Climate warming is associated with smaller body size and shorter lifespans in moose near their southern range limit.

Primary research article

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Running title: The shrinking moose of Isle Royale

Abstract

Despite the importance of body size for individual fitness, population dynamics and community dynamics, the influence of climate change on growth and body size is inadequately understood, particularly for long-lived vertebrates. Although temporal trends in body size have been documented, it remains unclear whether these changes represent the adverse impact of climate change (environmental stress constraining phenotypes) or its mitigation (via phenotypic plasticity or evolution). Concerns have also been raised about whether climate change is indeed the causal agent of these phenotypic shifts, given the length

of time-series analysed and that studies often do not evaluate – and thereby sufficiently rule out – other potential causes. Here, we evaluate evidence for climate-related changes in adult body size (indexed by skull size) over a 4–decade period for a population of moose (*Alces alces*) near the southern limit of their range whilst also considering changes in density, predation, and human activities. In particular, we document: (i) a trend of increasing winter temperatures and concurrent decline in skull size (decline of 19% for males and 13% for females) and (ii) a negative correlation between skull size and winter temperatures during the first year of life. These patterns could be plausibly interpreted as an adaptive phenotypic response to climate warming given that latitudinal/temperature clines are often accepted as evidence of adaptation to local climate. However, we also observed: (iii) that moose with smaller skulls had shorter lifespans, (iv) a reduction in lifespan over the 4-decade study period, and (v) a negative relationship between lifespan and winter temperatures during the first year of life. Those observations indicate that this phenotypic change is not an adaptive response to climate change. However, this decline in lifespan was not accompanied by an obvious change in population dynamics, suggesting that climate change may affect population dynamics and life-histories differently.

Introduction

Whilst the influence of climate change on species distributions and phenology has been studied across a number of taxa, the influence of climate change on growth and ultimately body size has received far less attention, particularly for long-lived vertebrates (Sheridan & Bickford, 2011). Nevertheless, climate-related changes in body size are expected to have important consequences for ecosystem functioning because body size influences almost all aspects of an organism's biology (Peters, 1983; Calder, 1984), including fitness-related traits that subsequently influence population dynamics (e.g. Ozgul *et al.*, 2010). Changes in body

size could also affect community dynamics because of the indirect influence body size has on the flow of energy through ecosystems (Brown *et al.* 2004).

Although body size trends which appear to be linked to contemporary changes in climate have now been documented in a wide range of species (Gardner *et al.*, 2011; Sheridan & Bickford, 2011), neither the underlying mechanisms nor the consequences of these changes are well understood. In particular, it is not clear whether such changes represent an adverse impact of climate change (environmental stress constraining growth and ultimately phenotypes) or its mitigation (via phenotypic plasticity or evolution). For example, latitudinal/temperature clines in size (i.e., body size tending to decline at lower latitudes where the climate is warmer) are often accepted as evidence of adaptation to local climatic conditions, because smaller body size is considered advantageous in warmer climates due to higher thermoregulatory efficiency (Olson *et al.*, 2009; Gardner *et al.*, 2011). Therefore, declines in size could be an adaptive response to climate change. Alternatively, declines in size could represent an adverse effect of climate change on growth, if climate warming represents deteriorating environmental conditions during development (Post *et al.*, 1997; Tafani *et al.*, 2013). The critical evidence that would distinguish adaptive change from adverse impact would be evidence on the relationship between body size and fitness-related traits. However, many of the studies documenting trends in body size do not assess whether these trends are accompanied by changes in survival or reproductive success.

Another underappreciated challenge of evaluating climate-related changes in phenotype is the robustness of inferences that assign climate as the causal agent (Boutin & Lane, 2014; Merilä & Hendry, 2014). This challenge arises because time series data of adequate length are often unavailable and because changes in climate are often correlated with other ecological

processes capable of inducing phenotypic change (e.g. habitat degradation and rates of human exploitation). An important case in point involves a red squirrel (*Tamiasciurus hudsonicus*) population in Kluane, Canada for which climate warming had been inferred as the cause of advances in first parturition date over the decade-long (3 generation) period (Réale *et al.*, 2003). This inference was based on having identified a plausible mechanism between ultimate cause (climate warming), proximate cause (food availability, represented by an increased likelihood of large cone mast years) and effect (phenotypic change). However, after another decade of data became available, further analysis revealed that the trend had reversed, indicating that the observed change in phenology was unlikely to be caused by climate warming (Boutin & Lane, 2014).

Climate warming is expected to have the greatest impact on phenology, phenotypes and distributions for species living at higher latitudes or altitudes and for populations residing near the southern limit of their species' geographic range (Parmesan & Yohe, 2003; Parmesan, 2006). In particular, moose (*Alces alces*) populations near their southern range limit in the Great Lakes region of United States are thought to be especially vulnerable (Lenarz *et al.*, 2010; Rempel, 2011) because: (i) winters are warming particularly rapidly in this region of North America (Pryor *et al.*, 2014), and (ii) moose are considered cold-adapted and intolerant of heat (Renecker & Hudson, 1986). For example, moose respond to relatively warm weather (above 5º C in winter and above 14º C in summer) with increased metabolic, heart, and respiration rates, and reduced food intake, which ultimately leads to a loss of body weight (Belovsky & Jordan, 1978; Renecker & Hudson, 1986, 1990). Warm winter temperatures are also thought to negatively influence moose survival (Lenarz *et al.*, 2009). Consequently, there are growing concerns about the extent that climate warming could negatively influence moose populations and how those influences would cascade to

negatively impact recreational and economic opportunities, the functioning of these ecosystems, and their cultural and ecological values.

Here we examine how adult body size (indexed as skull size) is influenced by climate warming over a 37–year period in a population of moose near the southern limit of the species' geographic range, in Isle Royale National Park, USA (48° N, 89° W). In particular, we assessed the relationship between skull size and average winter temperatures experienced during the first year of life. We focused on winter temperature in the first year of life because: (i) winter temperatures have steadily increased over the last half century (Fig. 1a), (ii) winter is warming faster than any other season in this portion of North America (Pryor *et al.*, 2014), (iii) winter is generally thought to be the most stressful time of year for moose, because adult mortality is highest in winter (Stubsjøen *et al.*, 2000), and (iv) warm winters temperatures during early development have previously been found to have a negative effect on growth and body size in other ungulate species (e.g. Post *et al.*, 1997). We also assessed whether climate warming and changes in body size were associated with a reduction in lifespan (measured here as age at death) because understanding whether phenotypic changes are accompanied by changes in fitness-related traits, such as lifespan, is essential for determining whether the change is adaptive. Lastly, to determine whether climate warming is indeed the causal agent of the observed phenotypic changes, we evaluated whether several other possible alternatives could be responsible for changes in moose body size, namely changes in density dependence, predation, hunting or anthropogenic changes in habitat quality.

Materials and Methods

Study system

Isle Royale National Park is a 544 km^2 island in Lake Superior, North America. The island is inhabited by a population of moose which has been continuously studied since 1959 (Vucetich & Peterson, 2004). Over this nearly 60–year time period the island's winter climate has been characterized by both considerable inter-annual variation and a long-term warming trend (Fig 1a). Wolves (*Canis lupus*) are the only predator of moose on Isle Royale and neither the moose, nor the forest have been harvested by humans for nearly a century (Vucetich & Peterson, 2004).

Focusing on skull size is appropriate because it is a good indicator of overall body size in adult moose (Haigh, Stewart & Mytton 1980) and because it has been used to evaluate temporal changes in body size in other mammals (Yom-Tov *et al.*, 2006, 2008). Although most other studies use body mass as an indicator of overall body size, there is still value in evaluating indicators of skeletal size because it does not fluctuate in fully grown adults. In contrast, body mass changes on a daily, seasonally, and yearly basis according to the stage of the individual's reproductive cycle, and also in response to both short term changes in weather and other environmental factors, as well as longer term changes in climate. Consequently, changes in body mass also reflect changes in body condition, rather than growth *per se*. Therefore, whilst evaluations of body mass are valuable, it is also important to evaluate climate-related changes in measures of skeletal size. Furthermore, it is often not feasible to obtain body mass measurements for wild populations of large species, such as moose, especially when they reside in remote locations with limited access, such as our study site.

Although moose do not attain full adult body size until four-to-five years of age, the rate of growth is substantially slower after the first year of life, and a large proportion (over 70%) of structural growth has already taken place by the end of the first year (Franzmann & Schwartz, 2007). For this reason, it is relevant to evaluate skull size in relation to the conditions experienced during the first year of life. We also included moose population density (experienced during the first year of life) as a predictor variable to account for a potentially confounding effect of density, which fluctuated substantially over the study period, especially during the 1990s when a large population decline occurred (Fig. 1b). Furthermore, population density has previously been shown to influence growth, body size, and survival in other ungulates (Festa-Bianchet *et al.*, 2003; Solberg *et al.*, 2004), and is liable to indicate the influence of several density-dependent processes on growth, such as intraspecific competition for food and predation risk. For example, low population densities are likely to reflect relatively low levels of intraspecific competition for food as well as high predation risk (Vucetich *et al.*, 2011). We could not include predation rate, the variable which is most closely related to predation risk, in our models because such data are not available for an important portion of the study period (before the 70's). However, predator (wolf) density is correlated with predation rate for the period 1971–1999 during which estimates of predation rate exist (*Correlation coefficient (r)* = 0.80). Therefore we include wolf density during the year of birth as a covariate in our models as a proxy for predation risk.

Data collection

Average winter temperatures (January-February) were recorded at a nearby weather station (approximately 50 km away; Western Regional Climate Center 2016). Moose and wolf population density have been estimated annually (as total number of moose and wolves on Isle Royale) since 1959 using methods described in Vucetich *et al.* (2011). Each year the

skeletal remains of deceased moose were detected via extensive hiking across the island in summer (~625 miles/summer) and island-wide aerial surveys in winter (~100 hours/winter) from 1959 onwards. Of the 4658 carcasses discovered and necropsied, it was possible to estimate skull size, age-at-death and year-of-birth for 662 individuals (346 males and 316 females). This sample only includes individuals that died after five years of age to ensure that we only included fully grown adults in our analyses. Furthermore, we only included individuals for which year-of-death could be reliably estimated (e.g. those detected shortly after death (Peterson, 1977)). The first cohort represented in our dataset is 1963, the first cohort for which we had all requisite information (i.e., skull size, year-of-birth, and age-at-death). We excluded cohorts born after 1999 because the longest-living moose (approximately upper quartile) in these cohorts could still be alive and are therefore not represented in our samples.

Skull size was estimated in a laboratory (after bones had been cleaned) as the product of three linear measures: cranial length (shortest distance from the external occipital protuberance to the lowest point of the left indentation on the suture where the frontal bone and nasal bone join), cranial width (distance between the temporal bones, which corresponds to the widest portion of the inner braincase), and cranial height (distance between the top of the parietal bone and the sphenoid bone). Age-at-death was reliably estimated by counting cementum lines in the teeth (Peterson 1977; Haagenrud 1978; Rolandsen *et al.* 2008). Year-of-birth was calculated by subtracting age-at-death from known year-of-death.

Analyses

To assess the influence of climate on body size we used linear mixed-effect models to quantify the extent to which skull size varied in relation to average winter temperature, moose density, and predator density during the individual's first year of life. We also evaluated models that account for an interactive effect of winter temperature and moose density and an interactive effect of winter temperature and predator density. Because the effect of climate on phenotypes may be non-linear (Mysterud *et al.*, 2001), we also evaluated the prospect that the influence of winter temperature on skull size was best characterized by a second-order polynomial. We fit winter temperature, moose density and predator density as continuous fixed-effect variables and individuals' year-of-birth was fit as a random effect.

We also assessed whether any climate-related changes in body size were associated with changes in lifespan because body size has previously been found to be an important determinant of survival in ungulates (e.g., Gaillard *et al.*, 2000). To do so, we first used mixed-effect models (with year-of-birth as a random effect) to quantify the extent to which skull size and lifespan (age at death) were related. We then used mixed-effect models to assess the extent to which lifespan was related to winter temperature and moose density. We did not include predator density as a covariate in models aiming to predict lifespan because doing so could result in misleading inferences about the effect of predation on lifespan. In particular, because our data set only included fully grown adults it would not account for the effects of predation on calves, yearlings and young adults. Lastly, we used simple linear regression to assess the presence of long-term temporal trends in average skull size and lifespan.

We conducted all analyses in R version 3.2.0 (R Core Development Team, 2015) and calculated the portion of variation explained by our best models (i.e., R^2) using the "MuMin" package (Barton, 2016). We based model selection on Akaike's information criterion (AIC; Burnham and Anderson 2002). We analysed data for males and females separately because moose are sexually dimorphic, with males having significantly larger skulls than females (Appendix S2). Moreover, in cases of sexual dimorphism, the faster growing sex (males; Garel et al. 2006), is thought to be more sensitive to growth setbacks in early life (Metcalfe & Monaghan, 2001). A third reason for sex-specific evaluation is because selective pressure for larger body size is likely greater in male ungulates, whose body size influences access to females (McElligott *et al.*, 2001).

Results

Skull size was negatively related to both winter temperature and moose density for both sexes (Table 1). That is, the smallest individuals were born in years when winter temperatures were relatively warm and moose density was high (Fig. 2). For both males and females, the most parsimonious model that we evaluated included all three main effects (winter temperature, moose density and predator density), and an interaction between winter temperature and moose density (Table 1). This interaction term indicated that the influence of winter temperature on skull size was more pronounced for individuals (particularly males) born in years when moose density was high; however, the effect size of this interaction was very weak for females (Fig. 2). For plots of the raw data showing how skulls size also varies with predator density see Appendix 3.

Skull size and lifespan were positively correlated in both males (Fig. 3a) and females (Fig. 3b, Table 2). For example, individuals with skull sizes in the upper quartile lived an average of 3.48 years longer for females and 3.49 years longer for males compared to individuals with skull sizes in the lowest quartile for each sex. There was also evidence to suggest that lifespan was negatively related to winter temperature and population density as the model including both these fixed-effects outperformed the null model and the density only model – a result consistent for both males and females (Table 3). The relationship between lifespan and winter temperature was best characterised using a second order polynomial (Table 3), with individuals experiencing particularly warm first winters tending to have shorter lifespans than those experiencing moderate or colder first winters. Lastly, mean skull size and lifespan both declined throughout the study period for both sexes (Fig.4; Table 4). Some of these relationships appeared non-linear, with an increasing rate of decline toward the end of the study period.

Discussion

Here we provide evidence of a decline in skull size (an important indicator of changes in overall body size), which appears to be at least partially attributable to climate warming in a population of moose (Fig. 2). More specifically, we observed a decline in skull size over a four-decade period (Fig. 4a and 4b) which was correlated with increasing winter temperatures experienced during the first year of life (Table 1). Earlier work has demonstrated that the environmental conditions experienced during development can affect adult body size and that these effects are greater for males, the faster growing sex (Toïgo *et al.*, 1999; Solberg *et al.*, 2004). Our work extends these insights to show how climate warming appears to have resulted in a multi-decadal trend in body size (Fig. 4a and b). Furthermore, our analysis also

indicates that this climate-related decline in size is associated with a reduction in lifespan (Fig. 3c and 3d; see also Table 2-4).

Is climate change the causal agent?

A major concern surrounding studies investigating climate-related phenotypic changes is whether climate change is really the causal agent. This is because climate change is often correlated with other ecological processes which could also cause phenotypic changes (Merilä & Hendry, 2014). However, several considerations support the rationale for thinking that the reduction in moose body size observed here is at least partly attributable to climate warming. In particular, we can account for what might otherwise be plausible causes of declines in body (density dependence, habitat degradation, hunting, and predation pressure). Firstly, the influence of winter temperature was apparent even when the influence of fluctuations in moose and wolf density were taken into account (Table 1). Moreover, winter temperature was not correlated with moose density or wolf abundance during the study period (Fig. 1 and Fig. S1). Second, whilst hunting can be a significant cause of selective pressure on body size for ungulates (Fenberg & Roy, 2008), this population has been protected from hunting for nearly a century. Third, changes in moose body size are unlikely to be due to habitat degradation associated with timber harvesting or changes in land-use because Isle Royale has been protected from those activities for nearly a century.

Is the change in body size adaptive?

It is often difficult to evaluate whether climate-related phenotypic changes are adaptive, despite it being crucial for understanding how species will cope with ongoing climate warming. Our analyses provide a practical example of such difficulties. For instance, if we did not have data to evaluate changes in lifespan, then we may well have concluded that the

observed decline in body size was adaptive (if only as a result of phenotypic plasticity). The basis for this inference would have been: (i) body mass is expected to decline in locations where the climate is warming because smaller body sizes are thought to be advantageous in warmer climates due to thermoregulatory efficiency (Teplitsky *et al.*, 2008; Teplitsky & Millien, 2014); and (ii) moose are thought to experience an adverse energetic balance in warm weather due to increased metabolic, heart, and respiration rates, and reductions in food intake (Belovsky & Jordan, 1978; Renecker & Hudson, 1986, 1990). However, the observed decline in body size was associated with a decline in an important determinant of fitness (lifespan). This conclusion is based on having observed: (i) a positive correlation between skull size and lifespan (Fig. 3; and Table 2), (ii) a negative relationship between winter temperatures and both body size and lifespan (Table 2 and 3), and (iii) a declining temporal trend in lifespan (Fig. 4 and Table 4), as well as an understanding that lifespan is a primary predictor of lifetime reproductive success in ungulates (Clutton-Brock, 1988; Gaillard *et al.*, 2000). Independently of changes in lifespan, we might also expect individuals' reproductive success to decline as moose become smaller because reproductive success is positively associated with body size in many species (Peters, 1983; Clutton-Brock, 1988; McElligott *et al.*, 2001). It therefore seems unlikely that the fitness could have been maintained by an increase in reproduction to compensate for the decline in lifespan. Indeed, recruitment has not increased over this time period (Peterson & Vucetich, 2016). Consequently, the concurrent decline in lifespan with body size is reasonably suggestive of fitness decline. Yet, moose abundance did not start to decline towards the end of the study period as one might have expected (Peterson & Vucetich, 2016). Nevertheless, the decline in lifespan still indicates that the observed phenotypic changes are not adaptive, but instead represent an adverse impact of an increasingly stressful environment.

To our knowledge, there are few cases where a climate driven change in body size was considered to be adaptive. In one case, an increasing temporal trend in body mass was associated with increased overwinter survival for yellow-bellied marmots (*Marmota flaviventris*); however, this study didn't directly assess the relationship between body mass and climatic variables (Ozgul *et al.*, 2010). In another case, a climate-driven decline in body size for Soay sheep (*Ovis aries*) was considered adaptive by Boutin and Lane (2014) because it was the result of an increase in the number of small individuals surviving as winters became more mild (Ozgul *et al.*, 2009). Otherwise, changes in climate are mostly thought to have resulted in nonadaptive changes in mammalian body size. In addition to our results, other examples of nonadaptive phenotypic changes include declines in body size which were accompanied by: (i) reduced condition and survival for polar bears (*Ursus maritimus*; Stirling and Derocher 2012), (ii) reduced litter size for alpine marmots (*Marmota marmot*) in the French Alps (Tafani *et al.*, 2013), and (iii) reduced fecundity for Norwegian red deer (*Cervus elaphus*; Post *et al.*, 1997). Consequently, most documented cases (including ours) which directly assessed the influence of climate warming on body size and fitness related traits in mammals found that the change was not adaptive. This suggests that most climate-driven declines in body size are primarily represent the result of environmental stress, rather than adaptation to new conditions.

Rate of phenotypic change

Concerns have been raised that most vertebrate species will not be able to evolve fast enough to keep pace with the rapid rate of climate change (Teplitsky & Millien, 2014). It is therefore pertinent to pay attention to the rates of phenotypic changes observed in wild populations. Previously, a 1.25% change per generation in body mass was observed in yellow-bellied marmots over a period of about 8 generations (assuming generation time of 4 years, Schwartz

et al. 1998) for a total 10% change in body mass over a 33–year period (Ozgul et al., 2010). That change was found to be mostly due to phenotypic plasticity rather than evolution by natural selection. By comparison, we observed a much faster rate of change: the cohort mean for skull size declined throughout the study period by approximately 19% for males (Fig. 3a) and 13% for females (Fig. 3b). This equates to approximately 3.8% (males) and 2.6% (females) per generation, over a period of approximately five generations (assuming a generation time of seven years; Gaillard 2007). Given that phenotypic plasticity is likely to lead to more rapid changes than natural selection, and the fact that our results suggest that the decline in skull size is not adaptive, we suspect that the rapid rate of change observed in this study is mostly likely attributable to phenotypic plasticity, rather than evolution. It is also important to recognize that some portion of the temporal changes in skull size and lifespan are attributable to changes in density (See Fig. 1 and Table 1).

Conclusions and future directions

The steep decline in lifespan over the study period adds to existing concerns that moose will be adversely affected by climate warming in the southern portions of their geographic range, such as the Upper Great Lakes region. For example, projections of moose dynamics under various climate change scenarios indicate that moose density will decline at the southern limit of their distribution in Ontario (Rempel, 2011). Furthermore, previous work indicates that overwinter survival rates of radio-collared moose were lower during warmer winters (Lenarz *et al.*, 2009). Those findings were based on 116 moose observed over a 6–year period in northeastern Minnesota. Our findings extend that insight considerably, by evaluting the effect of climate on lifespan in more than 600 moose over four decades. What is not yet known is which mechanisms are responsible for the relationship between warmer winter temperatures, growth, body size, survival, and lifespan. For example, although we hypothesed that climate

warming influenced moose growth by altering energy expenditure for thermoregulation, it is also possible that climate related changes in parasite abundance, specifically winter ticks (*Dermacentor albipictus;* Addison *et al.*, 1994) or the quality and quantity of food available to moose during winter, also play an important role. Furthermore, it is also not clear how and to what extent an apparently adverse impact of climate warming on life history will influence population dynamics. Previously, the population dynamics of Isle Royale moose were thought to have been influenced more by predation than by weather conditions (Vucetich & Peterson, 2004; Wilmers *et al.*, 2006; Peterson *et al.*, 2014). However, the influence of climate change on predator-prey dynamics is not well understood. One possiblity is that predator preferences may shift in response to climate-induced changes in prey body size because body size influences how accessible prey are to predators (Clements *et al.*, 2014). Another possibility is that kill rates may change in response to climate-induced changes in winter conditions, such as snow depth and the frequency of freeze-thaw and rain-on-snow events, (independently of any changes in body size), if these snow conditions affect moose mobility and vulnerability.

Despite almost 60 years of research and detailed knowledge of the moose population, its habitat, and main predator, there still are a number of uncertainties surrounding the impact of climate warming on moose. In particular, that the decline in an important life-history trait, lifespan, was not mirrored by a decline in population size was not entirely expected, especially given that the decline was not compensated for by an increase in recruitment (Peterson & Vucetich, 2016). The explanation may lie in accounting for the difference between a time-lagged effect of a cohort-based decline in lifespan (Fig. 4) and interannual variation in survival rates (not analysed here). In any case, these results have important implications for understanding the effect of climate change on wildlife populations and also

highlights the complexity and extent of challenges associated with trying to elucidate them. Future research might focus on understanding the extent to which climate change has disparate effects on population dynamics and life history and the mechanisms beneath it. More specifically, it could focus on the influence of climate change on predator-prey dynamics, moose foraging ecology, parasite loads and the overall nutritional condition of moose population, followed by studies examining the consequences of these changes for population dynamics.

Acknowledgements

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Tables

Table 1. Results of linear, mixed-effects models to assess the influence of average winter temperature, moose density (estimate of the total number of moose) and predator density (estimate of the total number of wolves) in the first year of life on skull size (measured using an index of cranial volume) for a population of moose in Isle Royale National Park. Predictor variables were standardized to enable their effect sizes to be compared as the units of these variables are all on different scales. ΔAIC is the AIC for the model of interest minus the smallest AIC for the set of models being considered. The best model has an ΔAIC of zero and is bold faced.

	Predictor variable(s)	Males			Females		
		Estimate	SE	ΔAIC	Estimate	SE	ΔAIC
1.	Null	-	-	30.2			31.6
2.	Winter temperature	-19.1	18.6	26.7	-16.4	11.5	24.9
3.	Moose density	-39.2	14.8	18.8	-27.7	9.2	19.7
4.	Predator density	33.8	15.4	20.3	30.8	9.3	18.0
5.	Winter temperature +	-19.9	16.6	11.9	-15.8	9.8	12.7
	Moose density	-39.8	14.8		-28.0	9.0	
6.	Winter temperature +	-13.6	17.9	14.2	-10.3	10.2	12.5
	Predator density	32.0	15.7		29.0	9.5	
7.	Moose density +	-30.1	16.4	11.7	-18.7	9.6	10.1
	Predator density	20.9	16.2		23.0	9.7	
8.	Winter temperature +	-16.6	16.9	5.3	-11.8	9.4	4.2
	Moose density +	-31.7	16.5		-19.9	9.6	
	Predator density	18.1	16.5		20.4	9.9	
9.	Winter temperature +	-19.9	16.9	6.7	-15.8	10.0	8.3
	Moose density +	-40.4	16.2		-27.4	9.3	
	Winter temperature: Moose density	-2.1	15.0		2.1	9.5	
10.	Winter temperature +	-13.7	18.2	8.6	-10.6	10.3	7.7
	Predator density +	32.2	16.2		29.2	9.7	
	Winter temperature: Predator density	1.4	17.7		5.0	11.0	
11.	Winter temperature +	**-16.5**	**17.1**	**0.0**	**-11.8**	**9.6**	**0**
	Moose density +	**-32.6**	**17.7**		**-19.6**	**9.8**	
	Predator density +	**18.2**	**16.7**		**20.4**	**10.1**	
	Winter temperature: Moose density	**-2.9**	**15.0**		**0.3**	**9.0**	

Table 2. Results of linear, mixed-effects models to assess the relationship between skull size (measured using an index of cranial volume) and lifespan (age at death in years) for a population of moose in Isle Royale National Park. See Table 1 for meanings of abbreviations.

Variable	Males			Females		
	Estimate	SE	ΔAIC	Estimate	SE	ΔAIC
Null	-	-	35.5	-	-	32.8
Lifespan	**22.1**	**3.4**	**0**	**11.8**	**1.9**	**0**

Table 3. Results of linear, mixed-effects models to assess the extent to which lifespan (age at death in years) varied in relation to average winter temperature and moose density (the total number of moose) for a moose population in Isle Royale National Park. Predictor variables were standardized to enable their effect sizes to be compared as the units of these variables are all on different scales. The relationship with winter temperature was best characterised using a second order polynomial, where there are two estimates, the first corresponds to the linear term.

Predictor variable(s)	Males			Females		
	Estimate	SE	ΔAIC	Estimate	SE	ΔAIC
Null	-	-	13.0	-	-	15.0
Winter temperature	-13.1; -8.7	7.0; 6.6	1.1	-6.4; -5.8	7.4; 6.8	6.0
Moose density	-0.6	0.3	12.4	-1.0	0.3	9.4
Winter temperature +	**-13.4; -9.1**	**6.7; 6.3**	**0**	**-5.9; 7.1**	**6.6; 6.1**	**0**
Moose density	**-0.6**	**0.3**		**-1.0**	**0.3**	

Table 4. Results of regression analyses assessing temporal trends in skull size (measured using an index of cranial volume), lifespan (age at death in years) in a population of moose in Isle Royale National Park. See Table 1 for meanings of abbreviations. The relationship between year of birth was best characterised using a second order polynomial and where there are two estimates, the first corresponds to the linear term.

Response Variable	Predictor variable	Males			Females		
		Estimate	SE	ΔAIC	Estimate	SE	ΔAIC
Skull size	Null	-	-	62.3	-	-	37.3
	Year of birth	**-1383.5; -505.0**	**173.0; 172.9**	**0**	**-748.6; -347.7**	**124.8; 124.8**	**0**
Lifespan	Null	-	-	131.0	-	-	88.6
	Year of birth	**-0.2**	**0.02**	**0**	**-33.5; -4.2**	**3.3; 3.3**	**0**

Figure captions

Fig. 1 Temporal variation in average winter (Jan-Feb) temperatures (a), the total number of moose (b), and total number of wolves in Isle Royale National Park for the study period, 1963-1999. For context, 1000 moose corresponds to a density of 1.8 moose/km^2 and 50 wolves corresponds to a density of 0.9 wolves/km^2.

Fig. 2 Skull size (measures using an index of cranial volume) shown in relation to average winter temperatures and moose density during the first year of life for male (a) and female (b) moose in Isle Royale National Park. Circles represent measurements from individual moose. Lines represent model predictions when predator abundance was fixed at the median value (0.04 wolves/km^2 or 22 wolves) and moose density was fixed at the 15th (1.5 moose/km^2; black lines) and 85th percentile (2.4 moose/km^2; grey lines). The median moose density for this time period was 1.9 moose/km^2 (1014 moose). Note, difference in scale of y-axes. See Appendix 3 for alternative plots of the raw data showing how skulls size also varies with predator density (Fig. S3).

Fig. 3 Lifespan and skull size (measured here using an index of cranial volume) were positively correlated for both (a) male and (b) female moose. Circles represent measurements of individual moose. Solid lines represent model predictions and dashed lines are the 95% confidence intervals.

Fig. 4 Temporal trends in skull size (measured using an index of cranial volume; a and b) and lifespan (c and d) for cohorts of adult males (left column) and females (right column) in Isle Royale National Park. Circles represent measurements of individual moose. Solid lines represent model predictions and dashed lines the 95% confidence intervals.

Supporting Information

Appendix S1 – Correlation between temporal covariates (winter temperatures, moose density and wolf density).

Appendix S2. – Sex-specific differences in skull size.

Appendix S3. – Plots of raw data showing how skull size varied in relation to environmental conditions during early life (winter temperatures, moose density and wolf density).

(a) $R^2 = 0.17$

Cranial volume (cm^3)

Year of birth

(b) $R^2 = 0.12$

Cranial volume (cm^3)

Year of birth

(c) $R^2 = 0.32$

Lifespan (age at death in years)

Year of birth

(d) $R^2 = 0.25$

Lifespan (age at death in years)

Year of birth