Are long penis bones an adaption to high latitude snowy environments?

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Animals adapted to high latitude environments typically live at relatively low densities and require large areas to acquire the requisites for successful reproduction. Also, the unpredictable distribution of energy across time and space, such as environmental seasonality, constrains the timing of mating and parturition and imposes limitations to reproductive strategies. For example, limited mobility due to snow accumulation may reduce mate encounters, and this selective pressure may have resulted in morphological adaptations to assess mate quality during serial encounters. We tested whether mammalian carnivores living in high latitude environments displayed greater use of copulatory competition via length of the penis bone or baculum, and whether females in such settings enhance competition among males via multi-male matings. We then examined how baculum length may correlate with other reproductive adaptations in high latitude environments such as delayed implantation and induced ovulation. Statistical methods that account for phylogeny revealed that longer bacula occur in carnivores living in high latitude environments with greater snow accumulation, and that larger bacula is also associated with delayed implantation and multi-male mating systems. In contrast, the smallest bacula were observed in polygynous species. Our results provide an example of the effects of ecology on the evolution of a secondary sexual character due to sexual selection. Selection pressures imposed by seasonality of resources and environmental conditions affecting locomotion may have led to sexual selection via mating systems for females, and counter morphological adaptations of long penis bones in males.

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The availability of resources, in both space and time, is a universal determinant of distribution and abundance of organisms. Environmental variation also affects the life history of species, as well as their behavioural ecology. Challenges imposed by such variability consequently translate into the basic strategies to enhance not only survival, but also fitness, and fundamental to the latter is the choice and evolution of reproductive strategies.

Seasonality in the availability of resources has several implications on the evolutions of animal life histories (Boyce 1979). For example, one hypothesis is that

evolution for life in high latitude environments has selected for slow life-history traits (Ferguson and Larivière 2002). In high latitude mammals, slow life histories are reflected in longer lifespans, larger litters of smaller neonates, and animals that typically value self-survival over offspring survival (Ferguson and Larivière 2002). Such strategies may be of significant adaptive value because of the uncertainty of environmental conditions encountered during mating and parturition. For example, the evolution of delayed implantation allows the uncoupling of the timing of mating and

parturition (Renfree and Shaw 2000), thereby providing for flexibility in the timing of parturition (Ferguson et al. 1996). Delayed implantation also may have evolved to allow mating when conditions provide for greater accessibility to mates (Sandell 1990), thereby promoting sexual selection. In high latitude environments, accumulation of snow during winter increases locomotory costs (Parker et al. 1984, Crête and Larivière 2003), and may impair movements, and hence mate searching, mate choice, and ultimately mating systems in carnivores.

Mating systems can be viewed as the outcome of evolutionary conflicts between the sexes (Chapman and Partridge 1996, Partridge and Hurst 1998, Arnqvist and Rowe 2002), and include the resolution of sexual antagonistic coevolution (Rice 1996, 2000, Rowe and Arnqvist 2002). Adaptations by one sex often reduce fitness for individuals of the other sex, leading to selection for counter adaptations in the other sex to mitigate costs imposed by such adaptations. Coevolution between the sexes results in the evolution of particular reproductive traits (Arnqvist 1998) that influences speciation and extinction (Parker and Partridge 1998, Rice 1998). Missing in research and discussions on evolutionary conflicts between the sexes is an understanding of the environmental selection pressures that drive and constrain evolutionary adaptation of mating system and reproductive traits. There are few examples linking environmental conditions and the evolution of secondary sexual characters and likewise few examples for primary sexual characters (Andersson 1994).

Unpredictable and seasonal environments may have numerous effects on animal mating systems and reproductive strategies, and comparative evidence was recently provided linking environment and delayed implantation (Ferguson et al. 1996), baculum length (Larivière and Ferguson 2002), induced ovulation (Larivière and Ferguson 2003), and mating system (McLoughlin et al. 2001). We expanded these investigations by probing further into the hypothesis that the mammalian penis bone (baculum) plays a role as an indicator of genetic quality in males (Larivière and Ferguson 2002), and is used by females as a way of assessing male quality when mate encounters are disjunct temporally and spatially (Larivière and Ferguson 2003). This would be especially important in solitary species that occupy large home ranges and live at low density. In social species, females may assess genotypic quality of males via phenotypic displays or physical competitions among males in short time small space. In contrast, females of solitary species generally encounter only one male at a time over large space limiting precopulatory sexual competition through sexual display or physical competitions among males. Possibly as a result, female selection has been for post-copulatory competition (e.g. sperm competition) or selection (differential

fertilization) providing alternative ways for females to evaluate genotypic quality of males.

In contrast to females, male strategies may seek to overcome the uncertainty of paternity, and the counter strategy to multi-male matings of females may be to develop behavioural or morphological attributes that enhance the odds of being selected over competitors and improving paternity odds (Davies 1983, Clutton-Brock and Parker 1995). The evolution of the baculum likely relates to post-copulatory competition as baculum morphology may assist mating via the size of erect penis or baculum or stimulation level associated with copulation (Short 1979, Eberhard 1985, Dixson 1998). For example, length and rigidity of the phallus maintains intromission during prolonged copulations while morphological features of the distal head contribute to displacing or damaging sperm from previous males (Fairbairn et al. 2003). These factors may dominate in species where females mate with multiple males, but previous tests have been inconclusive, possibly because of low number of species and phylogenetic relationships (Larivière and Ferguson 2002, Baryshnikov et al. 2003).

Herein, we test for the environmental conditions responsible for the evolution of baculum length in mammalian carnivores and the possible influence of induced ovulation, delayed implantation, and mating system. Mammalian carnivores provide a varied group for such comparisons. Their body mass ranges from 0.06 kg in *Mustela* to over 2200 kg in *Phoca,* and the length of their penis bones varies within and among families (Larivière and Ferguson 2002, Baryshnikov et al. 2003). Moreover, their life-history strategies vary from competitors, bet-hedgers, reproducers, to survivors (Ferguson and Larivière 2002), and their evolutionary histories contrast from Mustelids that arose in the Holarctic, pinnipeds in the Nearctic, to procyonids in the New World (Gittleman and Purvis 1998).

Material and methods

Data

We used the phylogenetic tree proposed by Bininda-Emonds et al. (1999) that used a super-tree technique to combine a large number of molecular and morphological phylogenies. Taxonomy followed that of Wozencraft (1993). The data consisted of 11 families, 88 genera, and 122 species of world mammalian carnivores (Appendix 1).

We obtained data on life history and behavioural traits from published sources (e.g. mammalian species articles, Appendix 1), complemented with data from Hayssen et al. (1993) and Silva and Downing (1995). Information on induced ovulation was supplemented by reviews on carnivore reproduction (Wright 1963, Weir and Rowlands 1973, Colby 1974, Milligan 1982,

Larivière and Ferguson 2003). We used the current beliefs of induced/spontaneous ovulation for each species although we acknowledge that only a few species such as the American mink (*Mustela vison*), striped skunk (*Mephitis mephitis*), wolverine (*Gulo gulo*), and black bear (*Ursus americanus*) have been intensively studied (Hansson 1947, Enders 1952, Wade-Smith and Richmond 1978, Mead et al. 1993, Boone et al. 1998).

Information on delayed implantation was summarized from Ferguson et al. (1996), Johnson et al. (2000) and mammalian species accounts. We considered species with a short delay (< 2 week; *Mustela vison*, *Mephitis mephitis*, *Conepatus mesoleucus*) to not have delayed implantation as likely these species were either in the evolutionary process of losing or gaining delayed implantation but had not evolved completely seasonal delays (> 1 month). All three species were of a similar body size (852–2000 g) in the mid-range of the Mustelidae-Mephitidae body size range (53–24,000 g) making body size an unlikely adaptive explanation for their short delay (Lindenfors et al. 2003).

Data on species' density and home range size were obtained from summary literature that included: Bininda-Emonds (1998), Kelt and Van Vuren (2001), and Ferguson and Larivière (2002). We used means of population estimates for species. Where large discrepancies occurred, we selected the lower population density and the larger home range size as biases in carnivore space-use are for studies of high-density populations and correspondingly small home ranges (Gaston and McArdle 1993, Smallwood and Schonewald 1998, Smallwood 1999).

Longitude and latitude of the midpoint of each species historical distribution was obtained. For North American species (Novak et al. 1987) we used GIS (IDRISI www.clarklabs.org) to obtain midpoints. For world carnivore species occurring outside of North America species distribution centre point was approximated visually using maps from mammalian species accounts and world carnivore maps (Nowak 1991, Macdonald and Barrett 1993, Wilson and Reeder 1993, Smithsonian Institute website www.mnh.si.edu/msw, The Animal Diversity Web: animaldiversity.ummz.umich.edu). For species occurring on separate continents, we took the midpoint of the larger continent (e.g. Eurasia versus North America). Similarly, for species occurring on northern and southern continents (e.g. North and South America) we took the midpoint distribution from the continent having the greater distribution. For terrestrial species we ensured that midpoint locations occurred on land and for marine species on an ocean. We recognize that hemisphere may have an influence on results for terrestrial mammals (Lyons and Willig 1999), however for the purpose of understanding environmental influences on the evolution of baculum size we

chose to limit our interpretations to global macroecological patterns.

Environmental variables (seasonality, primary productivity, snow on ground, and temperature) for the centre point of each species' historical distribution were obtained from Wilmott et al. (1985) website http:// climate.geog.udel.edu/ ∼ climate. Calculations were made using a water budget analysis that was based on a modified version of the method of Thornthwaite (1948) and used average monthly precipitation, snowcover, soil moisture, and an estimate of potential evapotranspiration derived from observed average monthly surface temperature. These calculations used data from 13,332 weather stations over the globe and then spatially interpolated results to a regular grid of 1° by 1° latitude-longitude intervals. Seasonality was calculated as the coefficient of variation of monthly (n = 12) values of actual evapotranspiration (Ferguson 2002). Actual evapotranspiration (mm m^{-2} yr^{-1}) was calculated using equations of Thornthwaite and Mather (1957) and was calculated from a site's latitude, soil and vegetation type, and mean monthly temperature and rainfall. Actual evapotranspiration generally increases with a site's solar input, precipitation, and soils water capacity and is highly correlated with primary productivity (Rosenzweig 1968). Hence, actual evapotranspiration is used as a productivity surrogate in a variety of studies (Currie 1991, Ferguson and McLoughlin 2000, Kaspari et al. 2000). We used Lieth's (1976) algorithm to convert actual evapotranspiration to total net primary productivity (g m^{-2} yr^{-1}). Larger primary productivity values indicated greater energy within a species geographic range. Similarly, larger coefficient of variation values indicated greater seasonality within the range of a species.

Phylogenetic correction

Not all factors are constrained by phylogeny. For example, variation in habitat selection may be best explained at the species level, and thus, comparative analyses controlling for genus or family effects may do little in explaining variation (Ferguson and Larivière 2002). Because behavioural plasticity may allow individuals within the same species to inhabit different environments and use different behavioural strategies, comparative analyses may not reflect the species variability as well as traditional non-phylogenetic methods.

Phylogenetic corrections are necessary when variation in the observed data-set is due to phylogenetic structure thereby violating the statistical assumption of independence of variants in general linear models (Harvey and Pagel 1991). We used a test for phylogenetic signal in comparative data (Blomberg et al. 2003) that compares the 'real' phylogenetic tree with a randomly permuted

tree (i.e. destroying any phylogenetic signal). Randomizing shuffles the data across the tips of the tree, without regard to phylogenetic hierarchy (Garland et al. 2001). Next, the data output from 1000 permutations was analyzed for variance. If the variance of the data on the real tree is smaller than 95% of the variance of the randomized data, then this provides evidence that related species do tend to resemble each other with respect to the analyzed trait. The test has reasonable statistical power for trees with > 20 species, such that there is a $> 80\%$ chance of detecting significant phylogenetic signal at alpha $= 0.05$ (Garland et al. 2001). The test assumes Brownian motion evolution.

Measurement error can have an adverse effect on the ability to detect phylogenetic signal, including error in the tip data themselves, errors in branch lengths, and errors in the topology of our tree. Therefore, we report results of both conventional and phylogenetically based statistical analyses. For traits that did not show a significant phylogenetic signal, we calculated standardized independent contrasts from a collapsed phylogeny (i.e. star phylogeny with arbitrary branch lengths using Grafen's (1989) rho value of zero).

Phylogenetic tests

First, we tested for the environmental correlates of population density and home range size for carnivore species. We used standardized independent contrasts to compare the behavioural traits of density and range size to six environmental variables: seasonality, primary productivity, latitude, annual temperature, and snow on ground. We calculated standardized independent contrasts (unstandardized contrast divided by standard deviation) using Felsenstein's (1985) method (PDTREE; Garland et al. 2001). Various diagnostic tests indicated that the branch lengths were standardized adequately, and that the Brownian motion model was appropriate for the data (Purvis and Rambaut 1995). General linear models of standardized independent contrasts were forced through the origin. We performed a multiple regression analysis of all environmental traits to test which variables contributed most to the relationship between baculum length and body size (partial correlation analysis of variance explained).

The same method of standardized independent contrasts and general linear models were used as above to test for the selective advantages of longer baculum that may be associated with high latitude environments characterized by high seasonality, low primary productivity, greater snow, and lower temperatures. Here, we used standardized independent contrasts to compare baculum length to each environmental trait separately while controlling for body size (male body size as covariate).

Next, we compared reproductive traits: implantation – delayed or not, ovulation – spontaneous or induced, and mating system – monogamy, multi-male, or polygyny with baculum length while statistically controlling for body size effects by including male body mass as covariate. Here, we used Garland et al.'s (1993) method of phylogenetic analysis of covariance by Monte Carlo simulations (PDSIM). We chose not to use residual regression analysis to control for body mass effects as residual analysis fails to take into account the correlation between the independent variable and the confounding variable(s) (Darlington and Smulders 2001). ANCOVA (general linear models) should be used as we are testing for an effect of the categorical variables of interest (reproductive traits) on the continuous variable of interest (baculum length), while controlling for the effect of the continuous confounding variable body size (covariate). We used Monte Carlo algorithms to incorporate phylogenetic structure (i.e. phylogenetic tree) to estimate statistical parameters for phylogenetic analysis of covariance (ANCOVA; Garland et al. 1993). Initial limits corresponding to life history and behavioral traits were obtained from the average of all species values. We performed simulations according to the gradual model of speciation that assumes variance changes are proportional to branch lengths. For each simulated data-set ($n = 1,000$), we calculated phylogenetically corrected estimates of analysis of covariance parameters using general linear models.

We tested the prediction that induced ovulators have different baculum length than non-induced ovulators and felids. Felids were found to be statistical outliers (Larivière and Ferguson 2003) and were treated as a separate group. Conventional ANCOVA statistics were calculated from the observed sample data and compared to the distribution of simulated test statistics as for delayed implantation (see above).

Mating systems are often coded as categorical data although the coarse information can also be interpreted as a continuous variable (Garland et al. 1993). Polygyny, promiscuity (multi-male mating), and monogamy can be considered groupings along a continuum from breeding group size greater than 5 for highly polygynous species, to breeding group size between 3 and 5 for weakly polygynous species associated with multi-male mating systems, to breeding group size of 1 or 2 for monogamous species (Clutton-Brock et al. 1980, Loison et al. 1999). Hence, we scored the mating system data as three category ordered variables: 3 = polygyny, 2 = multi-male, 1 = monogamy. Standardized contrasts were computed from the mating system coding and analysis of covariance was used to control body size effects. We used female mass as a covariate to control for the effect of body size on sexual size dimorphism and thus mating system (Loison et al. 1999).

Statistical analyses

We tested for normality of environmental and life history data using Wilk's Shapiro normality test. For environmental data (seasonality, latitude, primary productivity, temperature) we found the distributions did not differ significantly from normality. The exception was snow on ground, which was normalized after $\log_{10}$ transformation and adding $+0.5$ to remove 0 values. The sum of monthly mean temperatures was analyzed after adding a constant (300) to ensure all values were positive before log transformation. We used the absolute values for latitude to compare similar latitude locations in the northern (positive) and southern (negative) hemispheres. Density, home range size, baculum length, and body size (males and females) were $\log_{10}$ transformed before analyses.

Testing for a relationship between two variables, while controlling for the effects of a third variable, was carried out using multiple least-squares regression (GLM, Sokal and Rohlf 1995; forced through the origin for contrasts, Garland et al. 1992). Additionally, ANOVA and ANCOVA (GLM) were used to analyze species values. Tests for associations between contrasts where there was a mixture of continuous and categorical variables (i.e. between baculum length and mating system) were performed using a GLM models followed by a Tukey test for multiple comparison, which holds the experiment-wide alpha level to 0.05 (SAS Institute 1989). We present the results obtained from analysis of both species data and from phylogenetically independent contrasts, as recommended by Garland et al. (1999). We also examined all regressions for the presence of outliers (residuals > 3 SD from the mean; Kleinbaum and Kupper 1978) that might change the outcome (e.g. Genet).

ANCOVA adjusts for differences associated with body mass between groups and enabled us to assess differences in traits due to groups alone (i.e. variation in body mass has been statistically removed from the analysis). These adjusted trait values are known as least-squared means, and represent the predicted mean value for traits after regressing traits on body mass for each group. The ANCOVA model used Type III sum of squares to determine the statistical difference between the least-squared (adjusted) means associated with each group. The phylogenetically corrected critical value of differences due to group (three mating systems) was set at alpha $= 0.05$ from the 95th percentile of the simulated distribution. We report significant differences in least-squared means that control for body size variation using Tukey's multiple comparison tests.

Results

Strength of phylogenetic signal

Using a test for phylogenetic signal in comparative data, we found differences among life history, behavioral and environmental attributes (Table 1). Variation in three environmental attributes (primary productivity, seasonality, and latitude) and one behavioral trait (female home range) was best described using the species traits (Table 1). In contrast, variation in all three life-history (baculum length, male, and female body mass), two environmental (snow and temperature), and one behavioral (density) traits were best described while considering phylogeny. These results indicate that phylogenetic correction methods are necessary for the latter traits. Consequently, we used the results on conventional

Table 1. Test for phylogenetic signal using relative variance attributable to life history, behavior, and environmental traits for 122 carnivore species of North American carnivores (see text).

	Species values			Phylogenetic variance		
	Mean	Std	n	Observed	Expected	P
Life history traits						
Baculum length (mm)	74.6	82.0	122	0.008413	0.000617	< 0.01
Female body mass (kg)	54.47	128.4	122	0.03201	0.00906	< 0.01
Male body mass (kg)	117.7	417.2	122	0.03777	0.0114	< 0.01
Environmental attributes						
Primary productivity[1]	1,277	643	122	8.148×10^{-4}	3.250×10^{-8}	0.77
Seasonality[2]	83.8	52.2	122	792.5	7,7020	0.16
Latitude[3]	32.2	21.1	122	118.0	1,697.5	0.07
Snow on ground[4]	1,975	10,031	122	0.3116	0.05771	0.01
Temperature sum[5]	164.4	151.0	122	0.003812	0.00909	0.01
Behavioral traits						
Population density (km^2)	4.510	8.197	58	0.08426	0.001508	0.01
Female home range (km^2)	18.40	148.3	71	0.6861	0.01213	0.10

[1] primary productivity (g m^{-2} yr^{-1}).
[2] coefficient of variation among monthly actual evapotranspiration (mm m^{-2} yr^{-1}).
[3] degrees of latitude north or south of equator.
[4] sum of mean monthly snow on ground (mm).
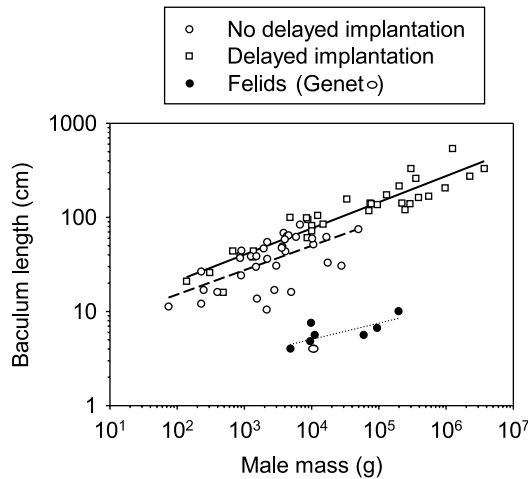[5] sum of mean monthly temperatures ($^\circ$C).

Fig. 1. Baculum length and male body size among carnivore species (n = 75 species) grouped into those with delayed implantation, those without delayed implantation, and felids.

analysis of covariance for traits where the variation was best described at the species level, and phylogenetically-corrected analyses for traits that varied due to phylogeny, although both results are reported.

Home range size and population density

We first tested our assumption that environmental variables were correlated with home range size and population density. Non-phylogenetic analyses revealed that female home range size was negatively correlated with female body mass (partial $r^2 = 0.56$) and seasonality (partial $r^2 = 0.16$).

In contrast to home range size, population density was significantly affected by phylogeny (P = 0.01). Independent contrasts revealed that population density was not significantly affected by environmental variables (all r < 0.15).

Evolution of longer baculum

Our primary hypothesis was that longer penis bones evolved as an adaptation to high latitude environments. Controlling for the effects of male mass on baculum length, phylogenetic analyses revealed that only latitude and snow accumulation correlated with baculum length; longer bacula occurred in carnivore species living in high latitude environments characterized by high snow accumulation (Table 2). A multiple regression analysis of standardized independent contrasts that included male mass, to control for this covariate (partial $r^2 = 8\%$, P = 0.001), indicated that snow accumulation was the best explanatory variable (partial $r^2 = 4\%$, P = 0.03) followed by latitude (partial $r^2 = 1\%$, P = 0.24).

Longer bacula were also associated with delayed implantation (Table 3, Fig. 1). Although slopes for male body mass and baculum length did not differ among the groups ($F_{2,75} = 0.29$, P = 0.59; with delayed implantation slope = 0.28, species without delayed implantation slope = 0.26, and felids + Genet slope = 0.17). However, elevation differed with species with delayed implantation having the largest intercept (0.78), followed by species without delayed implantation (0.74), and felids + Genet (0.11). Felids have been identified as an outlying group as they are characterized by very small baculum relative to their body size. However, removing felids from the analysis did not significantly change the observed relationships (Table 2). Baculum length was positively associated with male body mass using species values (slope = 0.402 ± 0.0100, n = 122, $r^2 = 0.29$, F = 49.9, P < 0.0001). Also, using standardized independent contrasts (one less degree of freedom) a positive relationship was found (slope = 0.137 ± 0.0412, n = 121, $r^2 = 0.08$, F = 49.9, P = 0.001).

In contrast to delayed implantation, baculum length was unrelated to induced ovulation (Table 3). Again, excluding felids did not change the relationship.

The relationship of baculum length and mating system was significant, but only after exclusion of the felids

Table 2. Analysis of covariance tests (ANCOVA) of difference between baculum length and environmental variables from 122 species of carnivores (df = 121 for independent contrasts). Male body mass is used as a covariate and type III sum of squares is reported to account for a possible interaction between environmental variables and body size. Values in bold represent statistical differences.

| | Conventional ANCOVA | | | | | | Phylogenetic (standardized independent contrasts) | | | |
| | All carnivores | | | Exclude cats | | | All carnivores | | Exclude cats | |
	n	F	P	n	F	P	F	P	F	P
Seasonality	122	8.01	0.006	109	2.60	0.11	2.47	0.12	1.71	0.19
Primary productivity	122	11.53	0.0009	109	1.41	0.24	1.94	0.17	1.20	0.27
Latitude	122	28.41	0.0001	109	13.4	0.001	4.29	**0.03**	3.93	**0.04**
Temperature	122	24.24	0.0001	109	12.8	0.001	1.08	0.30	0.66	0.42
Snow on ground	122	16.87	0.0001	109	8.46	0.004	4.96	**0.03**	3.89	**0.05**
Density	58	1.45	0.23	50	1.01	0.32	1.09	0.30	1.25	0.27
Home range size	71	0.03	0.86	59	0.00	0.97	1.86	0.18	2.11	0.15

Table 3. Analysis of covariance tests (ANCOVA) of differences in baculum length among carnivore species relative to delayed implantation, induced ovulation, and mating system. The covariate is male body mass. Models of evolutionary change were no phylogenetic (conventional ANCOVA) or gradual evolutionary change (proportional to branch lengths). Values in bold represent statistical differences.

	Conventional			Phylogenetic P	Least square means mean $\pm$ 1SE (n)		
	n	F	P				
Delayed implantation:					DI	No-DI	
All carnivores	75	58.4	0.0001	**0.001**	76.7$\pm$1.14 (42)	29.9$\pm$1.13 (33)	
Exclude cats	68	64.8	0.0001	**0.001**	74.7$\pm$1.10 (35)	53.0$\pm$1.12 (33)	
Induced ovulation:					IO	No-IO	
All carnivores	54	21.4	0.0001	0.13	44.5$\pm$1.18 (25)	78.3$\pm$1.16 (29)	
Exclude cats	49	0.29	0.59	0.90	82.8$\pm$1.10 (20)	77.4$\pm$1.08 (29)	
Mating system:					Monogamy	Multi-male	Polygyny
All carnivores	53	11.0	0.0001	0.18	a 70.8$\pm$1.33 (9)	a 61.7$\pm$1.16 (35)	a 60.3$\pm$1.39 (9)
Exclude cats	48	27.1	0.0001	**0.01**	a 93.1$\pm$1.15 (9)	a 79.9$\pm$1.08 (30)	b 60.9$\pm$1.17 (9)

(Fig. 2). Excluding felids, polygynous species had a significantly smaller baculum compared to species with monogamous or multi-male mating systems, while controlling for body size (Table 3). Carnivores with a polygynous mating system were larger than other carnivores; however baculum size was smaller after controlling for body size.

Discussion

Phylogenetic analyses of published data on behavioural and life history traits of worldwide carnivores suggest that longer penis bones have evolved in conjunction with high latitude and snowy environments, and that mating systems also affect length of the penis bone in mamma-

Fig. 2. Baculum length and male body size among carnivore species (n = 53 species) grouped into those with monogamous, multi-male, polygynous mating system, and felids (multi-male mating with exceptionally small bacula).

lian carnivores. These findings support our contention that penis bones evolved in carnivores as an adaptation to overcome the pressures imposed by environmental conditions at high latitudes, and the associated pressures or constraints on the reproduction of animals living therein.

Animals living in high latitude environments often occupy large home ranges, and having to roam across a large area, acts as a major selection pressure leading to the evolution of particular reproductive modes. For example, larger home range sizes and lower population density are associated with induced ovulation versus spontaneous ovulation (Larivière and Ferguson 2003), and carnivores with 'bet-hedging' life histories versus 'reproductive' life histories (Ferguson and Larivière 2002). Our study also indicates that high latitude environments exert pressure on mating system, and consequently, on the morphology of genital anatomy, particularly penis bones, in carnivores.

Selection pressures related to reproduction of animals may lead to adaptation not only of morphology, but also behaviour. In the case of carnivores that occupy high latitude environments, the negative effects of reduced mate encounters due to low animal density and reduced locomotion due to snow, may be mitigated by adoption of particular mating systems. For example, if environmental conditions preclude the pre-copulatory assessment of male quality by females, other mechanisms of mate choice such as post-copulatory sperm competition may nonetheless provide cues of mate quality. Our study showed that larger bacula are observed in species with multi-male mating systems, and smallest bacula in polygynous species, suggesting that multi-male mating may be the female's strategy to evaluate mate choice when mate availability is limited or sequential. Note that larger species are more likely to evolve a polygynous mating system and extreme sexual dimorphism (Perez-Barberia et al. 2002); however we controlled for body size in our analyses allowing for relative comparisons.

The mammalian penis bone (baculum) likely plays a larger role in monogamous (e.g. Canidae) and multi-
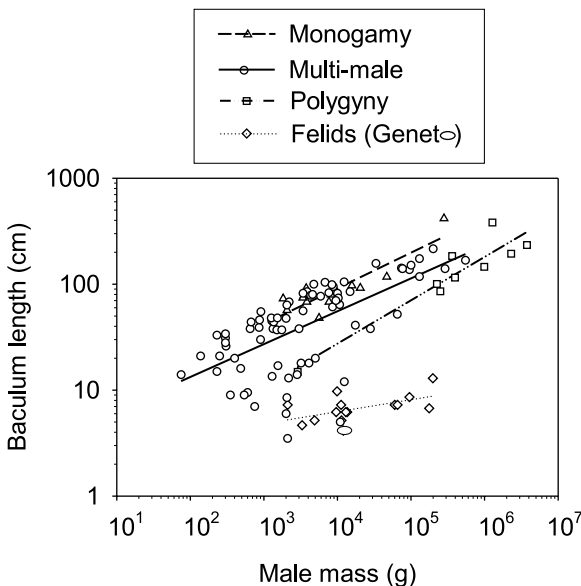
male mating systems (Mustelidae; Baryshnikov et al. 2003) as an indicator of genetic quality in males (Larivière and Ferguson 2002). Without the opportunity to assess males at one time and place as in polygynous mating species, females rely on baculum length as a way of assessing male size and age. For example, female walrus (*Odobenus*) that engage in multiple aquatic mating exhibit hypoallometric growth of the baculum after sexual maturity (Fay 1982). Thus, for carnivore species using monogamous and multi-male mating systems, female selection has likely occurred for post-copulatory competition (e.g. sperm competition) or selection (differential fertilization) providing alternative ways for females to evaluate genotypic quality of males. Empirical evidence for post-copulatory selection occurs in species that adopt multi-male matings and in which multiple paternity is observed (e.g. *Ursus americanus*; Schenk and Kovacs 1995 and *Microcebus murinus*; Radespiel et al. 2002).

Long intromittent organs have arisen independently in various animal groups in which aquatic mating occurs (Briskie and Montgomerie 1997), as water can damage mammalian sperm. The explanation for the terrestrially mating elephant seals (*Mirounga*) having a small baculum, and the aquatically mating walrus having a large one may be due to the greater risk of bacular fracture while mating on land for elephant seals (Dixson 1995). However, bacular fracture could occur while copulating in water (Miller et al. 2000) and a more parsimonious explanation between the sizes of baculum in these two species may be the difference between polygyny and multi-male matings. Elephant seals live in low latitude environments and mate on land whereby males can control mating access to females and therefore do not require sperm competition. In contrast, walrus live in high latitude environments and mate in water whereby males cannot control access to mates in a 3 dimensional aquatic environment and therefore rely on baculum length to secure success in sperm competition.

We found no correlation between induced ovulation and baculum length, a finding previously reported with a smaller data-set on North American carnivores (Larivière and Ferguson 2003). Induced ovulation is a process by which eggs are released following behavioral, hormonal, or physical stimuli (Milligan 1974, Taymor 1978). Females that are induced to ovulate by male copulation, may exercise choice through post-copulatory mechanisms that reduce the fertilization success of sperm from related males. Attributes of male intromission organs such as penile spines (Stoddart 1979) may increase the odds of inducing ovulation (Zarrow and Clark 1968). Evolution of induced ovulators is variable suggesting that selection pressures may differ among species (Larivière and Ferguson 2003).

Our results indicate a clear relationship between delayed implantation and baculum length, with larger

bacula occurring in species with delayed implantation. Parturition of most mammals living at high latitudes occurs in spring. Gestation length is strongly correlated with body size (Blueweiss et al. 1978). Therefore, time of mating determines the timing of parturition and, depending on body size, fixes the mating period to occur during winter. Winter in high latitude snowy environments is a season presenting limited movement opportunities for mates to encounter each other. However, evolution of delayed implantation allows the uncoupling of the timing of mating and parturition (Sandell 1990, Renfree and Shaw 2000), thereby providing for flexibility in the timing of parturition (Ferguson et al. 1996). Delayed implantation also likely evolved to allow mating when conditions provide for greater accessibility and opportunity to compare mates. Therefore, the evolution of larger bacula and delayed implantation likely co-evolved in high latitude environments as a selective need to provide sexual selection (i.e. mate choice) relative to mating systems adapted to local environmental conditions.

Species living in high latitude environments, associated with low densities and having to roam over large areas, have difficulty in getting together to mate. As a result a pattern of pre- and post-copulatory mechanisms have evolved to afford mate choice by females and maximization of mating opportunities by males. We suggest that multi-male mating systems, long penis bones, and delayed implantation all evolved to accommodate sexual selection in high latitude snowy environments.

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Appendix 1. Species specific data on reproduction, behaviour, and environment for 122 mammalian carnivores.

Family	Genus	Species	Male mass (g)	Female mass (g)	DI[1]	IO[1]	Mating system[2]	Female home range (km²)	Density (ind/km²)	Latitude[3]	Snow (mm)[4]	Temperature °C[5]	Primary productivity[6]	Seasonality[7]
Odobenidae	*Odobenus*	*rosmarus*	1,246,000	690,000	1	0	3	.	1.27	73	576	−158	202	189.3
Phocidae	*Phoca*	*groenlandicus*	130,000	130,000	1	0	2	.	0.1	51	117	25.6	436	116.9
Phocidae	*Phoca*	*fasciata*	74,000	74,000	1	0	2	.	.	69	273	−79.1	170	156.4
Phocidae	*Phoca*	*vitulina*	95,000	78,000	1	0	2	.	5.68	60	385	−32	330	150.5
Phocidae	*Phoca*	*hispida*	71,000	69,000	1	0	.	.	0.95	74	603	−101	228	168.9
Phocidae	*Halichoerus*	*grypus*	388,000	175,000	1	0	3	.	.	60	0	91.3	579	56.3
Phocidae	*Cystophora*	*cristata*	300,000	160,000	1	0	1	.	0.01	58	187	−19.8	341	144.9
Phocidae	*Mirouga*	*angustirostris*	2,250,000	900,000	1	0	3	.	.	34	0	184.1	388	63.9
Phocidae	*Mirounga*	*leonina*	3,692,000	359,000	1	0	3	.	.	60	183	−52.2	385	228.2
Phocidae	*Monachus*	*schauinslandi*	172,000	265,000	.	.	.	.	.	20	0	221.3	832	14.0
Phocidae	*Monachus*	*monachus*	260,000	301,000	.	.	.	.	.	18	0	333.5	906	55.5
Phocidae	*Lobodon*	*carcinophagus*	220,500	224,000	.	.	.	.	1.01	72	561	−234	20	181.5
Phocidae	*Hydrurga*	*leptonyx*	324,000	367,000	.	.	.	.	0.12	72	522	−291	3	180.9
Phocidae	*Leptonychotes*	*weddelli*	360,000	376,000	.	.	.	.	0.13	75	687	−233	24	182.2
Phocidae	*Erignathus*	*barbatus*	290,000	290,000	1	0	2	.	0.02	75	695	−163	207	193
Otariidae	*Callorhinus*	*ursinus*	220,000	43,000	1	0	3	.	18	55	0	93.4	582	69.0
Otariidae	*Eumetopias*	*jubatus*	968,000	333,000	1	0	3	.	.	55	0	91.2	576	73.6
Otariidae	*Zalophus*	*Californicus*	245,000	82,000	1	0	3	.	0.5	46	0	116	594	40.7
Otariidae	*Otaria*	*Byronia*	300,000	144,000	.	.	.	.	.	40	0	168.7	666	55.7
Otariidae	*Neophoca*	*Cinerea*	355,000	83,000	1	0	3	.	.	40	0	151.1	670	37.1
Otariidae	*Arctocephalus*	*Tropicalis*	152,500	50,000	.	.	2	.	.	40	0	184.1	303	52.1
Ursidae	*Ursus*	*Maritimus*	550,000	225,000	1	1	2	125,000	0.02	70	667	−139	245	185
Ursidae	*Ursus*	*Arctos*	200,000	118,670	1	1	2	723	0.02	50	230	89.9	344	100.9
Ursidae	*Ursus*	*Americanus*	76,650	54,050	1	1	2	153	0.28	47	403	47.1	530	109.1
Ursidae	*Ursus*	*Thibetanus*	130,100	77,500	.	.	2	0.92	.	44	97	98.8	217	122.9
Ursidae	*Melursus*	*Ursinus*	100,000	.	.	.	2	10	0.08	21	0	319.9	1,088	71.5
Ursidae	*Helarctos*	*Malayanus*	65,000	50,000	.	.	2	.	.	1	0	326.8	1,724	5.81
Ursidae	*Ailurus*	*Fulgens*	5,000	4,900	0	1	2	1.02	.	23	0	315.5	825	77.6
Procyonidae	*Bassariscus*	*Astutus*	900	700	0	0	2	0.20	3.2	29	0	179.5	439	99.6
Procyonidae	*Nasua*	*Narica*	5,900	3,500	0	0	2	0.6	26	18	0	306.1	1,241	37.5
Procyonidae	*Procyon*	*Lotor*	6,760	5,940	0	1	2	2.87	7.86	33	0	217.6	845	76.7
Procyonidae	*Procyon*	*Cancrivorus*	7,630	6,270	.	.	2	.	.	4	0	306	1,398	11.1
Procyonidae	*Nasua*	*Nasua*	3,863	3,000	0	0	2	1.05	17.8	23	0	288.5	1,284	41.0
Procyonidae	*Potos*	*Flavus*	2,200	2,000	0	1	2	0.08	41.18	15	0	292.4	1,077	33.8
Procyonidae	*Bassariscus*	*Sumichrasti*	1,280	530	.	.	2	.	.	5	0	311.1	1,325	27.0
Mustelidae	*Martes*	*Americana*	860	565	1	1	2	4.5	0.9	51	640	−3.3	454	121.9
Mustelidae	*Martes*	*Pennanti*	4,760	2,390	1	1	2	15	0.02	59	345	−41.4	314	137.2
Mustelidae	*Martes*	*Zibellina*	1,330	1,030	1	.	2	16.75	0.08	60	0	−83.4	172	145
Mustelidae	*Martes*	*Martes*	1,360	1,020	1	.	2	7	.	59	704	−8.4	432	129.5
Mustelidae	*Martes*	*Flavigula*	3,400	.	.	.	2	.	.	30	0	176.7	736	72.4
Mustelidae	*Martes*	*Foina*	2,050	1,300	.	.	2	1.8	.	50	150	54.6	190	128.6
Mustelidae	*Meles*	*Meles*	12,300	10,900	1	.	2	1	.	55	349	40.3	423	118.3
Mustelidae	*Mustela*	*Putorius*	1,260	800	0	1	2	1.25	0.1	50	39	95.1	572	90.8
Mustelidae	*Mustela*	*Lutreola*	871	543	0	.	2	0.23	0.08	46	0	124.8	651	75.1
Mustelidae	*Mustela*	*Africana*	300	.	.	.	2	.	.	7	0	289.6	1,313	16.2
Mustelidae	*Mustela*	*Nivalis*	75	53	0	1	2	0.04	18.36	35	0	195.5	790	82.5
Mustelidae	*Mustela*	*Erminea*	138	57	1	1	2	0.13	6.25	59	334	−77.6	340	137.9
Mustelidae	*Mustela*	*frenata*	305	165	1	1	2	0.79	0.76	53	425	−9.4	422	123.5

Appendix 1 (*Continued*)

Family	Genus	Species	Male mass (g)	Female mass (g)	DI[1]	IO[1]	Mating system[2]	Female home range (km²)	Density (ind/km²)	Latitude[3]	Snow (mm)[4]	Temperature °C[5]	Primary productivity[6]	Seasonality[7]
Mustelidae	*Mustela*	*vison*	1,523	852	0	1	2	2.77	2.5	49	229	28.3	496	112.7
Mustelidae	*Mustela*	*nigripes*	1,500	1,350	0	1	2	0.49	2	40	54	135	554	97.6
Mustelidae	*Mustela*	*altaica*	250	130	0	.	2	.	.	47	53	108.7	110	169.9
Mustelidae	*Mustela*	*nudipes*	650	500	.	.	2	.	.	1	0	321.6	1,674	5.4
Mustelidae	*Mustela*	*strigidorsa*	300	.	.	.	2	.	.	29	0	224.9	819	67.6
Mustelidae	*Lontra*	*canadensis*	8,760	7,860	1	1	2	70	1.13	47	202	54.5	523	110.1
Mustelidae	*Enhydra*	*lutris*	33,350	23,600	1	1	2	2.45	6.47	51	0	106.4	606	62.3
Mustelidae	*Gulo*	*gulo*	14,800	10,600	1	1	2	192	0.01	63	457	−98.8	213	148
Mustelidae	*Taxidea*	*taxus*	8,400	6,400	1	1	2	2.4	0.71	38	0	151	406	83.7
Mustelidae	*Arctonyx*	*collaris*	10,000	.	1	.	2	.	.	26	0	306.3	952	89.5
Mustelidae	*Galictis*	*vittata*	3,400	1,800	.	.	2	4.15	.	4	0	301.9	1,301	14.9
Mustelidae	*Galictis*	*cuja*	1,750	.	.	.	2	.	.	14	0	299.5	1,155	40.3
Mustelidae	*Ictonyx*	*libyca*	230	.	0	.	2	.	.	32	0	239.9	114	67.4
Mustelidae	*Vormela*	*peregusna*	670	530	1	.	2	.	.	42	4	104.9	123	106.3
Mustelidae	*Lyncodon*	*patagonicus*	300	.	.	.	2	.	.	35	0	192.1	261	59.4
Mustelidae	*Melogale*	*moschata*	2,000	.	.	.	2	.	.	22	0	161.1	800	55.9
Mustelidae	*Eira*	*barbara*	4,320	3,950	0	.	2	14.62	.	3	0	324.7	1,677	11.0
Mustelidae	*Ictonyx*	*striatus*	910	630	0	.	2	.	.	9	0	252.3	792	40.2
Mustelidae	*Mellivora*	*capensis*	8,570	7,590	1	.	2	.	.	6	0	308.2	1,090	39.6
Mustelidae	*Lutra*	*lutra*	10,700	7,100	0	.	2	28.08	0.85	44	52	112.1	112	170.7
Mustelidae	*Lontra*	*longicaudis*	10,000	8,000	1	0	2	.	.	0	0	311.5	1,453	8.6
Mustelidae	*Lutra*	*perspicillata*	10,260	7,300	0	.	2	7	.	31	0	238.2	66	123.2
Mustelidae	*Amblonyx*	*cinerea*	3,000	.	0	.	2	.	.	21	0	231.6	971	50.0
Mustelidae	*Lutra*	*maculicollis*	4,580	3,500	0	.	2	.	.	2	0	280.1	816	36.7
Mustelidae	*Pteronura*	*brasiliensis*	28,000	24,000	0	.	2	113.1	.	9	0	242.2	1,016	21.6
Mephitidae	*Mephitis*	*mephitis*	2,820	2,000	0	1	3	3.74	10.45	43	153	90.8	632	104.7
Mephitidae	*Spilogale*	*gracilis*	483	397	1	0	2	.	.	36	0	223.2	112	48.2
Mephitidae	*Spilogale*	*putorius*	399	283	0	0	2	0.64	22.5	40	157	136.1	725	95.8
Mephitidae	*Spilogale*	*pygmaea*	230	.	0	.	2	.	.	14	0	296.9	1,160	35.1
Mephitidae	*Conepatus*	*mesoleucus*	2,168	1,152	0	.	2	0.36	.	20	0	156.4	565	31.1
Canidae	*Canis*	*lupus*	50,000	36,500	0	0	1	562	0.01	56	247	−32.7	462	128.4
Canidae	*Canis*	*latrans*	16,750	13,620	0	0	1	51.75	0.45	32	0	202.8	221	67.2
Canidae	*Urocyon*	*cinereoargenteus*	3,700	3,500	0	0	1	2.09	0.61	26	0	270.6	552	56.1
Canidae	*Urocyon*	*littoralis*	1,950	1,900	0	0	1	0.14	3.45	38	0	176	400	71.2
Canidae	*Vulpes*	*vulpes*	4,100	3,400	0	0	1	15.1	1.35	49	772	−3.9	457	121.8
Canidae	*Alopex*	*lagopus*	3,620	3,220	0	0	1	21.2	.	67	325	−175	137	194.7
Canidae	*Vulpes*	*macrotis*	2,200	1,900	0	0	1	7.53	2.94	32	0	228.1	348	71.5
Canidae	*Canis*	*aureus*	8,790	8,320	.	.	1	10	.	15	0	343.3	318	151.3
Canidae	*Nyctereutes*	*procyonides*	4,020	4,870	0	0	1	0.89	12.02	56	279	−62.8	433	134
Canidae	*Vulpes*	*zerda*	1,500	1,500	.	.	1	.	.	17	0	322.1	23	218.5
Canidae	*Cerdocyon*	*thous*	6,000	6,000	.	.	1	1.13	.	12	0	299.4	1,275	23.3
Canidae	*Canis*	*mesomelas*	8,200	7,200	.	.	1	14.6	0.37	10	0	258.6	795	51.4
Canidae	*Cuon*	*alpinus*	17,500	11,500	0	0	2	35	0.63	30	0	213.6	919	71.4
Canidae	*Lycaon*	*pictus*	21,800	22,200	.	.	1	2,288	0.01	23	0	241.1	459	97.8
Felidae	*Lynx*	*canadensis*	9,870	8,430	0	1	2	30	0.47	57	287	−51.7	413	132.6
Felidae	*Lynx*	*rufus*	9,600	6,800	0	1	2	24.39	0.14	35	0	202.9	804	82.0
Felidae	*Panthera*	*onca*	94,900	67,000	0	.	2	44.72	0.14	11	0	288.8	1,063	47.3
Felidae	*Puma*	*concolor*	60,000	40,000	0	1	2	331	0.02	34	0	209.1	728	80.3

Appendix 1 (*Continued*)

Family	Genus	Species	Male mass (g)	Female mass (g)	DI[1]	IO[1]	Mating system[2]	Female home range (km²)	Density (ind/km²)	Latitude[3]	Snow (mm)[4]	Temperature °C[5]	Primary productivity[6]	Seasonality[7]
Felidae	*Leopardus*	*pardalis*	11,200	7,800	0	.	2	7.93	0.4	3	0	299.3	1,337	5.7
Felidae	*Felis*	*sylvestris*	4,880	4,090	0	1	2	1.01	.	8	0	268.2	918	31.8
Felidae	*Prionailurus*	*viverrinus*	11,300	6,300	.	.	2	.	.	25	0	306.9	1,015	85.4
Felidae	*Prionailurus*	*bengalensis*	3,300	2,250	.	.	2	2.41	.	20	0	296.8	1,205	53.8
Felidae	*Caracal*	*caracal*	13,500	9,680	.	.	2	376.63	.	8	0	275.9	824	66.5
Felidae	*Leptailurus*	*serval*	13,000	10,400	.	.	2	2.4	.	6	0	253.6	647	66.9
Felidae	*Panthera*	*leo*	176,100	135,500	.	.	2	210	0.1	0	0	300.4	1,383	8.6
Felidae	*Panthera*	*pardus*	65,500	39,300	.	.	2	23.6	0.04	9	0	252.4	717	57.4
Felidae	*Panthera*	*tigris*	198,000	116,000	0	1	2	75	0.03	24	0	297.4	919	84
Felidae	*Neofelis*	*nebulosa*	12,000	9,450	.	.	2	.	.	23	0	258.6	1,142	63.8
Viverridae	*Genetta*	*tigrina*	2,100	2,020	.	.	2	0.06	.	1	0	301.3	1,390	7.8
Viverridae	*Civettictis*	*civetta*	12,380	11,920	.	.	2	.	.	16	0	264.4	635	84.4
Viverridae	*Genetta*	*genetta*	10,900	11,600	0	.	2	25.7	.	30	0	261.8	44	80.9
Viverridae	*Viverricula*	*indica*	2,830	2,490	.	.	2	.	.	23	0	303.8	739	102.3
Viverridae	*Nandinia*	*binotata*	2,050	1,900	.	.	2	0.73	5	1	0	274.1	612	57.4
Viverridae	*Eupleres*	*goudotii*	2,100	2,100	.	.	2	.	.	18	0	277	920	63.0
Viverridae	*Fossa*	*fossana*	2,000	1,600	.	.	2	1	.	19	0	321.5	1,073	74.1
Viverridae	*Cryptoprocta*	*ferox*	9,500	7,000	.	.	2	1	.	20	0	201.9	780	33
Herpestidae	*Crossarchus*	*obscurus*	1,550	1,310	0	1	2	.	.	8	0	311.9	1,340	26.2
Herpestidae	*Atilax*	*paludinosus*	4,100	3,300	.	.	2	2.22	.	5	0	260	1,019	10.1
Herpestidae	*Cynictis*	*penicillata*	750	640	.	.	2	10.18	18	25	0	228.3	503	90.3
Herpestidae	*Dologale*	*dybowskii*	350	.	.	.	2	.	.	6	0	312.1	1,290	29.2
Herpestidae	*Herpestes*	*ichneumon*	3,200	2,900	.	.	2	2.8	.	28	0	253.7	11	118.2
Herpestidae	*Mungos*	*mungo*	1,290	1,230	.	.	2	2.15	18	1	0	261.7	1,014	6.0
Herpestidae	*Salanoia*	*concolor*	600	.	.	.	2	.	.	21	0	299.5	645	114.5
Herpestidae	*Galerella*	*sanguinea*	540	440	.	.	2	0.88	.	13	0	333.2	658	101.2

[1] DI = Delayed implantation, IO = induced ovulation; 1 = yes, 0 = no.
[2] Mating system: 1 = monogamous, 2 = multi-male mating, 3 = polygynous.
[3] Absolute value of latitude.
[4] Cumulative snow on ground over winter (mm).
[5] Sum of mean monthly temperature (Jan–Dec).
[6] Primary productivity measured in (g m^{-2} yr^{-1}).
[7] Seasonality measured as coefficient of variation of monthly actual evapotranspiration (mm m^{-2}).