How Social Behaviour Links Environment and Body Size in Mammalian Carnivores

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Abstract: Many hypotheses for larger body size with increasing latitude invoke environmental explanations, such as decreasing temperature. We propose a novel explanation that links environmental selection pressures and body size with spacing behaviour. We test for causal pathways between (1) environment (snow, latitude, primary productivity, seasonality, and temperature) and (2) spacing behaviour (home range size and population density) and (3) body size and sexual size dimorphism using structural equation modelling of independent contrasts derived from 101 mammalian terrestrial carnivore species. Although strong intercorrelations existed among all five environmental variables, primary productivity and seasonality best related to body size and size dimorphism. Using information-theoretic approach to select optimal model fit established that body size was not influenced directly by environment but rather through the intermediary variables, home range or density. For example, species living in highly seasonal environments were associated with larger home ranges and low density that in turn selected for larger body mass and greater sexual size dimorphism. Thus, spacing behaviour provides an important evolutionary link explaining interspecific body size variation.

INTRODUCTION

Two general rules in evolutionary ecology are that species evolved larger body size and greater sexual size dimorphism at higher latitudes. Various factors have been attributed as responsible for increasing body size with latitude, including latitudinal clines in primary productivity [1, 2]; ability to survive environmental unpredictability characteristic of higher latitudes by enhancing thermoregulation and/or resisting starvation [3-5]; decreased competition or increased predation [6]; life-history adjustment to colder environments [7]; and Bergmann's rule [8], which has been interpreted as a prediction that surface area/mass for larger animals provides better adaptations against cold temperatures [9]. Body size influences and is influenced by behaviour, population dynamics and life history. Body size has been proposed to relate to latitudinal and seasonal variation [10] and clines of size *vs* latitude are similar in northern and southern hemispheres [11]. Although previous authors mentioned that environmental stability might be a factor determining body size diversity, they have not suggested specific mechanisms by which this could happen [12, 13].

A possibly mechanism for terrestrial mammals is seasonal snow conditions that affect the movements of animals and subsequently lead to adaptations, such as delayed implantation, to overcome limitations posed by social behaviour [14]. Similarly, Bergmann's rule may be more related to seasonality than to temperature [15, 16]. Thus among terrestrial animals, a novel explanation for the relationship of larger size with latitude is the hypothesis that (1) animals living at high latitudes exist at lower density and occupy larger home ranges because of seasonality and snow fall, and consequently, (2) have evolved the adaptation of large body size to facilitate movement as a means of overcoming the difficulties of acquiring food and mates while living in seasonally cold environments. Thus, life-history traits, such as body size, may ultimately be derived from living in specific environments whereas the proximate selection pressure is social behaviour and mating systems [17-19].

For mating, the one sex (usually males) that is responsible for finding the other sex (usually females) needs to move about more during the mating season [14, 20]. Therefore, a consequence of living at low densities and occupying large ranges is that greater sexual size dimorphism will also occur with increasing latitude. This leads to the additional expectation that species inhabiting high latitudes would display greater size dimorphism than low latitude species. Social behaviour does not always have to be the recipient of environmental selection pressure; behaviour is a life-history force of its own, and capable of modifying morphological traits [21, 22]. Both large-scale patterns of body size variation may have similar underlying causes [23].

We used data on terrestrial mammalian carnivores to test for a relationship between environment (snow, temperature, productivity, and seasonality) and spacing behaviour (density and home range size) and body size or sexual dimorphism. We used phylogenetic independent contrasts because species do not represent independent data points [24, 25]. Path analysis using structural equation modeling [26] was the statistical analysis technique used to test causal hypotheses explaining the evolution of body size and sexual size dimorphism. We generate plausible hypotheses represented by graphical path models (Fig. **1**) that estimate the relative contributions of species' traits to the evolution of body size patterns. We test among the multiple causal hypotheses explaining the evolution of body size using an information-theoretic approach. Here, Akaike's information criterion (AIC) provides the quantitative method to choose a final

*Address correspondence to this author at the Fisheries and Oceans Canada, 501 University Crescent, Winnipeg, MB, R3T 2N6, Canada; E-mail: steve.ferguson@dfo-mpo.gc.ca

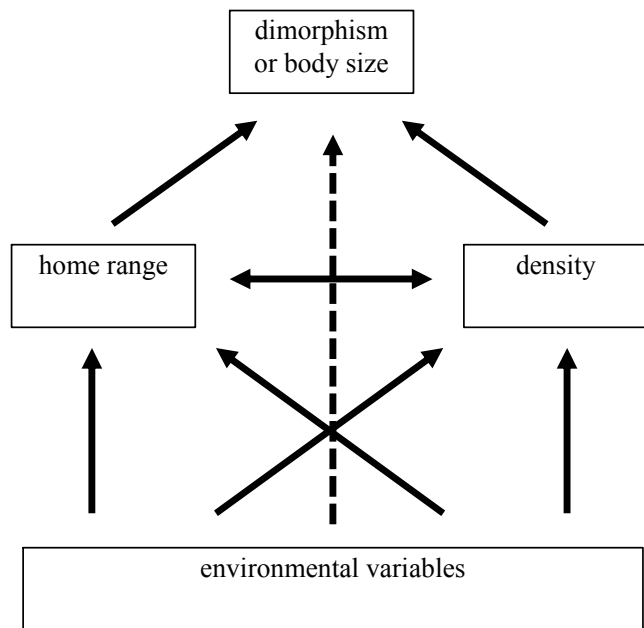model that has both simplicity and high predictive power [27].

Fig. (1). Hypothesized path models predicting the influence of environment (5 variables) on behaviour (population density, home range size) and body size/sexual size dimorphism. Environmental characteristics are the assumed explanatory causal pattern and subsequent tests assessed model fit with (solid lines) or without (dashed line) the intermediate social behaviour variables.

MATERIALS AND METHODS

Data Sources

We obtained published data on species' traits from 8 families (of 12), 60 genera, and 101 species of terrestrial mammalian carnivores (e.g., *Mammalian Species* articles) [28]. We calculated an index of sexual size dimorphism as the ratio of male mass/female mass [29]. Data on density and home range of species were obtained from summary literature and means of population estimates were calculated for species. Summaries of population studies across a species' geographic range were used to represent species means although we recognize the assumptions inherent to this approach [30] and the bias in geographic distribution of species well enough studied to be included (e.g, 25% of species from southern hemisphere). We used the phylogenetic tree and branch lengths proposed by Bininda-Emonds [31] and the taxonomy of Wozencraft [32].

Longitude and latitude of the midpoint of each species historical distribution was obtained using maps from *Mammalian Species* accounts and world maps [28]. We used the absolute values for latitude to compare similar latitude locations in the northern (positive; n = 90) and southern (negative; n = 30) hemispheres. Environmental variables included seasonality, primary productivity, snow accumulation, and temperature, and were calculated using data from 13,332 weather stations distributed over the globe and then temporally averaged from 30-year normals and spatially interpolated to a regular grid of 1° by 1° latitude-longitude intervals [33]. Seasonality was calculated as the coefficient of varia-

tion of monthly (n = 12) values of actual evapotranspiration ($mm·m^{-2}$) using a water budget analysis [34, 35]. Actual evapotranspiration generally increases with solar input, precipitation, and soil water holding capacity and is highly correlated with primary productivity [12, 36, 37]. Lieth's [38] algorithm was used to convert actual evapotranspiration to total net primary productivity ($g·m^{-2}·y^{-1}$). Larger primary productivity values and larger coefficients of variation indicated greater energy and seasonality within a species' geographic range, respectively.

Statistical Analyses

For all traits, log_{10}-transformed data distributions did not differ significantly from normality using Wilk-Shapiro normality test. Data points that vary with phylogenetic history violate the statistical assumption of independence and therefore require phylogenetic corrections [24]. Consequently, we used phylogenetically corrected analyses. Standardized independent contrasts were calculated by dividing the unstandardized contrast by the standard deviation [39] using the Phenotypic Diversity Analysis Program (PDAP version 5) PDTREE module [25, 40]. General linear models of standardized independent contrasts were forced through the origin. Diagnostic tests were used to determine if branch lengths were standardized properly and that the assumption of Brownian evolution was appropriate [41].

Since the benefits of larger body size may be multiple [42, 43], we tested for relationships among the reduced variable set using the multiple hypothesis structure [44] of path analysis and structural equations [45]. An *a priori* path model approach was used to generate multiple models based on a proposed hypothesis and mechanistic understanding of relationships between variables (Fig. **1**). The logic for the selected models was to select a subset of best fit models that included (1) environment as the initial causal variable [14] and (2) body size or sexual dimorphism as the final outcome [46]. The social behaviour hypothesis was tested by comparing model fit between those models having spacing behaviour traits (home range and density) included as intermediate variables between 1 and 2 and those models that linked 1 and 2 directly. Fit was assessed according to the information-theoretic approach (Akaike's information criterion).

The adjusted trait values were used in model comparisons with the Covariance Analysis of Structural Equations (SAS 1999 Version 8.02; SAS Institute Inc, Cary: PROC CALIS). The variables are assumed to have an approximately multivariate normal distribution for the maximum-likelihood estimation procedure. The option NOINT was used to specify that no intercept be used in the linear equations as required with the use of phylogenetic independent contrasts [40]. The coefficients were parameterized using iterative normal-theory maximum likelihood.

Model appropriateness was indicated by the following model information. The optimization parameters include the goodness-of-fit statistics, which indicate the appropriateness of the linear structural equation model for the given data set (covariance matrix). Chi-square measure is the likelihood ratio test statistic for the null hypothesis that the predicted matrix has specified model structure against the alternative that the matrix is unconstrained. The probability denotes the likelihood under the null hypothesis of obtaining a greater

Chi-square statistic and here, a larger *p* indicates better model fit. The Bayesian information criteria (BIC or Schwarz's information criterion; [47]) is similar to AIC and helps to determine the best number of parameters with the smallest value being considered more appropriate. For small sample sizes and with maximum–likelihood estimation, AIC is the preferred measure of model appropriateness [48]. Thus, statistically the model that yields the smallest value of BIC or AIC was considered best.

All 40 models (20 for body size and 20 for dimorphism) were tested for absolute fit as well as relative fit by comparing models based on goodness-of-fit statistics [27]. Model comparisons were done using the Kullback-Leibler information approach with modified Akaike's Information Criterion for small samples [27]. AIC_c was calculated as

$$AIC_c = -2\ln L(\Theta) - 2K + 2K(K + 1)/(n - K - 1)$$

where $\ln L(\Theta)$ is the value of the maximized log-likelihood over the unknown parameters (Θ) given the data and the model, K is the number of parameters, and n is the sample size. Akaike differences (Δ_i) and normalized Akaike weights were calculated (w_i). In general, where $\Delta_i < 2.0$, the models were considered to have substantial support [49].

RESULTS

Many of the independent contrast traits were correlated, particularly among the five environmental variables (Table 1). Some relevant relationships included: male mass better

related to sexual size dimorphism than female mass; density decreased and home range increased with body mass; and greater sexual size dimorphism was associated with greater snow on ground.

Body Size Models

We tested for the directional cause and effect of environment, behaviour, and body size relationships among 20 separate models. Seven models were supported statistically based on the Kullback-Leibler information approach (Table 2). For the body size model, the best cause and effect grouping of explanatory variables ($\Delta_i < 1.0$) indicated relationships between primary productivity or seasonality, home range size or density, and body size (Fig. 2A). Snow and latitude were adequate explanatory variables only with reduced model acceptance $1.0 < \Delta_i < 2.0$ and having range or density as intermediate variables. For none of the seven acceptable pathways, did density significantly affect home range or home range affect density (i.e., only one intermediate variable was supported). In other words, either environment acted on home range and then body size or environment acted on density and then body size never did environment act on home range which acted on density which acted on body size.

In the case of density, seasonality was negatively related to density and density was negatively related to body size. Thus, higher latitude and greater seasonality related to lower population density, which favored the evolution of larger

Table 1. **Correlation Matrix of Independent Contrasts for Nine Traits from 101 Carnivore Species. Pearson's Correlation Coefficient, Probability, Sample Size**

Trait	Female Mass	Male Mass	Dimorphism	Latitude	Primary Productivity	Temperature	Snow	Seasonality	Density
Male mass	+0.933 0.0001 101								
Dimorphism	-0.045 0.63 101	0.266 0.003 101							
Latitude	+0.129 0.16 101	+0.150 0.10 101	+0.089 0.33 101						
Primary Productivity	-0.028 0.76 101	-0.018 0.85 101	+0.018 0.84 101	-0.749 0.0001 101					
Temperature	-0.142 0.12 101	-0.170 0.06 101	-0.122 0.18 101	-0.596 0.0001 101	+0.460 0.0001 101				
Snow	+0.035 0.70 101	+0.104 0.26 101	+0.265 0.003 101	+0.468 0.0001 101	-0.271 0.003 101	-0.639 0.0001 101			
Seasonality	+0.065 0.48 101	+0.087 0.34 101	+0.139 0.13 101	+0.792 0.0001 101	-0.782 0.0001 101	-0.535 0.0001 101	+0.521 0.0001 101		
Density	-0.476 0.0001 59	-0.490 0.0001 59	-0.027 0.84 59	-0.096 0.47 59	+0.055 0.68 59	+0.128 0.33 59	-0.087 0.51 59	-0.146 0.27 59	
Home Range	+0.502 0.0001 70	+0.535 0.0001 70	+0.137 0.26 70	+0.137 0.26 70	-0.134 0.27 70	-0.245 0.04 70	+0.129 0.29 70	+0.191 0.11 70	-0.376 0.008 49

Table 2. **Results from a Comparison of 40 Structural Equation Models Derived Using Data for 101 Species of Mammalian Carnivores**

Model Rank (Best to Worst)	R^2	Chi-Square	p	BIC	AIC_c	$\Delta_i AIC_c$	w_i
(A) Female Body Size Models:							
pp→range→size	0.252	0.04	0.83	-4.20	-1.61	0.00	0.1475
season→range→size	0.253	0.06	0.80	-4.19	-1.59	0.02	0.1462
pp→density→size	0.228	0.16	0.69	-3.92	-1.49	0.12	0.1391
season→density→size	0.238	0.88	0.35	-3.20	-0.78	0.83	0.0974
snow→range→size	0.268	1.44	0.23	-2.81	-0.212	1.40	0.0733
latitude→range→size	0.270	1.68	0.195	-2.56	0.028	1.64	0.0650
latitude→density→size	0.251	1.85	0.174	-2.23	0.196	1.81	0.0598
(B) Sexual Size Dimorphism Models:							
pp→range→density→dim	0.100	3.93	0.269	-7.74	-1.55	0.00	0.253
season→density→dimorphism	0.071	0.71	0.100	-3.37	-0.95	0.60	0.187
lat→range→density→dimorphism	0.106	4.69	0.200	-6.98	-0.78	0.77	0.172
snow→density→dimorphism	0.023	1.32	0.251	-2.76	-0.34	1.21	0.138

Only the models with substantial support are presented (see methods). (**A**) The two environment variables, seasonality (season) and primary productivity (pp) influenced body size via home range size and population density. (**B**) Environmental variables influences sexual size dimorphism (dim = male/female body mass) via home range size (range) and population density. Variables are standardized contrasts that control for phylogenetic effects.

Statistics used to assess model appropriateness: R^2 estimates model explanatory power and were derived using general linear models. Chi-square measure is the optimum function value F multiplied by (N-1). A greater Chi-square statistic with a higher p value indicates a more reliable model. BIC = Bayesian information criteria (Schwarz's Information Criterion) = -2log(£) + K * log(n). AIC = second order Akaike information criteria (AIC = n log(σ^2) + 2K) is a general criterion for choosing the best number of parameters to include in a model. AIC_c = bias adjusted AIC for small sample size = AIC+(2K(K+1))/(n-K-1) where K is the total number of estimated regression parameters including σ^2 (no intercept) and n is sample size. Δ_i = AIC differences computed as AIC_i – AIC_{min}. w_i = exp(-1/2Δ_i)/$\sum$exp(-1/2Δ_r).

body size. The explained variation (R^2) was consistent among body size models with approximately 25% of the variation explained (0.23 – 0.27).

In the case of home range, primary productivity was positively related to home range size while seasonality was negatively related, and home range size was positively related to body size. Thus, greater snow, at high latitudes, with low primary productivity, and high seasonality related to individuals occupying larger home ranges and this favored the evolution of larger body size. We tested for all pathways that started with environment as the cause and in no instance did temperature provide a significant model (results not shown).

Sexual Dimorphism Models

Of the 20 sexual dimorphism models tested, the three best causal grouping of variables (Δ_i < 1.0) indicated that the environment acted directly on density or indirectly through home range, which then influenced dimorphism (Fig. **2B**). Here, greater seasonality related to lower population density which related to greater sexual size dimorphism. Alternatively, living at high latitudes with low primary productivity related to individuals occupying large home ranges, which related to reduced population density and greater dimorphism.

Two models were supported with lower acceptance criteria (1.0 < Δ_i < 2.0). One model indicated that snow on the ground directly influenced dimorphism with greater snowfall being correlated with greater dimorphism. In the other model, greater latitude was associated with greater range size which in turn correlated with lower population density and then finally low density was associated with greater sexual size dimorphism. This latter model was the only complex (4 variable) model supported of the 40 models tested. In none of the pathways did temperature provide a statistically adequate explanation of the evolution of sexual size dimorphism. The explained variation (R^2) was approximately 10% (0.03 – 0.11) among size dimorphism models.

DISCUSSION

Here, we have formulated a novel hypothesis and provided evidence that environment may affect body size through the intermediate, social behaviour. Current evidence already suggests that Carnivora follow Bergmann's rule with greater body size associated with high latitudes [43, 50] and that evolution of body size and sexual size dimorphism in mammals is likely a result of multiple factors [46, 51]. Larger body size at northern latitudes (i.e., Bergmann's rule) was originally explained in terms of advantages for heat conservation [52]; but see [53]. However, non-physiological benefits of larger body size may include greater mobility and ability to range more widely to overcome local fluctuations in abundance of food and mates. For example, reproductive strategies may ultimately be derived from living in high-latitude environments but the proximate selection pressure is social behaviour and mating systems [14, 18, 54]. Indirectly we test whether body size and dimorphism evolve together and found that both responded to the same environmental pressures. Thus, these relationships support that both are under similar environmental selection pressure and may be responding to similar relationships [23].
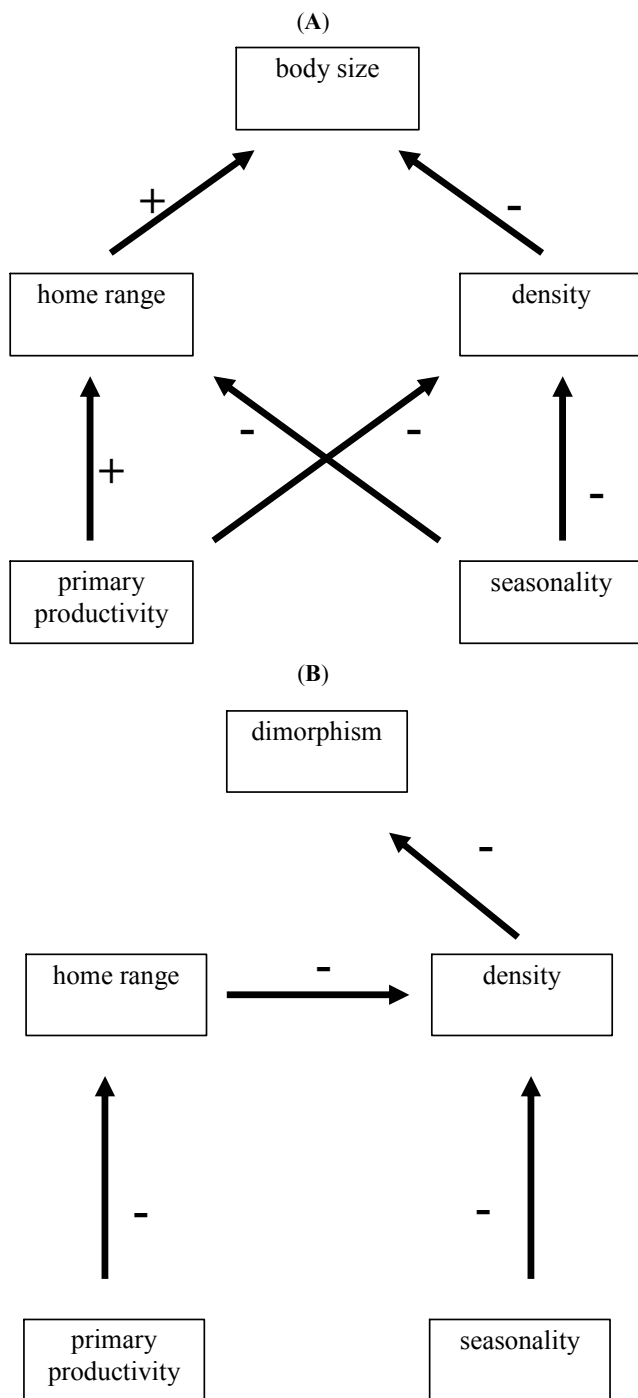
(A)

(B)

Fig. (2). Two structural equation models representing the relationships among explanatory variables influencing (**A**) body size and (**B**) sexual size dimorphism for 101 species of mammalian carnivores. Relationships shown were derived from models with $\Delta_i < 1.0$ (Table **2**). Arrows depict the proposed links between variables. Positive (+) and negative (-) parameterized regression coefficients are associated with each link (see Table **2** error terms = $1 - R^2$).

Our results suggest that a potential link between environmental selection pressures and body size both among (species) and within (intrasexual) is spacing behaviour. The evolution of larger body size with high-latitude environments provides for greater mobility as a means of overcoming spatio-temporal fluctuations in food and mate availability. For terrestrial mammals, greater mobility is beneficial to

overcome seasonal fluctuations in food availability and larger body size may ameliorate the costs associated with travel through the season of snow and ice. In high latitude environments, accumulation of snow during winter increases relative locomotory costs [55, 56], and may reduce movement distances or exact an energetic cost. Similarly, areas of greater seasonality, e.g., fluctuations in ice, are associated with large home ranges [57, 58]. Not surprising, home range scales with body mass for a wide range of taxonomic groups, including carnivores [4, 57, 59-62]. The link between body size and mobility is evidenced by the positive correlation between body sizes and both home range size and dispersal distance [63]. Thus, greater body size may have evolved in high latitude environments to reduce locomotory costs and allow travel over large distances in areas of dispersed and/or reduced food availability, particularly during winter and with snow cover.

A latitudinal gradient results in greater temporal fluctuations at high latitudes [64] and increased randomness [65, 66]. Similarly, seasonality has been shown to influence sexual size dimorphism through its effect on the distribution and abundance of resources, both food and mates [10, 67]. In the current analysis, terrestrial mammalian carnivores were characterized by (1) greater relative body size with greater mobility (larger home ranges) and lower population density; (2) higher latitude and greater seasonality reduced population density, which increased body size; (3) higher latitude and lower primary productivity increased home range size, which favoured larger body size; and (4) body size was not influenced by temperature either directly or through spacing behaviour.

Additionally, increased mobility associated with larger size may facilitate mate searching, influence mate choice, and ultimately select for different mating systems. Here, the evolution of larger body size was related to the increased likelihood of greater sexual dimorphism in size, a relationship referred to as "Rensch's rule" [67-70] but see [71] and was best associated with primary productivity and seasonality [15, 72]. Most carnivores (95 of 109; 8 females larger and 6 monomorphic) are male-biased sexually dimorphic (males larger than females [28]. Structural equation modelling indicated that (1) changes in sexual size dimorphism occurred *via* the intermediates of home range or density but not both, (2) density decreased with seasonality causing greater dimorphism, (3) greater latitude and lower primary productivity resulted in greater home range, which resulted in lower population density, which resulted in greater dimorphism, and (4) temperature did not affect spacing or dimorphism. Sexual dimorphism among mammalian carnivores has been related to mating systems [28] with polygynous species associated with greater latitude (45°) relative to monogamous (34°) or multi-male mating species (29°). Polygynous species had a mean male/female body mass ratio of 4.01; species with monogamous mating system had a mean ratio of 1.15; and multi-male species a mean of 1.33.

One mechanistic explanation for why home range size links seasonality with body size is that the allometric relationship of home range size (1.0) [73] and density (0.75) [74, 75] increase at different rates (body mass exponents) resulting in greater overlap of individuals within populations for larger bodied species [76]. Hence, the evolution of large bod-

ied males with latitude may be for the selective advantages afforded by greater mobility and increased opportunities for mating [20, 77]. For most species, mating and spacing systems covary with ecological conditions [78], especially with local density. For example, male mating system depends on female dispersion, which itself depends on resource dispersion and predation [79-81]. The effects of environmental selection pressure and evolution of sociality leading to sexual dimorphism has been postulated for ungulates [51, 82]. For example, high population density affects food availability and subsequently growth rates which likely affect males and females differentially [67]. Similarly, population density will affect the contact between individuals influencing mating synchrony which can affect polygyny and degree of sexual size dimorphism [46]. However, population adjustments connecting environment and body size are proximate mechanisms that occur at the individual-population level, whereas our current analysis refers to ultimate explanations (evolutionary why questions) that emerge at the species level.

Natural selection acts to adapt life histories to particular environmental selection pressures. However, environment may act on certain life history parameters that then cause a mosaic shift in a suite of parameters. We substantiated previous research that illustrates the importance of energy (primary productivity) and variation in the distribution of energy (e.g., seasonality as temporal distribution) as predominant environmental characteristics influencing evolution ([83-86]. Knowledge of life-history evolution has progressed to the stage whereby evolutionary ecology can ask how these multiple interactions occur. Environmental seasonality has been proposed as an important selection pressure on animals occupying northern environments [4, 87-89]. Here, carnivores in more seasonal high latitude environments have tended to evolve to greater body size and to greater sexual size dimorphism. Selection pressures associated with the unpredictability of high-latitude environments may have (1) favoured terrestrial mammalian carnivores occupying larger home ranges and living at lower density relative to animals living in less variable environments and (2) species living at low densities and having to roam over large areas evolved greater relative body size and/or male size to counter the difficulty of finding food and mates, respectively. Presumably, large body size facilitates greater movement distances and ease of locomotion in winter through snow in terrestrial environments and selection for greater body mass in these environments is stronger for males.

ACKNOWLEDGEMENTS

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