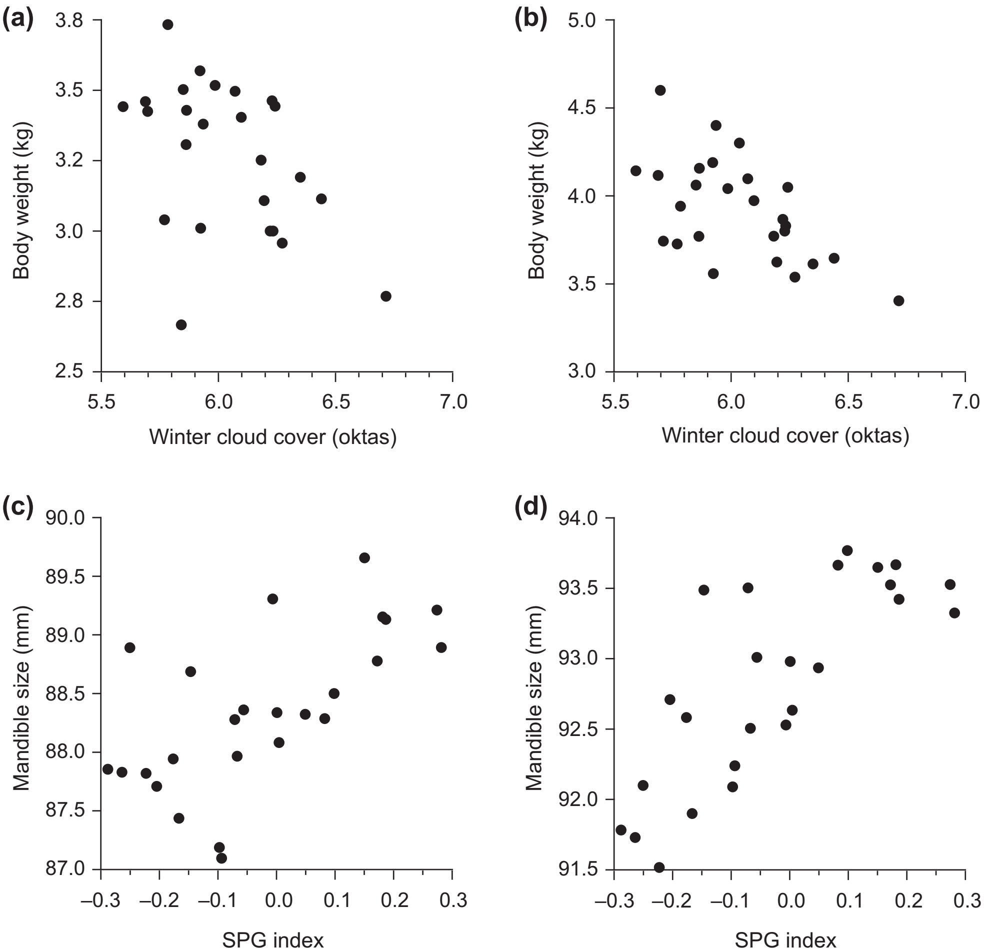

Figure 4. Effect of Iceland climatic variables on Arctic fox morphology. Correlation plots between mean winter cloud cover and body weight of eastern females ((a) $r^2 = -0.167$, $p = 0.042$) and western males ((b) $r^2 = 0.258$, $p = 0.008$), and mean SPG index and mandible size of females ((c) $r^2 = 0.418$, $p = 0.0005$) and males ((d) $r^2 = 0.622$, $p < 0.0001$) in eastern Iceland.

Although western Iceland comprises only a quarter of the total surface area of the country, its productive seashores are twice as long as those of all the rest of the country. Of the three most populous species of guillemots, between 91% and 97% nest in the cliffs of western Iceland (Gardarsson 1995).

In contrast, in most of eastern Iceland, food type and availability are poorer and scarcer. The foxes switch their diet in spring from ptarmigans *Lagopus mutus*, snow buntings *Plectrophenax nivalis*, and caches from the previous summer and carcasses, to migrant birds (geese, waders, and passerines) (Hersteinsson and Macdonald 1996). Thus, in eastern Iceland, where poor conditions exist in comparison to the western region, the effect of climate on body size will be more profound.

NAO was included in two of the eight selected models. NAO is also a proxy for various climate parameters that may affect fox body size, either directly through their effect on energy expenditure, or indirectly through their effect on food availability. For example, at high latitudes, ambient temperature is a major factor determining net primary productivity (NPP). The warmer the summer, the higher the NPP (Kimball et al. 2007), which in turn also affects the higher links in the food chain on which the Arctic foxes depend. Nevertheless, in spite of the frequent mention in the literature that temperature is the prominent factor affecting body size, especially in Arctic regions, temperature relates to a smaller proportion of the variation in body size than do the two indices (SPG and NAO). Our findings indicate that body size is affected by multiple climate variables rather than one key factor. They also indicate that climate variables vary greatly geographically, even in a relatively small area such as Iceland, as different variables were selected as significant for in eastern and western Iceland.

It is noticeable that SPG and winter NAO positively affect mandible size and body weight, but negatively affect fat deposits (see arrows in Table 1). We see the same kind of trends in summer and winter temperatures (Table 1). We suggest that foxes particularly accumulate fat in food-poor areas, while in food-rich areas they rely on the abundant food and do not accumulate the large fat deposits that may hinder their movement.

In conclusion, body size, body mass, and RTF of the Arctic fox in Iceland have been shown here to be significantly affected by the environmental parameters that prevailed during their year of death. SPG was the most prominent, followed by NAO, while ambient temperature and cloud cover were selected as significant in fewer models. We suggest that the stronger effect of the two indices rather than any direct climate parameter is explained by the fact that both indices incorporate several direct climate parameters, such as temperature and cloud cover. Furthermore, SPG reflects the conditions in the oceans surrounding Iceland more than the other climatic variables we used in this study, which are largely land related. Because Arctic foxes in Iceland feed largely on marine birds and invertebrates, the SPG seems to encompass more accurate information on the direct ocean forces that affect food availability to the foxes.

The effect of environmental conditions on the dependent variables was stronger in the less productive eastern-Iceland region, apparently because in areas where food availability is scarce, a small difference in climate may tilt the balance from food sufficiency to food shortage. Thus, in eastern Iceland, where poor conditions exist in comparison to its western region, the effect of climate on body size will be more profound than in the west.

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Supplementary material (Appendix ECOG-01782 at <www.ecography.org/appendix/ecog-01782>). Appendix 1.