

# Life on the edge: carnivore body size variation is all over the place

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Evolutionary biologists have long been fascinated by both the ways in which species respond to ecological conditions at the edges of their geographic ranges and the way that species' body sizes evolve across their ranges. Surprisingly, though, the relationship between these two phenomena is rarely studied. Here, we examine whether carnivore body size changes from the interior of their geographic range towards the range edges. We find that within species, body size often varies strongly with distance from the range edge. However, there is no general tendency across species for size to be either larger or smaller towards the edge. There is some evidence that the smallest guild members increase in size towards their range edges, but results for the largest guild members are equivocal. Whether individuals vary in relation to the distance from the range edges often depends on the way edge and interior are defined. Neither geographic range size nor absolute body size influences the tendency of size to vary with distance from the range edge. Therefore, we suggest that the frequent significant association between body size and the position of individuals along the edge-core continuum reflects the prevalence of geographic size variation and that the distance to range edge *per se* does not influence size evolution in a consistent way.

**Keywords:** abundance; Bergmann's rule; body size; Carnivora; range edge

## 1. INTRODUCTION

Range edges are usually thought to constitute suboptimal habitats. At the range edge at least one niche axis must be limiting to a peripheral population, or it would expand its range. Populations at range edges are therefore often seen as existing in unfavourable ecological conditions. If range edges are harsher environments for a species, climates may be less suitable and resource abundance may be lower (Brown 1984; Brown *et al.* 1995; Pitt *et al.* 2008), and hence body condition may be poorer (Perez-Tris *et al.* 2000).

Body size is a major factor influencing animal morphology, physiology, ecology, evolution and extinction probability (Haldane 1928; Stanley 1973; Peters 1983; Schmidt-Nielsen 1984; Cardillo *et al.* 2005), and has therefore been studied intensively. The ecology, genetics and evolution of populations at range edges are also the focus of much research (Brown 1984; Channell & Lomolino 2000; Sagarin & Gaines 2002*b*). The effects of range edges on ecological variables such as density have often been investigated (Brown 1984; Brown *et al.* 1995; Enquist *et al.* 1995; Blackburn *et al.* 1999). Populations near their range limits are thought to be facing harsh ecological conditions (such as different climate, abundance, competitors, prey and predator species). These factors are often thought to influence size evolution but, surprisingly, the relationship between body size and the gradient in niche optimality, which may exist from the core

to the marginal areas of a species distribution, is seldom studied (e.g. Perez-Tris *et al.* 2000; Hallas *et al.* 2002; Fukui *et al.* 2005). Owing to the strong relationship between size and animal life history, ecology and evolution, studying the mode of size evolution near the limits of species' distributions may illuminate the ecological circumstances facing populations living on the edge. Furthermore, general patterns in the direction of body size evolution towards range margins might distinguish among the mechanisms by which the ranges of species become limited.

It is difficult, however, to hypothesize *a priori* about the direction and effect size of trends in body size towards the range edge, because plausible mechanisms from existing theory generate contrasting predictions. Applicable mechanisms are broadly categorized into inter- and intraspecific competition, resource and competitor density, climatic variation and effects of geographic and phenotypical scale.

Given a strong relationship between resource abundance and body size (Bonnet *et al.* 2002; Jessop *et al.* 2006; Raia & Meiri 2006), a plausible hypothesis may be that body sizes should decrease from core areas towards the edge of a species' range. Indeed, Allen (1876) hypothesized that body size should covary positively with abundance and increase towards the central distribution of the species.

However, both the relationship between abundance and position within the range, and abundance and body size, are much debated. Although it has been argued repeatedly that population abundances tend to be low at range edges, other patterns are often reported (e.g. Blackburn *et al.* 1999; Sagarin & Gaines 2002*a*; Sagarin *et al.* 2006). Furthermore, size is often thought to be positively correlated with density, because large

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size confers a competitive advantage within species (Melton 1982). However, low density may actually allow individuals access to more resources, and body size is sometimes negatively correlated with density (Boucher *et al.* 2004; Fiori & Defeo 2006). If peripheral populations inhabit areas where competitors are absent, then small guild members may increase in size and exploit the niche of a missing larger competitor (McNab 1971), whereas large species may decrease in size (Dayan & Simberloff 1998). However, if range edges are characterized by low resource abundance it may be that large species will decrease in size, while smaller species may be less affected (McNab 1971; Heaney 1978; Dayan & Simberloff 1998).

Core individuals may be larger than those living near range edges if core areas have more continental climates and if the higher seasonality of such areas selects for large body size (Brodie 1975; Boyce 1979; Millar & Hickling 1990; cf. Ferguson & McLoughlin 2000; Meiri *et al.* 2005*b*). Body size frequently varies clinally across space, often (in endotherms) in accordance with Bergmann's rule, which predicts that size will increase with decreasing temperatures and by proxy with increasing latitude (Mayr 1963; Freckleton *et al.* 2003; Meiri & Dayan 2003; Meiri *et al.* 2007). Therefore, size may be large at the colder edges of the range, small at the hotter edges, and, if core areas of the range are characterized by intermediate temperatures, intermediate there. The (few) studies that have explicitly examined intraspecific size variation in relation to population position along the core—range edge axis usually did not account for such overriding clinal variation (e.g. Hallas *et al.* 2002; Diaz *et al.* 2007).

Finally, the distance to range edges may not affect size evolution in any consistent manner but may appear to do so owing to factors that are not directly related to this distance. Thus, we would expect that species with larger ranges, where the scope for geographic variation in size is greater (Meiri *et al.* 2007), would more often show a significant relationship between size and distance to the range edge than would species with smaller ranges. Likewise, we would expect that species that vary more in size will more likely show a significant relationship between size and distance to the range edge.

Here, we examine the relationship between distance from the distribution edge and body size in carnivores (Mammalia: Carnivora) using digitized distribution maps and a large dataset of carnivore cranial measurements (Meiri *et al.* 2005*c*), while statistically accounting for clinal geographic variation. We test whether there is a general tendency for carnivores to be smaller towards the edges of their geographic range (Allen 1876). We further test whether (i) a tendency towards smaller sizes near the range edges is stronger in larger species, owing to low resource abundance (McNab 1971), (ii) small guild members tend to grow larger near their range edges, while larger species grow smaller owing to reduced interspecific competition near the range edges (McNab 1971; Dayan & Simberloff 1998); this hypothesis differs from the previous one in that small members of one guild (e.g. American black bears *Ursus americanus*) can be larger than even the largest members of other guilds (e.g. the wolverine, *Gulo gulo*), and vice versa, and (iii) sizes of species with larger geographic ranges, and greater size variability across their ranges, tend to respond to the

distance from range ends more than to sizes of species with smaller ranges.

## 2. MATERIAL AND METHODS

We use condylobasal skull length (CBL) as a measure of body size. This commonly used size index is associated with low measurement error, does not increase in adults and is independent of body condition (Gould 1974; Gittleman & Van Valkenburgh 1997; Dayan *et al.* 2002; Meiri *et al.* 2005*c*). We measured skulls in natural history museums (see acknowledgments) and use only wild-caught, sexed adult specimens. Log transforming CBL has no qualitative effect on our results (not shown), and we therefore use raw CBL values. Here, we use only species for which our sample size is greater than or equal to 100 specimens with relatively precise locality data (less than 1° error, although in the vast majority of cases precision was much higher; figure 1).

Some studies compare populations they consider to be peripheral with those they consider to inhabit core areas (e.g. Sexton *et al.* 1992; Fukui *et al.* 2005). Kark *et al.* (2008) have argued that such a dichotomy may miss important aspects of the between-population variation, and have used a third category of 'sub-periphery'. They showed that genetic variability peaks at the sub-periphery (see also Schwartz *et al.* 2003). We use two ways to divide specimens into edge, sub-edge and interior categories. In the first, we find, for each species separately, the distance to range edge attained by the specimen furthest away from the edge. We then divide the logarithm of this distance by three, and note for each specimen of that species whether it falls in the furthest segment, the intermediate one or the one closest to the range edge. Under this classification, approximately 20, 29 and 51 per cent of the specimens are assigned to the edge, sub-edge and interior categories, respectively. In the second, we assign equal numbers of specimens to the three categories (but in case of ties, we classify specimens as edge and interior in preference to sub-edge). In a separate analysis, we treat distance to the nearest edge of the range (log transformed in all analyses) as a continuous predictor of size (following Blackburn *et al.* 1999; Komonen *et al.* 2004). Because specimen localities are often labelled in quite general terms we repeat this analyses at three levels of precision, with distances rounded up to the nearest 1, 5 and 30 km.

We treat populations of three species inhabiting both North America and the Palearctic (*Mustela erminea*, *Mustela nivalis* and *Vulpes vulpes*) separately, owing to intraspecific size differences between North America and Eurasia (e.g. the first two species are larger in Eurasia, and response of their sizes to latitude differs between continents). We study *Alopex lagopus*, *Canis lupus*, *G. gulo* and *Ursus arctos* in their Nearctic range only, because we measured fewer than 100 Palearctic specimens. While island populations are often peripheral, insularity may be associated with a host of selection pressures unrelated to position relative to the range end. Thus, at a similar distance to the near coast, even adjacent insular and mainland individuals may differ greatly in size. Furthermore, we have extensively examined the effects of insularity on body size elsewhere (Meiri *et al.* 2005*a,b*, 2006, 2008), so we opt to exclude all insular specimens from the present study.

Range edges can reflect either physiological–ecological or dispersal barriers such as mountain chains or oceans. Because we mainly measured specimens in order to compare island and mainland populations (see above), most (approx. 91%)

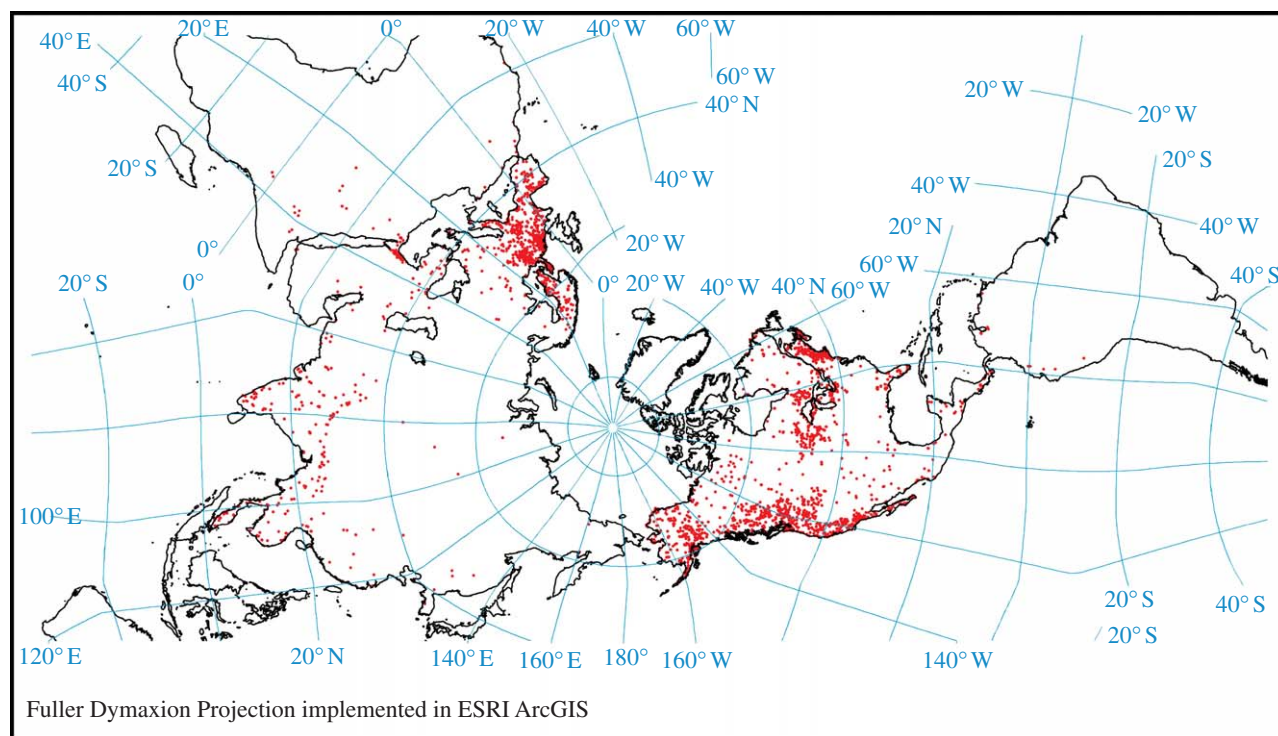


Figure 1. Specimen data localities for all species plotted onto the Fuller Dymaxion projection used for distance calculations.

of the specimens we study here were collected closer to coasts than to inland range edges. It is reasonable to believe that inland edges more likely reflect physiological or ecological barriers rather than dispersal barriers. If similar ecological or ecophysiological conditions affect body size, then the distance to inland edges may be a more informative size predictor than distance to coastal edges. We therefore introduce another analysis using only specimens that are closer to an inland than to a coastal edge. For this analysis, we use a minimum sample size of 20 specimens.

We digitized polygon range maps for each species used in Grenyer *et al.* (2006), modified, where necessary, using other published sources (see appendix 1 in the electronic supplementary material) and extended these range maps, where needed, to include specimen localities using ArcGIS v. 9.2 (ESRI, 2005). We used VMAP level 0 (NIMA 1997) to define the global extent of land. We generalized this outline and the digitized range maps to force 1 km between vertices to reduce computational demands.

Linear distances from specimen point localities were calculated to both the nearest coastal edge and the nearest inland edge. It proved computationally unfeasible to calculate geodesic distances (i.e. the 'true' distance between points on the surface of the Earth) between every specimen and the coastal or inland range edges. Consequently, the distances between specimens and range edges (and therefore the decision as to which point was nearest) were computed with the projected data. Since it was not feasible to produce over 7800 equidistant projections centred upon each specimen location, a compromise projection had to be chosen to minimize distortion across the analytical domain.

The Buckminster Fuller's Dymaxion projection (Fuller 1954) has two appealing properties for our purpose. Since it is a projection of the globe onto an icosahedron with each face subtending a separate centred gnomonic projection, both scale and conformal error are kept low across the global

extent. The standard Dymaxion projection also positions the world's coastline such that it remains unbroken across discontinuities in the projection, and so facilitates the calculation of distances.

Because in carnivores males are almost always larger than females, and because both latitudinal and longitudinal size clines are common (Meiri *et al.* 2005*d*, 2007), we modelled CBL for each species as a function of sex, latitude, longitude and the distance to the edge of the range, or one of the three distance categories discussed above. Because specimen locality data are often imprecise, we repeated the analysis with distances binned to either 5 or 30 km intervals of distances from range edges. Slopes of CBL as a function of distance had identical signs for all three categories (see appendix 2 in the electronic supplementary material) in all species associated with significant (log) distance/CBL slopes. All the significant results (at  $p < 0.05$ ) obtained using 1 km bins remained significant using 5 and 30 km bins, and no result became significant using coarser distance measures. We are therefore confident that minor imprecision in locality data has negligible effects on our analysis, and we proceed using the 1 km precision data only.

We performed exploratory data analysis with generalized additive models (GAMs). CBL was modelled as a function of specimen sex and a multidimensional smooth function of latitude and longitude (following Wood 2006), using a thin plate regression spline as the smooth function basis, and determining the degree of smoothing by generalized cross-validation. Model summaries and maps of the spatial components and ranges for all species are presented in the electronic supplementary material, appendix 3. Exemplar plots of the spatial components for three species showing opposing patterns are shown in figure 2.

We test whether the response of size to distance from range edge is related to carnivore body mass (data from Meiri *et al.* 2005*e*) or position along the large-to-small axis within guilds,

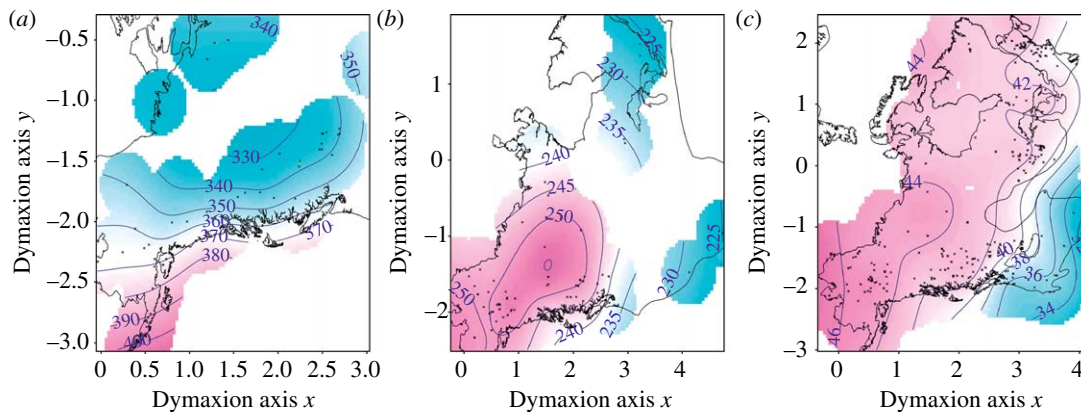


Figure 2. Three exemplar species from North America showing contrasting patterns of within-range variation in CBL. Contours and surfaces are marginal predicted CBL surfaces on the scale of the response variable from GAMs of CBL as a parametric function of sex and a smooth multidimensional function of position in projected (Fuller's Dymaxion) space (units are thousands of km, small-large gradient shaded as cyan to magenta). Only male specimen surfaces are shown. Points show specimen locations. (a) *Ursus arctos*, (b) *Canis lupus* and (c) *Mustela erminea* Nearctic.

defined on the basis of morphological similarities that reflect similarities in movement and killing behaviour (see Simberloff & Dayan (1991) for discussion of ecological guilds): we classify *U. arctos*, *C. lupus* and *G. gulo* as the largest members of their guilds, and *A. lagopus*, *Urocyon procyonoides*, *Viverricula indica* and *M. nivalis* as the smallest guild members. Other species are deemed intermediate and are not used in this analysis.

### 3. RESULTS

#### (a) Distance to range edge as a continuous predictor

Our dataset contains 7871 specimens belonging to 25 species (three of which are examined separately in the Nearctic and Palearctic; mean sample size  $281 \pm 49$  s.e., range 102–1227). The models of distance from range edge as a continuous predictor are presented in the electronic supplementary material, appendix 4A. Sex significantly affected CBL in all models (males were always larger). Latitude and longitude were significantly correlated with CBL in 16 and 19 of 28 cases, respectively. (CBL significantly increased with latitude in 12 cases and significantly decreased in 4 cases. It significantly increased eastwards in five cases and westwards in 14.) Slopes and probabilities for the effect of distance from range edge are shown in table 1. Twelve relationships were significant. Size increases towards the range interior in four cases and the range edge in eight cases. Adding a quadratic term to the log distance variable, to account for nonlinearity, resulted in significantly better models in 5 of 28 cases (determined by both ANOVA and AIC scores; see the electronic supplementary material appendices 4B and 4C).

#### (b) Distance to range edge as a categorical predictor

The models with all predictor variables are shown in the electronic supplementary material, appendix 4D. With equal distances categorization, edge specimens are significantly larger than core ones in seven cases and smaller in five cases (table 2). Edge specimens are significantly larger than sub-edge ones in four cases and smaller in two cases. With equal numbers of specimen categories, edge

Table 1. Slopes and probabilities for the effect of distance from range edge (km) on CBL (mm). (The results are slopes and probabilities for a linear model of CBL as a function of sex, latitude, longitude and distance to range edge. P, Palearctic sample; N, Nearctic sample. Coefficients for other variables are given in the electronic supplementary material, appendix 4A.)

species	n	slope (mm CBL per log (km) distance)	p-value
<i>Alopex lagopus</i>	153	0.087	0.900
<i>Canis aureus</i>	108	-1.255	0.153
<i>Canis latrans</i>	176	-0.251	0.741
<i>Canis lupus</i>	173	3.879	0.0002
<i>Gulo gulo</i>	128	-0.201	0.689
<i>Herpestes edwardsii</i>	103	0.751	0.172
<i>Lontra canadensis</i>	153	-1.868	0.0001
<i>Lutra lutra</i>	105	-1.128	0.105
<i>Lynx canadensis</i>	197	-0.145	0.748
<i>Martes americana</i>	307	-0.678	0.001
<i>Martes foina</i>	264	-0.190	0.482
<i>Martes martes</i>	145	0.232	0.637
<i>Meles meles</i>	328	0.730	0.061
<i>Mustela erminea</i> (N)	1227	0.199	0.014
<i>Mustela erminea</i> (P)	437	0.256	0.135
<i>Mustela frenata</i>	714	-0.589	<0.0001
<i>Mustela nivalis</i> (N)	149	-0.473	0.001
<i>Mustela nivalis</i> (P)	823	-1.492	<0.0001
<i>Mustela putorius</i>	467	1.380	<0.0001
<i>Mustela vison</i>	404	0.211	0.285
<i>Paradoxurus hermaphroditus</i>	109	3.181	0.001
<i>Procyon lotor</i>	131	0.902	0.123
<i>Spilogale gracilis</i>	102	-1.839	0.002
<i>Urocyon cinereoargenteus</i>	174	-0.063	0.906
<i>Ursus arctos</i>	151	-8.817	<0.0001
<i>Viverricula indica</i>	108	-1.201	0.028
<i>Vulpes vulpes</i> (N)	235	-0.332	0.481
<i>Vulpes vulpes</i> (P)	300	0.747	0.224

specimens are significantly larger than core ones in eight cases and smaller in six cases. Edge specimens are significantly larger than sub-edge ones in four cases and smaller in four others (table 2).

Table 2. Comparison of edge individuals to those at the sub-edge and core. (Sample sizes as in Table 1. For each species, categories of edge, sub-edge and interior were based on either (i) equal distances, or (ii) equal numbers of specimens. Edge specimens are compared with (a) interior ones, and (b) sub-edge ones. P, Palaeartic sample; N, Nearctic sample. The results are  $t$  values from a linear model of CBL as a function of sex latitude, longitude and distance to range edge categories. Sample sizes in Table 1. Precise  $p$  values and coefficients for other variables are given in appendix 4D in the electronic supplementary material. \* $p < 0.05$ ; \*\* $p < 0.01$ ; \*\*\* $p < 0.001$ .)

	(a) comparison of edge to interior		(b) comparison of edge to sub-edge	
	(i) categories based on equal distances	(ii) categories based on equal sample sizes	(i) categories based on equal distances	(ii) categories based on equal sample sizes
<i>Alopex lagopus</i>	-0.601	0.614	1.090	-0.842
<i>Canis aureus</i>	-1.083	-1.440	-1.027	-0.945
<i>Canis latrans</i>	0.305	0.126	-0.688	-0.979
<i>Canis lupus</i>	3.454**	2.877**	1.227	0.952
<i>Gulo gulo</i>	0.141	-0.236	0.290	0.625
<i>Herpestes edwardsii</i>	1.451	0.114	1.609	-0.266
<i>Lontra canadensis</i>	-4.421***	-3.571***	-0.835	-2.335*
<i>Lutra lutra</i>	-1.123	-1.028	0.237	0.461
<i>Lynx canadensis</i>	-0.911	0.681	-1.486	0.517
<i>Martes americana</i>	-4.911***	-4.354***	1.466	-0.238
<i>Martes foina</i>	-1.342	1.090	-2.127*	0.480
<i>Martes martes</i>	-0.303	0.698	-0.569	-0.595
<i>Meles meles</i>	2.162*	2.916**	0.524	0.222
<i>Mustela erminea</i> (N)	2.383*	2.762**	-0.743	2.557*
<i>Mustela erminea</i> (P)	0.484	1.394	0.971	-0.732
<i>Mustela frenata</i>	-2.896**	-3.672***	-2.414*	-2.442*
<i>Mustela nivalis</i> (N)	-3.343**	-3.006**	-1.979*	-1.925
<i>Mustela nivalis</i> (P)	-11.171***	-13.445***	-2.996**	-8.470***
<i>Mustela putorius</i>	4.695***	5.318***	2.699**	2.190*
<i>Mustela vison</i>	0.481	2.053*	-0.674	-0.515
<i>Paradoxurus hermaphroditus</i>	3.136**	2.250*	1.480	2.467*
<i>Procyon lotor</i>	0.653	0.900	1.322	1.668
<i>Spilogale gracilis</i>	-3.369**	-3.247**	2.469*	2.477*
<i>Urocyon cinereoargenteus</i>	-0.219	-1.093	0.790	0.673
<i>Ursus arctos</i>	-5.454***	-4.788***	-1.848	-2.551*
<i>Viverricula indica</i>	-0.866	-2.561*	1.434	-1.856
<i>Vulpes vulpes</i> (N)	-1.054	-0.204	-0.794	-1.715
<i>Vulpes vulpes</i> (P)	1.749	0.241	0.788	-0.996

In four species, all five tests (distance as a continuous variable, edge versus sub-edge and edge versus interior with both equal distances and equal number of specimens) are significant. *Mustela putorius* is larger in the interior of its range, whereas *Mustela frenata* and Palaeartic *M. nivalis* are larger towards the edges. Specimens of *Spilogale gracilis* increase linearly in size towards the range edge, and edge specimens are larger than interior ones. However, they are smaller than sub-edge ones (although a quadratic term for distance in this species was not significant). *Ursus arctos*, *Lontra canadensis* and Nearctic *M. nivalis* are significantly larger closer to the range edge in four of five tests, while *Paradoxurus hermaphroditus* and Nearctic *M. erminea* are significantly smaller closer to the edge in four tests.

Twelve species showed no significant response to range edge in any test (including *V. vulpes* in both the Nearctic and the Palaeartic). The other six species showed significant change in size in relation to range edges in one to three of five tests.

By examining the effect of distance to range edge using only specimens closer to an inland edge than to a coastal one (table 3, see appendix 4E in the electronic supplementary material), we found that size significantly increased towards range edges in 3 of 11 cases and

significantly decreased in two others. In just one case (*M. frenata*) was the direction of size change similar to that found for the whole dataset. In one case (Nearctic *M. erminea*), the direction of size changes was opposite to that found in the whole dataset, and three species showing no significant response to distance in the whole dataset showed significant size changes when only specimens closer to an inland edge than to a coastal one were considered.

### (c) Correlates of response to range ends

Body size *per se* does not influence the response of CBL to distance from range edges: of three large (more than 10 kg) species in our dataset, one (*C. lupus*) increases in size away from range edges (all comparisons here refer to distance treated as a continuous variable; table 1); one (*U. arctos*) decreases (figure 2); and a third (the coyote, *Canis latrans*) shows no significant change. Small (up to approx. 1 kg) species either increase in size towards the range edge (*M. nivalis* in both Palaeartic and Nearctic, *M. frenata*, *S. gracilis* and *Martes americana*), increase in size away from the range edge (Nearctic *M. erminea* and *M. putorius*) or show no response (Palaeartic *M. erminea*, *Mustela vison* and Eurasian *Martes*). The standardized slope for the distance to range edge/CBL relationship is not correlated with body mass ( $n=28$ ,  $t=0.70$ ,  $R^2=0.019$ ,  $p=0.49$ ), nor is the

absolute value of this standardized slope correlated with mass ( $t=0.10$ ,  $R^2<0.001$ ,  $p=0.92$ ).

One largest guild member (*C. lupus*) decreases in size towards the edge of its range, in agreement with the prediction of McNab (1971), while one other (the wolverine, *G. gulo*) shows no trend and a third (*U. arctos*) shows the opposite pattern. Two of the smallest members of their guilds (*M. nivalis* and *V. indica*) increase in size towards the edges of their range, in accordance with the predictions of McNab (1971), whereas the two small members of the canid guild, the arctic and grey foxes (*A. lagopus* and *Urocyon cinereoargenteus*), show no response.

Range size (log transformed) did not differ between carnivores that show a significant linear relationship between CBL and distance to range edge (mean log range size = 6.97) and those that did not (mean log range size = 7.09  $t = -1.22$ ,  $p = 0.23$ ). Furthermore, there was no correlation between range size and the standardized slope for the distance to range edge/CBL relationship (slope  $-0.056 \pm 0.10$ ,  $R^2 = 0.011$ ,  $p = 0.59$ ) or the absolute value of this slope (slope  $-0.05 \pm 0.07$ ,  $R^2 = 0.019$ ,  $p = 0.48$ ).

The range sizes of the carnivores we examine are uniformly large, with just one order of magnitude covering the entire range size (2.9 million km<sup>2</sup> for *S. gracilis* to 42 million km<sup>2</sup> for Palearctic red foxes (*V. vulpes*); see appendix 5 in the electronic supplementary material).

Carnivores showing a significant linear relationship between CBL and distance to range edge have higher overall geographic variation in size (measured as the average of the coefficients of variation for male and female CBL, to control for sexual dimorphism) to those that do not (mean CV = 5.99 versus 4.59;  $t = 2.41$ ,  $p = 0.027$ ).

#### 4. DISCUSSION

Size change in response to distance from range edge is relatively common: between 21 and 50 per cent of our results in the different analyses are significant. We are unsure, however, whether this high prevalence of significant results truly reflects an effect of range edge *per se*. Apart from species' tendencies to vary in size, none of the factors we examined seem to predict the direction and magnitude of size evolution consistently. There does not seem to be an excess of species in which body size is smaller near the range edges (cf. Allen 1876). In fact, individuals inhabiting range edges are often larger than core-area conspecifics (Thurber & Peterson 1991; Law *et al.* 2002; Goltsman *et al.* 2005; this study), but again this pattern is not general. Neither does there seem to be a general tendency for similar patterns to be obtained in relation to range size or absolute body size. There is some indication that small carnivores and small guild members may increase in size towards the edges of their ranges in line with McNab's (1971) hypothesis that small-bodied members of guilds are likely to increase in size away from their mid-latitude distribution. However, even these results are equivocal, and there is no general pattern of size decrease towards the edge of the range in the largest guild members.

Body sizes may often differ greatly between range edges and core area in parallel with clinal responses to latitude or temperature (i.e. according to Bergmann's rule, Mayr 1963; Meiri & Dayan 2003). Such a pattern, for example,

Table 3. Data of specimens closer to inland than to coastal edges. (Slopes and probabilities for the effect of distance from range edge (km) on CBL (mm). Only specimens inhabiting areas closer to an inland edge than to a coastal edge are used. The results are slopes and probabilities for a linear model of CBL as a function of sex, latitude, longitude and distance to range edge. P, Palearctic sample; N, Nearctic sample. Coefficients for other variables are given in the electronic supplementary material, appendix 4E.)

species	<i>n</i>	slope	<i>p</i> -value
<i>Herpestes edwardsii</i>	54	0.603	0.575
<i>Martes americana</i>	53	-1.669	0.488
<i>Meles meles</i>	22	6.744	0.008
<i>Mustela erminea</i> (N)	143	-1.996	0.0002
<i>Mustela erminea</i> (P)	37	5.091	0.031
<i>Mustela frenata</i>	111	-0.869	0.033
<i>Mustela nivalis</i> (N)	28	0.399	0.701
<i>Mustela nivalis</i> (P)	23	-0.644	0.851
<i>Mustela vison</i>	28	-11.607	0.0001
<i>Viverricula indica</i>	30	2.435	0.337
<i>Vulpes vulpes</i> (N)	78	-3.145	0.117

is seen in Nearctic *M. erminea* (figure 2). However, whether an animal will be small or large at the range edge depends on which edge it inhabits and is not a response to living on the edge *per se*. The common occurrence of insular dwarfs and giants (Foster 1964; Clegg & Owens 2002; Meiri *et al.* 2008) also probably depends on an interaction between the biology of a given species and the autecological conditions present on each island (Case 1978; Lawlor 1982; Raia & Meiri 2006; Meiri 2007).

The high variability of responses to range edge in body size of carnivores suggests the occurrence of different forces that block range expansion in different species (see, for example, Hersteinsson and Macdonald 1992) and differing directions, and a probable diversity in causes of size variation. In brown bears, for example, Ferguson & McLoughlin (2000) found that coastal populations with access to salmon had large body sizes, whereas inland bears were smaller (see also Meiri *et al.* 2007). However, barren-ground bears were smaller still, despite also living near the species' range edge. Thus, Ferguson & McLoughlin (2000) concluded that food abundance determines bear body size. We think body size variation often reflects autecological conditions interacting with species' biology.

We therefore believe that the common but somewhat idiosyncratic response of body size to distance from range edge we report here is more of a manifestation of the remarkable variability of carnivore body size than a reflection of a common response of size to position along the range edge–core continuum. Our finding that carnivores that vary more geographically also tend to show greater response to distance from the range edge supports this view. We hope that the finding that size often evolves in relation to the position of individuals within the geographic range will lead to further efforts to reveal the mechanisms that underpin such an impressive tendency for geographic variation in size.

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## REFERENCES

- Allen, J. A. 1876 Geographical variation among North American mammals, especially in respect to size. *Bull. U.S. Geol. Geogr. Surv. Territories* **2**, 309–344.
- Blackburn, T. M., Gaston, K. J., Quinn, R. M. & Gregory, R. D. 1999 Do local abundances of British birds change with proximity to range edge? *J. Biogeogr.* **26**, 493–505. (doi:10.1046/j.1365-2699.1999.00298.x)
- Bonnet, X., Pearson, D., Ladyman, M., Lourdais, O. & Bradshaw, D. 2002 'Heaven' for serpents? A mark-recapture study of tiger snakes (*Notechis scutatus*) on Carnac Island, Western Australia. *Austral Ecol.* **27**, 442–450. (doi:10.1046/j.1442-9993.2002.01198.x)
- Boucher, S., Crete, M., Ouellet, J. P., Daigle, C. & Lesage, L. 2004 Large-scale trophic interactions: white-tailed deer growth and forest understory. *Ecoscience* **11**, 286–295.
- Boyce, M. S. 1979 Seasonality and patterns of natural selection for life histories. *Am. Nat.* **114**, 569–583. (doi:10.1086/283503)
- Brodie, P. F. 1975 Cetacean energetics, an overview of intraspecific size variation. *Ecology* **56**, 152–161. (doi:10.2307/1935307)
- Brown, J. H. 1984 On the relationship between abundance and distribution of species. *Am. Nat.* **124**, 255–279. (doi:10.1086/284267)
- Brown, J. H., Mehlman, D. W. & Stevens, G. C. 1995 Spatial variation in abundance. *Ecology* **76**, 2028–2043. (doi:10.2307/1941678)
- Cardillo, M., Mace, G. M., Jones, K. E., Bielby, J., Bininda-Emonds, O. R. P., Sechrest, W., Orme, C. D. L. & Purvis, A. 2005 Multiple causes of high extinction risk in large mammal species. *Science* **309**, 1239–1241. (doi:10.1126/science.1116030)
- Case, T. J. 1978 A general explanation for insular body size trends in terrestrial vertebrates. *Ecology* **59**, 1–18. (doi:10.2307/1936628)
- Channell, R. & Lomolino, M. V. 2000 Dynamic biogeography and conservation of endangered species. *Nature* **403**, 84–86. (doi:10.1038/47487)
- Clegg, S. M. & Owens, I. P. F. 2002 The 'island rule' in birds: medium body size and its ecological explanation. *Proc. R. Soc. B* **269**, 1359–1365. (doi:10.1098/rspb.2002.2024)
- Dayan, T. & Simberloff, D. 1998 Size patterns among competitors: ecological character displacement and character release in mammals, with special reference to island populations. *Mamm. Rev.* **28**, 99–124. (doi:10.1046/j.1365-2907.1998.00029.x)
- Dayan, T., Wool, D. & Simberloff, D. 2002 Variation and covariation of skulls and teeth: modern carnivores and the interpretation of fossil mammals. *Paleobiology* **28**, 508–526. (doi:10.1666/0094-8373(2002)028<0508:VACOSA>2.0.CO;2)
- Diaz, J. A., Perez-Tris, J., Bauwens, D., Perez-Aranda, D., Carbonell, R., Santos, T. & Telleria, J. L. 2007 Reproductive performance of a lacertid lizard at the core and the periphery of the species' range. *Biol. J. Linn. Soc.* **92**, 87–96. (doi:10.1111/j.1095-8312.2007.00877.x)
- Enquist, B. J., Jordan, M. A. & Brown, J. H. 1995 Connections between ecology, biogeography, and paleobiology: relationship between local abundance and geographic distribution in fossil and recent molluscs. *Evol. Ecol.* **9**, 586–604. (doi:10.1007/BF01237657)
- Ferguson, S. H. & McLoughlin, P. D. 2000 Effect of energy availability, seasonality, and geographic range on brown bear life history. *Ecography* **23**, 193–200. (doi:10.1111/j.1600-0587.2000.tb00275.x)
- Fiori, S. & Defeo, O. 2006 Biogeographic patterns in life-history traits of the yellow clam, *Mesodesma mactroides*, in sandy beaches of South America. *J. Coast. Res.* **22**, 872–880. (doi:10.2112/04-0409.1)
- Foster, J. B. 1964 Evolution of mammals on islands. *Nature* **202**, 234–235. (doi:10.1038/202234a0)
- Freckleton, R. P., Harvey, P. H. & Pagel, M. 2003 Bergmann's rule and body size in mammals. *Am. Nat.* **161**, 821–825. (doi:10.1086/374346)
- Fukui, D., Maeda, K., Hill, D. A., Matsumura, S. & Agetsuma, N. 2005 Geographical variation in the cranial and external characters of the little tube-nosed bat, *Murina silvatica* in the Japanese archipelago. *Acta Therio.* **50**, 309–322.
- Fuller, R. B. 1954 Fluid Geography, a Primer for the Airocean [sic] World. *North Carolina State School of Design Journal*, 41–48.
- Gittleman, J. L. & Van Valkenburgh, B. 1997 Sexual dimorphism in the canines and skulls of carnivores: effects of size, phylogeny and behavioural ecology. *J. Zool.* **242**, 97–117.
- Goltsman, M., Kruchenkova, E. P., Sergeev, S., Volodin, I. & Macdonald, D. W. 2005 'Island syndrome' in a population of Arctic foxes (*Alopex lagopus*) from Mednyi Island. *J. Zool.* **267**, 405–418. (doi:10.1017/S0952836905007557)
- Gould, S. J. 1974 The origin and function of 'bizarre' structures: antler size and skull size in the 'Irish elk', *Megaloceros giganteus*. *Evolution* **28**, 191–220. (doi:10.2307/2407322)
- Grenyer, R. *et al.* 2006 Global distribution and conservation of rare and threatened vertebrates. *Nature* **444**, 93–96. (doi:10.1038/nature05237)
- Haldane, J. B. S. 1928 *On being the right size. Possible worlds*. New York, NY: Harper, pp. 20–28
- Hallas, R., Schiffer, M. & Hoffmann, A. A. 2002 Clinal variation in *Drosophila serrata* for stress resistance and body size. *Genet. Res.* **79**, 141–148. (doi:10.1017/S0016672301005523)
- Heaney, L. R. 1978 Island area and body size of insular mammals: evidence from the tri-colored squirrel (*Callosciurus prevosti*) of southeast Asia. *Evolution* **32**, 29–44. (doi:10.2307/2407408)

- Hersteinsson, P. & Macdonald, D. W. 1992 Interspecific competition and the geographical distribution of red and arctic foxes *Vulpes vulpes* and *Alopex lagopus*. *Oikos* **64**, 505–515. (doi:10.2307/3545168)
- Jessop, T. S., Madsen, T., Sumner, J., Rudiharto, H., Phillips, J. A. & Ciofi, C. 2006 Maximum body size among insular Komodo dragon populations covaries with large prey density. *Oikos* **112**, 422–429. (doi:10.1111/j.0030-1299.2006.14371.x)
- Kark, S., Hadany, L., Safriel, U. N., Noy-Meir, I., Eldredge, N., Tabarroni, C. & Randi, E. 2008 How does genetic diversity change towards the range periphery? An empirical and theoretical test. *Evol. Ecol. Res.* **10**, 391–414.
- Komonen, A., Grapputo, A., Kaitala, V., Kotiaho, J. S. & Paivinen, J. 2004 The role of niche breadth, resource availability and range position on the life history of butterflies. *Oikos* **105**, 41–54. (doi:10.1111/j.0030-1299.2004.12958.x)
- Law, B. S., Reinhold, L. & Pennay, M. 2002 Geographic variation in the echolocation calls of *Vespertilio* spp. (Vespertilionidae) from New South Wales and Queensland, Australia. *Acta Chiro.* **4**, 201–215.
- Lawlor, T. E. 1982 The evolution of body size in mammals: evidence from insular populations in Mexico. *Am. Nat.* **119**, 54–72. (doi:10.1086/283890)
- Mayr, E. 1963 *Animal species and evolution*. Cambridge, MA: Belknap Press.
- McNab, B. K. 1971 On the ecological significance of Bergmann's rule. *Ecology* **52**, 845–854. (doi:10.2307/1936032)
- Meiri, S. 2007 Size evolution in island lizards. *Glob. Ecol. Biogeogr.* **16**, 702–708. (doi:10.1111/j.1466-8238.2007.00327.x)
- Meiri, S. & Dayan, T. 2003 On the validity of Bergmann's rule. *J. Biogeogr.* **30**, 331–351.
- Meiri, S., Dayan, T. & Simberloff, D. 2005a Area, isolation, and size evolution in insular carnivores. *Ecol. Lett.* **8**, 1211–1217. (doi:10.1111/j.1461-0248.2005.00825.x)
- Meiri, S., Dayan, T. & Simberloff, D. 2005b Biogeographic patterns in the western Palearctic: the fasting-endurance hypothesis and the status of Murphy's rule. *J. Biogeogr.* **32**, 369–375. (doi:10.1111/j.1365-2699.2005.01197.x)
- Meiri, S., Dayan, T. & Simberloff, D. 2005c Variability and correlations in carnivore crania and dentition. *Funct. Ecol.* **19**, 337–343. (doi:10.1111/j.1365-2435.2005.00964.x)
- Meiri, S., Dayan, T. & Simberloff, D. 2005d Variability and sexual size dimorphism in carnivores: testing the niche variation hypothesis. *Ecology* **86**, 1432–1440. (doi:10.1890/04-1503)
- Meiri, S., Simberloff, D. & Dayan, T. 2005e Insular carnivore biogeography: island area and mammalian optimal body size. *Am. Nat.* **165**, 505–514. (doi:10.1086/428297)
- Meiri, S., Dayan, T. & Simberloff, D. 2006 The generality of the island rule reexamined. *J. Biogeogr.* **33**, 1571–1577. (doi:10.1111/j.1365-2699.2006.01523.x)
- Meiri, S., Yom-Tov, Y. & Geffen, E. 2007 What determines conformity to Bergmann's rule? *Glob. Ecol. Biogeogr.* **16**, 788–794. (doi:10.1111/j.1466-8238.2007.00330.x)
- Meiri, S., Cooper, N. & Purvis, A. 2008 The island rule: made to be broken? *Proc. R. Soc. B* **275**, 141–148. (doi:10.1098/rspb.2007.1056)
- Melton, R. H. 1982 Body size and island *Peromyscus*: a pattern and a hypothesis. *Evol. Theor.* **6**, 113–126.
- Millar, J. S. & Hickling, G. J. 1990 Fasting endurance and the evolution of mammalian body size. *Funct. Ecol.* **4**, 5–12. (doi:10.2307/2389646)
- NIMA 1997 *Vector Map Level 0 (VMAP0)*. 4th ed. Fairfax, VA: National Imagery and Mapping Agency (NIMA).
- Perez-Tris, J., Carbonell, R. & Telleria, J. L. 2000 Abundance distribution, morphological variation and juvenile condition of robins, *Erithacus rubecula* (L.), in their Mediterranean range boundary. *J. Biogeogr.* **27**, 879–888. (doi:10.1046/j.1365-2699.2000.00457.x)
- Peters, H. R. 1983 *The ecological implications of body size*. New York, NY: Cambridge University Press.
- Pitt, J. A., Lariviere, S. & Messier, F. 2008 Survival and body condition of raccoons at the edge of the range. *J. Wildl. Manag.* **72**, 389–395. (doi:10.2193/2005-761)
- Raia, P. & Meiri, S. 2006 The island rule in large mammals: paleontology meets ecology. *Evolution* **60**, 1731–1742. (doi:10.1554/05-664.1)
- Sagarin, R. D. & Gaines, S. D. 2002a Geographical abundance distributions using 1-dimensional ranges to test biogeographic hypotheses. *J. Biogeogr.* **29**, 985–998. (doi:10.1046/j.1365-2699.2002.00705.x)
- Sagarin, R. D. & Gaines, S. D. 2002b The 'abundant centre' distribution: to what extent is it a biogeographical rule? *Ecol. Lett.* **5**, 137–147. (doi:10.1046/j.1461-0248.2002.00297.x)
- Sagarin, R. D., Gaines, S. D. & Gaylord, B. 2006 Moving beyond assumptions to understand abundance distributions across the ranges of species. *Trends Ecol. Evol.* **21**, 524–530. (doi:10.1016/j.tree.2006.06.008)
- Schmidt-Nielsen, K. 1984 *Scaling. Why is animal size so important?* Cambridge, MA: Cambridge University Press.
- Schwartz, M. K., Mills, L. S., Ortega, Y., Ruggiero, L. F. & Allendorf, F. W. 2003 Landscape location affects genetic variation of Canada lynx (*Lynx canadensis*). *Mol. Ecol.* **12**, 1807–1816. (doi:10.1046/j.1365-294X.2003.01878.x)
- Sexton, O. J., Andrews, R. M. & Bramble, J. E. 1992 Size and growth rate characteristics of a peripheral population of *Crotaphytus collaris* (Sauria: Crotaphytidae). *Copeia* **1992**, 968–980. (doi:10.2307/1446626)
- Simberloff, D. & Dayan, T. 1991 The guild concept and the structure of ecological communities. *Annu. Rev. Ecol. Syst.* **22**, 115–143. (doi:10.1146/annurev.es.22.110191.000555)
- Stanley, S. M. 1973 An explanation for Cope's rule. *Evolution* **27**, 1–26. (doi:10.2307/2407115)
- Thurber, J. M. & Peterson, R. O. 1991 Changes in body size associated with range expansion in the coyote (*Canis latrans*). *J. Mammal.* **72**, 750–755. (doi:10.2307/1381838)
- Wood, S. N. 2006 *Generalized additive models: an introduction with R*. Boca Raton, FL: Chapman and Hall/CRC Press.

## APPENDICES

**Appendix 1 – origin of carnivore range maps**

**Appendix 2 – sensitivity analysis with three distance categories**

**Appendix 3 – General additive model maps of the spatial components of size for all species**

**Appendix 4 – A. models with distance to range edge as a continuous linear predictor**

**B. models with distance to range edge as a continuous linear and quadratic predictor**

**C. comparison of models with and without quadratic terms**

**D. models with distance to range edge as a categorical predictor**

**E. models for specimens closer to an inland edge than to a coastal edge, with distance to range edge as a continuous predictor**

**Appendix 5 – species level data**

### Appendix 1– origin of carnivore range maps

<b>Species</b>	<b>Range map from</b>
<i>Alopex lagopus</i>	Sechrest 2003, Grenyer et al. 2006*
<i>Canis aureus</i>	Sechrest 2003, Grenyer et al. 2006, Van Valkenburgh and Wayne 1994*
<i>Canis latrans</i>	Hall 1981*
<i>Canis lupus</i>	Hall 1981
<i>Gulo gulo</i>	Hall 1981
<i>Herpestes edwardsii</i>	Harrison and Bates 1991*
<i>Lontra canadensis</i>	Hall 1981
<i>Lutra lutra</i>	Macdonald et al. 2002
<i>Lynx canadensis</i>	Hall 1981
<i>Martes americana</i>	Hall 1981*
<i>Martes foina</i>	Corbet and Hill 1992, Mitchell-Jones et al. 1993, Sechrest 2003, Grenyer et al. 2006, IUCN 2007
<i>Martes martes</i>	Sechrest 2003, Grenyer et al. 2006*
<i>Meles meles</i>	Bevanger and Lindström 1995, Mendelssohn and Yom-Tov 1999, Sechrest 2003, Grenyer et al. 2006
<i>Mustela erminea</i> (N)	Sechrest 2003, Grenyer et al. 2006*
<i>Mustela erminea</i> (P)	Mitchell-Jones et al. 1993, Sechrest 2003, Grenyer et al. 2006
<i>Mustela frenata</i>	Hall 1951, Sheffield and Thomas 1997
<i>Mustela nivalis</i> (N)	Hall 1981
<i>Mustela nivalis</i> (P)	Sheffield and King 1994*
<i>Mustela putorius</i>	Macdonald et al. 2002
<i>Mustela vison</i>	Hall 1981
<i>Paradoxurus hermaphroditus</i>	Sechrest 2003, Grenyer et al. 2006

<i>Procyon lotor</i>	Hall 1981*
<i>Spilogale gracilis</i>	Verts et al. 2001*
<i>Urocyon cinereoargenteus</i>	Hall 1981
<i>Ursus arctos</i>	Hall 1981, Servheen et al. 1998
<i>Viverricula indica</i>	Helin et al. 1999, Sechrest 2003, Grenyer et al. 2006
<i>Vulpes vulpes</i> (N)	Hall 1981
<i>Vulpes vulpes</i> (P)	Harrison and Bates 1991, Sechrest 2003, Grenyer et al. 2006*

(N) = Nearctic; (P) = Palaeartic.

**Literature cited:**

- Bevanger, K. and Lindström, E. R. 1995. Distributional history of the European badger *Meles meles* in Scandinavia during the 20th century. *Annales Zoologica Fennici* 32: 5-9.
- Corbet, G. B. and Hill, J. E. 1992. The mammals of the IndoMalayan region. Oxford University Press. Oxford.
- Grenyer, R., Orme, C. D. L., Jackson, S. F., Thomas, G. H., Davies, R. G., Davies, T. J., Jones, K. E., Olson, V. A., Ridgely, R. S., Rasmussen, P. C., Ding, T-S., Bennett, P. M., Blackburn, T. M., Gaston, K. J., Gittleman, J. L. and Owens, I. P. F. 2006 Global distribution and conservation of rare and threatened vertebrates. *Nature* 444, 93-96.
- Hall, R. E. 1951. American Weasels. University of Kansas Publications Museum of Natural History 4: 1-466.
- Hall, R. E. 1981. The mammals of North America. 2nd edition. John Wiley & Sons. New York.
- Harrison, D. L. L. and Bates, P. J. J. 1991. The mammals of Arabia. 2nd ed. Harrison Zoological Museum Publications, Sevenoaks.
- Helin, S., Ohtaishi, N. and Houji, L. 1999. The mammalian of China. China Forestry Publishing House, Beijing.
- IUCN (2007) European mammal assessment. Available at: <http://ec.europa.eu/environment/nature/conservation/species/ema/> (accessed 01 September 2008).
- Macdonald, D. W., Sidorovich, V. E., Maran, T. and Krunk. H. 2002. European mink, *Mustela lutreola*: analyses for conservation. Wildlife Conservation Research Unit. Oxford.
- Mendelssohn, H. and Yom-Tov, Y. 1999. Mammalia of Israel. The Israel academy of sciences and humanities, Jerusalem.
- Mitchell-Jones, A. J., Amori, G., Bogdanowicz, B., Krystufek, B., Reijnders, P. H. J., Spitzenberger, F., Stubbe, M., Thirssen, J. B. M., Vohralik, V. and Zima, J. 1999. The atlas of European mammals. Academic Press. London.
- Sechrest, W. W. 2003. Global diversity, endemism, and conservation of mammals. PhD Thesis, University of Virginia.
- Servheen, C., Herrero, S. and Peyton, B. 1998. Bears status survey and conservation. Action plan. IUCN/SSC Bear Specialist Group. IUCN, Gland, Switzerland.
- Sheffield, S. R. and King, C. M. 1994. *Mustela nivalis*. *Mammalian Species* 454: 1-10.
- Sheffield, S. R. and Thomas, H. H. 1997. *Mustela frenata*. *Mammalian Species* 570: 1-9.

Van Valkenburgh, B. and Wayne, R. K. 1994. Shape divergence associated with size convergence in sympatric East African jackals. *Ecology* 75: 1567-1581.

Verts, B. J., Carraway, L. N., and Kinlaw, A. 2001. *Spilogale gracilis*. *Mammalian Species* 674: 1-10.

\*Range further modified by the authors to include specimens that fall outside published map

## Appendix 2 – sensitivity analysis with three distance categories

Slopes and probabilities of the relationship between condylo-basal length (CBL, in mm) and distance to range edge, controlling for latitude, longitude and sex.

Distances are in km, 5 km and 30 km units. Sample sizes as in Table 1.

(N) = Nearctic; (P) = Palearctic.

Species	Slope of CBL vs. distance	Slope of CBL vs. distance	Slope of CBL vs. distance	p value	p value	p value
units	mm / log km	mm / log (5 km)	mm / log (30 km)	mm / log km	mm / log (5 km)	mm / log (30 km)
<i>Alopex lagopus</i>	-0.015	-0.077	-0.541	0.205	0.194	0.146
<i>Canis aureus</i>	-0.006	-0.030	-0.177	0.125	0.128	0.133
<i>Canis latrans</i>	0.000	0.001	0.011	0.953	0.949	0.917
<i>Canis lupus</i>	0.018	0.088	0.522	0.0001	0.0002	0.0002
<i>Gulo gulo</i>	-0.005	-0.025	-0.154	0.106	0.104	0.096
<i>Herpestes edwardsii</i>	0.002	0.009	0.054	0.412	0.405	0.394
<i>Lontra canadensis</i>	-0.009	-0.042	-0.231	0.029	0.033	0.051
<i>Lutra lutra</i>	-0.002	-0.011	-0.058	0.484	0.477	0.536
<i>Lynx canadensis</i>	0.001	0.005	0.029	0.657	0.660	0.647
<i>Martes americana</i>	-0.007	-0.035	-0.215	0.0002	0.0002	0.0002
<i>Martes foina</i>	0.001	0.004	0.035	0.560	0.564	0.414
<i>Martes martes</i>	0.003	0.013	0.078	0.290	0.285	0.282
<i>Meles meles</i>	0.001	0.007	0.032	0.565	0.567	0.671
<i>Mustela erminea</i> (N)	0.001	0.003	0.015	0.250	0.245	0.272
<i>Mustela erminea</i> (P)	0.002	0.009	0.050	0.121	0.129	0.159
<i>Mustela frenata</i>	-0.004	-0.018	-0.106	<0.0001	<0.0001	<0.0001
<i>Mustela nivalis</i> (N)	-0.002	-0.011	-0.063	0.006	0.006	0.007
<i>Mustela nivalis</i> (P)	-0.008	-0.038	-0.220	<0.0001	<0.0001	<0.0001
<i>Mustela putorius</i>	0.008	0.042	0.249	<0.0001	<0.0001	<0.0001
<i>Mustela vison</i>	0.001	0.005	0.023	0.462	0.454	0.599
<i>Paradoxurus hermaphroditus</i>	0.000	0.000	-0.017	0.988	0.990	0.938
<i>Procyon lotor</i>	0.009	0.049	0.183	0.179	0.170	0.407
<i>Spilogale gracilis</i>	-0.033	-0.163	-1.021	0.005	0.007	0.012
<i>Urocyon cinereoargenteus</i>	-0.002	-0.010	-0.080	0.606	0.592	0.490
<i>Ursus arctos</i>	-0.040	-0.198	-1.170	0.004	0.004	0.006
<i>Viverricula indica</i>	-0.006	-0.030	-0.195	0.028	0.028	0.020
<i>Vulpes vulpes</i> (N)	-0.001	-0.004	-0.013	0.781	0.786	0.887
<i>Vulpes vulpes</i> (P)	0.005	0.027	0.165	0.072	0.069	0.069

### Appendix 3 – General additive model maps of the spatial components of size for all species

Spatial components of GAMs of CBL (in mm) as a function of location.

- a. GAM statistics
- b. GAM maps
- c. Range maps and specimens locations

(N) = Nearctic; (P) = Palaeartic.

Species	% Deviance explained by full model	Smooth term equivalent degrees of freedom	Approximate significance of smoothing	N
<i>Alopex lagopus</i>	37.4	10.7	0.0239	153
<i>Canis aureus</i>	78.5	25.33	<10E-5	108
<i>Canis latrans</i>	58.3	12.37	<10E-5	176
<i>Canis lupus</i>	46.2	13.64	<10E-5	173
<i>Gulo gulo</i>	53.1	4.394	0.0154	128
<i>Herpestes edwardsii</i>	60.5	8.921	0.00106	103
<i>Lontra canadensis</i>	56.5	17.17	<10E-5	153
<i>Lutra lutra</i>	68.4	20.753	<10E-5	105
<i>Lynx canadensis</i> *	48.4	2	<10E-5	197
<i>Martes americana</i>	73.7	23.21	<10E-5	307
<i>Martes foina</i>	56.1	19.23	<10E-5	264
<i>Martes martes</i> *	42.5	2	0.0227	145
<i>Meles meles</i>	67.8	20.49	<10E-5	328
<i>Mustela erminea</i> (N)	72.9	27.2	<10E-5	1227
<i>Mustela erminea</i> (P)	54.6	21.29	<10E-5	437
<i>Mustela frenata</i>	65.2	25.32	<10E-5	714
<i>Mustela nivalis</i> (N)	62.5	15.73	<10E-5	149
<i>Mustela nivalis</i> (P)	81.2	26.91	<10E-5	823
<i>Mustela putorius</i>	59.1	15.46	<10E-5	467
<i>Mustela vison</i>	70	24.43	<10E-5	404
<i>Paradoxurus hermaphroditus</i>	65.4	17.41	<10E-5	109
<i>Procyon lotor</i>	63.9	22.07	<10E-5	131
<i>Spilogale gracilis</i>	78.4	9.99	<10E-5	102
<i>Urocyon cinereoargenteus</i>	56.1	11.77	<10E-5	174
<i>Ursus arctos</i>	78.9	11.41	<10E-5	151
<i>Viverricula indica</i>	59.9	14.85	<10E-5	108
<i>Vulpes vulpes</i> (N)	68.1	22.47	<10E-5	235
<i>Vulpes vulpes</i> (P)	67.5	22.84	<10E-5	300

\*Possible convergence failure

## Appendix 4A

CBL (=condylo-basal length, in mm) as a function of sex (male CBL minus female CBL), latitude, longitude and (log) distance to range edge. Distance to range edge treated as a continuous predictor. For sample sizes see Table 1.

species	factor	Estimate	Std. Error	t	p
<i>Alopex lagopus</i>	distance to range edge	0.087	0.690	0.126	0.900
<i>Alopex lagopus</i>	Intercept	118.860	9.543	12.455	<0.0001
<i>Alopex lagopus</i>	Latitude	0.031	0.193	0.162	0.872
<i>Alopex lagopus</i>	Longitude	0.017	0.028	0.610	0.543
<i>Alopex lagopus</i>	sex	4.378	0.607	7.211	<0.0001
<i>Canis aureus</i>	distance to range edge	-1.255	0.871	-1.441	0.153
<i>Canis aureus</i>	Intercept	152.670	3.273	46.650	<0.0001
<i>Canis aureus</i>	Latitude	0.197	0.072	2.752	0.007
<i>Canis aureus</i>	Longitude	-0.148	0.030	-4.924	<0.0001
<i>Canis aureus</i>	sex	5.058	1.400	3.612	0.0005
<i>Canis latrans</i>	distance to range edge	-0.251	0.759	-0.331	0.741
<i>Canis latrans</i>	Intercept	168.128	2.841	59.171	<0.0001
<i>Canis latrans</i>	Latitude	0.440	0.049	8.903	<0.0001
<i>Canis latrans</i>	Longitude	0.097	0.026	3.759	0.0002
<i>Canis latrans</i>	sex	6.586	1.116	5.904	<0.0001
<i>Canis lupus</i>	distance to range edge	3.879	1.008	3.849	0.0002
<i>Canis lupus</i>	Intercept	199.302	6.675	29.860	<0.0001
<i>Canis lupus</i>	Latitude	0.185	0.155	1.195	0.234
<i>Canis lupus</i>	Longitude	-0.163	0.056	-2.898	0.004
<i>Canis lupus</i>	sex	7.774	1.341	5.797	<0.0001
<i>Gulo gulo</i>	distance to range edge	-0.201	0.501	-0.401	0.689
<i>Gulo gulo</i>	Intercept	119.515	4.896	24.413	<0.0001
<i>Gulo gulo</i>	Latitude	0.157	0.087	1.794	0.075
<i>Gulo gulo</i>	Longitude	-0.045	0.029	-1.555	0.123
<i>Gulo gulo</i>	sex	10.233	0.961	10.651	<0.0001
<i>Herpestes edwardsii</i>	distance to range edge	0.751	0.545	1.377	0.172
<i>Herpestes edwardsii</i>	Intercept	69.673	3.078	22.634	<0.0001
<i>Herpestes edwardsii</i>	Latitude	-0.063	0.045	-1.413	0.161
<i>Herpestes edwardsii</i>	Longitude	0.060	0.038	1.584	0.116
<i>Herpestes edwardsii</i>	sex	4.535	0.561	8.081	<0.0001
<i>Lontra canadensis</i>	distance to range edge	-1.868	0.454	-4.112	0.0001
<i>Lontra canadensis</i>	Intercept	108.656	2.516	43.190	<0.0001
<i>Lontra canadensis</i>	Latitude	-0.018	0.063	-0.287	0.774
<i>Lontra canadensis</i>	Longitude	-0.039	0.016	-2.492	0.014

<i>Lontra canadensis</i>	sex	2.974	0.726	4.097	0.0001
<i>Lutra lutra</i>	distance to range edge	-1.128	0.689	-1.637	0.105
<i>Lutra lutra</i>	Intercept	110.660	3.278	33.761	<0.0001
<i>Lutra lutra</i>	Latitude	0.025	0.063	0.396	0.693
<i>Lutra lutra</i>	Longitude	-0.061	0.023	-2.613	0.010
<i>Lutra lutra</i>	sex	7.630	0.990	7.703	<0.0001
<i>Lynx canadensis</i>	distance to range edge	-0.145	0.452	-0.321	0.748
<i>Lynx canadensis</i>	Intercept	103.386	2.361	43.797	<0.0001
<i>Lynx canadensis</i>	Latitude	0.126	0.061	2.048	0.042
<i>Lynx canadensis</i>	Longitude	-0.032	0.015	-2.114	0.036
<i>Lynx canadensis</i>	sex	5.195	0.477	10.890	<0.0001
<i>Martes americana</i>	distance to range edge	-0.678	0.200	-3.398	0.001
<i>Martes americana</i>	Intercept	55.362	1.668	33.188	<0.0001
<i>Martes americana</i>	Latitude	0.400	0.037	10.679	<0.0001
<i>Martes americana</i>	Longitude	0.017	0.008	2.110	0.036
<i>Martes americana</i>	sex	5.892	0.375	15.727	<0.0001
<i>Martes foina</i>	distance to range edge	-0.190	0.269	-0.704	0.482
<i>Martes foina</i>	Intercept	69.034	1.355	50.942	<0.0001
<i>Martes foina</i>	Latitude	0.178	0.030	5.942	<0.0001
<i>Martes foina</i>	Longitude	0.012	0.013	0.906	0.366
<i>Martes foina</i>	sex	3.900	0.277	14.080	<0.0001
<i>Martes martes</i>	distance to range edge	0.232	0.491	0.473	0.637
<i>Martes martes</i>	Intercept	70.158	3.758	18.670	<0.0001
<i>Martes martes</i>	Latitude	0.190	0.071	2.668	0.009
<i>Martes martes</i>	Longitude	-0.063	0.038	-1.671	0.097
<i>Martes martes</i>	sex	5.288	0.539	9.812	<0.0001
<i>Meles meles</i>	distance to range edge	0.730	0.388	1.881	0.061
<i>Meles meles</i>	Intercept	107.612	2.128	50.578	<0.0001
<i>Meles meles</i>	Latitude	0.406	0.038	10.608	<0.0001
<i>Meles meles</i>	Longitude	-0.083	0.015	-5.645	<0.0001
<i>Meles meles</i>	sex	3.101	0.532	5.831	<0.0001
<i>Mustela erminea</i> (N)	distance to range edge	0.199	0.081	2.469	0.014
<i>Mustela erminea</i> (N)	Intercept	23.875	0.493	48.394	<0.0001
<i>Mustela erminea</i> (N)	Latitude	0.310	0.012	24.890	<0.0001
<i>Mustela erminea</i> (N)	Longitude	0.033	0.003	9.854	<0.0001
<i>Mustela erminea</i> (N)	sex	5.285	0.151	34.992	<0.0001
<i>Mustela erminea</i> (P)	distance to range edge	0.256	0.171	1.497	0.135
<i>Mustela erminea</i> (P)	Intercept	44.254	1.035	42.738	<0.0001
<i>Mustela erminea</i> (P)	Latitude	-0.032	0.018	-1.790	0.074
<i>Mustela erminea</i> (P)	Longitude	-0.007	0.003	-2.007	0.045
<i>Mustela erminea</i> (P)	sex	3.811	0.238	15.980	<0.0001
<i>Mustela frenata</i>	distance to range edge	-0.589	0.137	-4.285	<0.0001
<i>Mustela frenata</i>	Intercept	43.609	0.645	67.568	3.54443721801929e-311

<i>Mustela frenata</i>	Latitude	-0.029	0.012	-2.443	0.015
<i>Mustela frenata</i>	Longitude	-0.013	0.005	-2.749	0.006
<i>Mustela frenata</i>	sex	5.294	0.206	25.728	<0.0001
<i>Mustela nivalis</i> (N)	distance to range edge	-0.473	0.135	-3.495	0.001
<i>Mustela nivalis</i> (N)	Intercept	30.156	0.791	38.124	<0.0001
<i>Mustela nivalis</i> (N)	Latitude	-0.045	0.029	-1.559	0.121
<i>Mustela nivalis</i> (N)	Longitude	-0.023	0.011	-2.155	0.033
<i>Mustela nivalis</i> (N)	sex	2.673	0.238	11.221	<0.0001
<i>Mustela nivalis</i> (P)	distance to range edge	-1.492	0.120	-12.476	<0.0001
<i>Mustela nivalis</i> (P)	Intercept	52.654	0.615	85.660	<0.0001
<i>Mustela nivalis</i> (P)	Latitude	-0.336	0.011	-29.804	<0.0001
<i>Mustela nivalis</i> (P)	Longitude	0.003	0.005	0.703	0.482
<i>Mustela nivalis</i> (P)	sex	4.507	0.181	24.908	<0.0001
<i>Mustela putorius</i>	distance to range edge	1.380	0.263	5.241	<0.0001
<i>Mustela putorius</i>	Intercept	53.468	2.626	20.359	<0.0001
<i>Mustela putorius</i>	Latitude	0.081	0.050	1.610	0.108
<i>Mustela putorius</i>	Longitude	-0.081	0.034	-2.359	0.019
<i>Mustela putorius</i>	sex	7.235	0.322	22.450	<0.0001
<i>Mustela vison</i>	distance to range edge	0.211	0.197	1.072	0.285
<i>Mustela vison</i>	Intercept	51.641	1.534	33.664	<0.0001
<i>Mustela vison</i>	Latitude	0.016	0.033	0.491	0.624
<i>Mustela vison</i>	Longitude	-0.072	0.007	-10.764	<0.0001
<i>Mustela vison</i>	sex	5.423	0.372	14.558	<0.0001
<i>Paradoxurus hermaphroditus</i>	distance to range edge	3.181	0.915	3.477	0.001
<i>Paradoxurus hermaphroditus</i>	Intercept	103.081	9.514	10.835	<0.0001
<i>Paradoxurus hermaphroditus</i>	Latitude	0.063	0.091	0.689	0.493
<i>Paradoxurus hermaphroditus</i>	Longitude	-0.067	0.085	-0.786	0.434
<i>Paradoxurus hermaphroditus</i>	sex	4.428	1.250	3.543	0.001
<i>Procyon lotor</i>	distance to range edge	0.902	0.582	1.551	0.123
<i>Procyon lotor</i>	Intercept	98.462	2.508	39.263	<0.0001
<i>Procyon lotor</i>	Latitude	-0.120	0.043	-2.798	0.006
<i>Procyon lotor</i>	Longitude	-0.131	0.028	-4.750	<0.0001
<i>Procyon lotor</i>	sex	4.119	0.839	4.910	<0.0001
<i>Spilogale gracilis</i>	distance to range edge	-1.839	0.566	-3.249	0.002
<i>Spilogale gracilis</i>	Intercept	59.494	17.668	3.367	0.001
<i>Spilogale gracilis</i>	Latitude	-0.123	0.113	-1.083	0.282
<i>Spilogale gracilis</i>	Longitude	0.011	0.179	0.061	0.951
<i>Spilogale gracilis</i>	sex	4.830	0.726	6.650	<0.0001
<i>Urocyon cinereoargenteus</i>	distance to range edge	-0.063	0.537	-0.118	0.906
<i>Urocyon cinereoargenteus</i>	Intercept	106.911	2.430	44.000	<0.0001
<i>Urocyon cinereoargenteus</i>	Latitude	0.443	0.045	9.811	<0.0001
<i>Urocyon cinereoargenteus</i>	Longitude	0.057	0.017	3.264	0.001
<i>Urocyon cinereoargenteus</i>	sex	3.051	0.593	5.141	<0.0001
<i>Ursus arctos</i>	distance to range edge	-8.817	1.815	-4.857	<0.0001

<i>Ursus arctos</i>	Intercept	261.545	22.946	11.398	<0.0001
<i>Ursus arctos</i>	Latitude	-1.112	0.336	-3.307	0.001
<i>Ursus arctos</i>	Longitude	-0.977	0.098	-9.959	<0.0001
<i>Ursus arctos</i>	sex	42.688	2.881	14.815	<0.0001
<i>Viverricula indica</i>	distance to range edge	-1.201	0.539	-2.230	0.028
<i>Viverricula indica</i>	Intercept	83.858	3.075	27.268	<0.0001
<i>Viverricula indica</i>	Latitude	0.169	0.050	3.398	0.001
<i>Viverricula indica</i>	Longitude	0.105	0.026	3.952	0.0001
<i>Viverricula indica</i>	sex	2.009	0.716	2.806	0.006
<i>Vulpes vulpes</i> (N)	distance to range edge	-0.332	0.470	-0.706	0.481
<i>Vulpes vulpes</i> (N)	Intercept	115.039	1.916	60.038	<0.0001
<i>Vulpes vulpes</i> (N)	Latitude	0.284	0.049	5.813	<0.0001
<i>Vulpes vulpes</i> (N)	Longitude	-0.042	0.017	-2.459	0.015
<i>Vulpes vulpes</i> (N)	sex	6.904	0.720	9.595	<0.0001
<i>Vulpes vulpes</i> (P)	distance to range edge	0.747	0.613	1.218	0.224
<i>Vulpes vulpes</i> (P)	Intercept	106.366	2.087	50.973	<0.0001
<i>Vulpes vulpes</i> (P)	Latitude	0.581	0.043	13.640	<0.0001
<i>Vulpes vulpes</i> (P)	Longitude	-0.021	0.016	-1.334	0.183
<i>Vulpes vulpes</i> (P)	sex	6.628	0.736	9.006	<0.0001

## Appendix 4B

CBL (=condylo-basal length, in mm) as a function of sex (male CBL minus female CBL), latitude, longitude, (log) distance to range edge, and its squared term. Distance to range edge treated as a continuous predictor. For sample sizes see Table 1.

<b>species</b>	<b>factor</b>	<b>Estimate</b>	<b>Std. Error</b>	<b>t</b>	<b>p</b>
<i>Alopex lagopus</i>	Distance	2.412	1.578	1.529	0.128
<i>Alopex lagopus</i>	Distance Squared	-1.365	0.834	-1.637	0.104
<i>Alopex lagopus</i>	Intercept	116.058	9.642	12.036	<0.0001
<i>Alopex lagopus</i>	Latitude	0.072	0.193	0.374	0.709
<i>Alopex lagopus</i>	Longitude	0.021	0.028	0.740	0.461
<i>Alopex lagopus</i>	Sex	4.425	0.604	7.321	<0.0001
<i>Canis aureus</i>	Distance	0.318	3.190	0.100	0.921
<i>Canis aureus</i>	Distance Squared	-0.577	1.125	-0.513	0.609
<i>Canis aureus</i>	Intercept	152.476	3.306	46.119	<0.0001
<i>Canis aureus</i>	Latitude	0.180	0.079	2.288	0.024
<i>Canis aureus</i>	Longitude	-0.149	0.030	-4.929	<0.0001
<i>Canis aureus</i>	Sex	5.155	1.418	3.635	0.0004
<i>Canis latrans</i>	Distance	-4.345	2.568	-1.692	0.092
<i>Canis latrans</i>	Distance Squared	1.502	0.900	1.668	0.097
<i>Canis latrans</i>	Intercept	170.307	3.114	54.693	<0.0001
<i>Canis latrans</i>	Latitude	0.440	0.049	8.959	<0.0001
<i>Canis latrans</i>	Longitude	0.100	0.026	3.888	0.0001
<i>Canis latrans</i>	Sex	6.552	1.110	5.903	<0.0001
<i>Canis lupus</i>	Distance	-0.137	3.943	-0.035	0.972
<i>Canis lupus</i>	Distance Squared	1.462	1.388	1.053	0.294
<i>Canis lupus</i>	Intercept	201.525	6.998	28.797	<0.0001
<i>Canis lupus</i>	Latitude	0.114	0.169	0.676	0.500
<i>Canis lupus</i>	Longitude	-0.186	0.060	-3.083	0.002
<i>Canis lupus</i>	Sex	7.895	1.346	5.868	<0.0001
<i>Gulo gulo</i>	Distance	2.632	2.302	1.143	0.255
<i>Gulo gulo</i>	Distance Squared	-1.113	0.883	-1.261	0.210
<i>Gulo gulo</i>	Intercept	120.013	4.900	24.493	<0.0001
<i>Gulo gulo</i>	Latitude	0.162	0.087	1.853	0.066
<i>Gulo gulo</i>	Longitude	-0.035	0.029	-1.201	0.232
<i>Gulo gulo</i>	Sex	10.136	0.962	10.541	<0.0001
<i>Herpestes edwardsii</i>	Distance	3.037	2.134	1.423	0.158
<i>Herpestes edwardsii</i>	Distance Squared	-0.705	0.636	-1.108	0.271
<i>Herpestes edwardsii</i>	Intercept	67.383	3.705	18.187	<0.0001
<i>Herpestes edwardsii</i>	Latitude	-0.063	0.045	-1.419	0.159
<i>Herpestes edwardsii</i>	Longitude	0.070	0.039	1.789	0.077
<i>Herpestes edwardsii</i>	Sex	4.530	0.561	8.081	<0.0001
<i>Lontra canadensis</i>	Distance	-3.952	1.616	-2.446	0.016
<i>Lontra canadensis</i>	Distance Squared	0.843	0.627	1.343	0.181
<i>Lontra canadensis</i>	Intercept	110.179	2.753	40.020	<0.0001

<i>Lontra canadensis</i>	Latitude	-0.032	0.064	-0.502	0.616
<i>Lontra canadensis</i>	Longitude	-0.037	0.016	-2.376	0.019
<i>Lontra canadensis</i>	Sex	2.969	0.724	4.101	0.0001
<i>Lutra lutra</i>	Distance	-2.473	2.774	-0.892	0.375
<i>Lutra lutra</i>	Distance Squared	0.453	0.903	0.501	0.618
<i>Lutra lutra</i>	Intercept	111.655	3.843	29.051	<0.0001
<i>Lutra lutra</i>	Latitude	0.021	0.064	0.334	0.739
<i>Lutra lutra</i>	Longitude	-0.062	0.024	-2.647	0.009
<i>Lutra lutra</i>	Sex	7.549	1.007	7.493	<0.0001
<i>Lynx canadensis</i>	Distance	-2.315	1.699	-1.363	0.175
<i>Lynx canadensis</i>	Distance Squared	0.758	0.572	1.325	0.187
<i>Lynx canadensis</i>	Intercept	104.962	2.639	39.773	<0.0001
<i>Lynx canadensis</i>	Latitude	0.111	0.062	1.791	0.075
<i>Lynx canadensis</i>	Longitude	-0.033	0.015	-2.201	0.029
<i>Lynx canadensis</i>	Sex	5.222	0.477	10.959	<0.0001
<i>Martes americana</i>	Distance	2.298	0.861	2.668	0.008
<i>Martes americana</i>	Distance Squared	-1.277	0.360	-3.549	0.0004
<i>Martes americana</i>	Intercept	51.847	1.913	27.099	<0.0001
<i>Martes americana</i>	Latitude	0.464	0.041	11.337	<0.0001
<i>Martes americana</i>	Longitude	0.020	0.008	2.518	0.012
<i>Martes americana</i>	Sex	5.857	0.368	15.923	<0.0001
<i>Martes foina</i>	Distance	-2.304	1.030	-2.237	0.026
<i>Martes foina</i>	Distance Squared	0.718	0.338	2.126	0.034
<i>Martes foina</i>	Intercept	71.510	1.780	40.176	<0.0001
<i>Martes foina</i>	Latitude	0.152	0.032	4.724	<0.0001
<i>Martes foina</i>	Longitude	0.004	0.013	0.320	0.749
<i>Martes foina</i>	Sex	3.933	0.276	14.272	<0.0001
<i>Martes martes</i>	Distance	-1.598	2.224	-0.719	0.474
<i>Martes martes</i>	Distance Squared	0.595	0.705	0.844	0.400
<i>Martes martes</i>	Intercept	72.241	4.499	16.058	<0.0001
<i>Martes martes</i>	Latitude	0.171	0.075	2.295	0.023
<i>Martes martes</i>	Longitude	-0.074	0.040	-1.854	0.066
<i>Martes martes</i>	Sex	5.289	0.539	9.804	<0.0001
<i>Meles meles</i>	Distance	1.227	1.556	0.789	0.431
<i>Meles meles</i>	Distance Squared	-0.178	0.538	-0.330	0.742
<i>Meles meles</i>	Intercept	107.240	2.411	44.472	<0.0001
<i>Meles meles</i>	Latitude	0.408	0.039	10.543	<0.0001
<i>Meles meles</i>	Longitude	-0.082	0.015	-5.389	<0.0001
<i>Meles meles</i>	Sex	3.116	0.534	5.830	<0.0001
<i>Mustela erminea</i> (N)	Distance	0.334	0.347	0.962	0.336
<i>Mustela erminea</i> (N)	Distance Squared	-0.050	0.125	-0.400	0.689
<i>Mustela erminea</i> (N)	Intercept	23.716	0.633	37.453	<0.0001
<i>Mustela erminea</i> (N)	Latitude	0.312	0.014	22.002	<0.0001
<i>Mustela erminea</i> (N)	Longitude	0.033	0.003	9.684	<0.0001
<i>Mustela erminea</i> (N)	Sex	5.287	0.151	34.977	<0.0001
<i>Mustela erminea</i> (P)	Distance	0.464	0.636	0.729	0.466
<i>Mustela erminea</i> (P)	Distance Squared	-0.079	0.233	-0.339	0.735
<i>Mustela erminea</i> (P)	Intercept	44.197	1.050	42.091	<0.0001
<i>Mustela erminea</i> (P)	Latitude	-0.033	0.018	-1.811	0.071
<i>Mustela erminea</i> (P)	Longitude	-0.007	0.003	-2.017	0.044

<i>Mustela erminea</i> (P)	Sex	3.816	0.239	15.952	<0.0001
<i>Mustela frenata</i>	Distance	0.749	0.543	1.380	0.168
<i>Mustela frenata</i>	Distance Squared	-0.463	0.182	-2.548	0.011
<i>Mustela frenata</i>	Intercept	42.252	0.835	50.614	<0.0001
<i>Mustela frenata</i>	Latitude	-0.025	0.012	-2.140	0.033
<i>Mustela frenata</i>	Longitude	-0.018	0.005	-3.527	0.0004
<i>Mustela frenata</i>	Sex	5.305	0.205	25.873	<0.0001
<i>Mustela nivalis</i> (N)	Distance	-0.801	0.618	-1.296	0.197
<i>Mustela nivalis</i> (N)	Distance Squared	0.120	0.220	0.543	0.588
<i>Mustela nivalis</i> (N)	Intercept	30.516	1.033	29.543	<0.0001
<i>Mustela nivalis</i> (N)	Latitude	-0.051	0.031	-1.643	0.103
<i>Mustela nivalis</i> (N)	Longitude	-0.024	0.011	-2.209	0.029
<i>Mustela nivalis</i> (N)	Sex	2.668	0.239	11.168	<0.0001
<i>Mustela nivalis</i> (P)	Distance	-0.145	0.483	-0.300	0.764
<i>Mustela nivalis</i> (P)	Distance Squared	-0.494	0.171	-2.881	0.004
<i>Mustela nivalis</i> (P)	Intercept	52.297	0.624	83.768	<0.0001
<i>Mustela nivalis</i> (P)	Latitude	-0.341	0.011	-30.030	<0.0001
<i>Mustela nivalis</i> (P)	Longitude	0.003	0.004	0.580	0.562
<i>Mustela nivalis</i> (P)	Sex	4.495	0.180	24.946	<0.0001
<i>Mustela putorius</i>	Distance	0.510	0.962	0.530	0.597
<i>Mustela putorius</i>	Distance Squared	0.329	0.350	0.940	0.347
<i>Mustela putorius</i>	Intercept	53.458	2.627	20.353	<0.0001
<i>Mustela putorius</i>	Latitude	0.090	0.051	1.761	0.079
<i>Mustela putorius</i>	Longitude	-0.092	0.036	-2.537	0.011
<i>Mustela putorius</i>	Sex	7.238	0.322	22.456	<0.0001
<i>Mustela vison</i>	Distance	1.264	0.865	1.461	0.145
<i>Mustela vison</i>	Distance Squared	-0.412	0.330	-1.250	0.212
<i>Mustela vison</i>	Intercept	51.012	1.614	31.616	<0.0001
<i>Mustela vison</i>	Latitude	0.026	0.034	0.768	0.443
<i>Mustela vison</i>	Longitude	-0.071	0.007	-10.470	<0.0001
<i>Mustela vison</i>	Sex	5.363	0.375	14.288	<0.0001
<i>Paradoxurus hermaphroditus</i>	Distance	8.592	2.885	2.978	0.004
<i>Paradoxurus hermaphroditus</i>	Distance Squared	-2.424	1.227	-1.975	0.051
<i>Paradoxurus hermaphroditus</i>	Intercept	100.073	9.507	10.526	<0.0001
<i>Paradoxurus hermaphroditus</i>	Latitude	0.219	0.120	1.825	0.071
<i>Paradoxurus hermaphroditus</i>	Longitude	-0.066	0.084	-0.784	0.435
<i>Paradoxurus hermaphroditus</i>	Sex	4.087	1.245	3.283	0.001
<i>Procyon lotor</i>	Distance	0.797	2.014	0.396	0.693
<i>Procyon lotor</i>	Distance Squared	0.050	0.910	0.055	0.956
<i>Procyon lotor</i>	Intercept	98.470	2.521	39.056	<0.0001
<i>Procyon lotor</i>	Latitude	-0.121	0.044	-2.736	0.007
<i>Procyon lotor</i>	Longitude	-0.131	0.029	-4.594	<0.0001
<i>Procyon lotor</i>	Sex	4.117	0.843	4.885	<0.0001
<i>Spilogale gracilis</i>	Distance	1.112	1.895	0.587	0.559
<i>Spilogale gracilis</i>	Distance Squared	-1.524	0.934	-1.631	0.106
<i>Spilogale gracilis</i>	Intercept	61.933	17.583	3.522	0.001
<i>Spilogale gracilis</i>	Latitude	-0.100	0.113	-0.879	0.382
<i>Spilogale gracilis</i>	Longitude	0.046	0.178	0.255	0.799
<i>Spilogale gracilis</i>	Sex	4.803	0.720	6.667	<0.0001
<i>Urocyon cinereoargenteus</i>	Distance	1.015	1.800	0.564	0.574
<i>Urocyon cinereoargenteus</i>	Distance Squared	-0.409	0.652	-0.628	0.531

<i>Urocyon cinereoargenteus</i>	Intercept	106.204	2.682	39.596	<0.0001
<i>Urocyon cinereoargenteus</i>	Latitude	0.445	0.045	9.812	<0.0001
<i>Urocyon cinereoargenteus</i>	Longitude	0.056	0.018	3.194	0.002
<i>Urocyon cinereoargenteus</i>	Sex	3.034	0.595	5.099	<0.0001
<i>Ursus arctos</i>	Distance	-5.017	6.737	-0.745	0.458
<i>Ursus arctos</i>	Distance Squared	-1.620	2.765	-0.586	0.559
<i>Ursus arctos</i>	Intercept	268.989	26.274	10.238	<0.0001
<i>Ursus arctos</i>	Latitude	-1.142	0.341	-3.350	0.001
<i>Ursus arctos</i>	Longitude	-0.931	0.125	-7.463	<0.0001
<i>Ursus arctos</i>	Sex	42.600	2.892	14.731	<0.0001
<i>Viverricula indica</i>	Distance	1.280	1.754	0.730	0.467
<i>Viverricula indica</i>	Distance Squared	-0.877	0.590	-1.485	0.141
<i>Viverricula indica</i>	Intercept	83.215	3.088	26.949	<0.0001
<i>Viverricula indica</i>	Latitude	0.167	0.049	3.388	0.001
<i>Viverricula indica</i>	Longitude	0.098	0.027	3.681	0.0004
<i>Viverricula indica</i>	Sex	2.113	0.715	2.953	0.004
<i>Vulpes vulpes (N)</i>	Distance	-0.028	1.872	-0.015	0.988
<i>Vulpes vulpes (N)</i>	Distance Squared	-0.114	0.678	-0.168	0.867
<i>Vulpes vulpes (N)</i>	Intercept	114.834	2.274	50.491	<0.0001
<i>Vulpes vulpes (N)</i>	Latitude	0.285	0.049	5.776	<0.0001
<i>Vulpes vulpes (N)</i>	Longitude	-0.042	0.017	-2.459	0.015
<i>Vulpes vulpes (N)</i>	Sex	6.907	0.721	9.576	<0.0001
<i>Vulpes vulpes (P)</i>	Distance	-0.763	2.281	-0.335	0.738
<i>Vulpes vulpes (P)</i>	Distance Squared	0.515	0.749	0.687	0.492
<i>Vulpes vulpes (P)</i>	Intercept	107.288	2.482	43.221	<0.0001
<i>Vulpes vulpes (P)</i>	Latitude	0.579	0.043	13.563	<0.0001
<i>Vulpes vulpes (P)</i>	Longitude	-0.022	0.016	-1.388	0.166
<i>Vulpes vulpes (P)</i>	Sex	6.654	0.738	9.021	<0.0001

## Appendix 4C

### comparison of models with and without quadratic terms

AIC scores are for the full models with sex, latitude, longitude, (log) distance and, for AIC (Quadratic model) only, squared (log) distance.

F and p values are output of an ANOVA comparing the quadratic and linear models.

Species	AIC (Linear model)	AIC (Quadratic model)	$\Delta$ AIC	F	p- value
<i>Alopex lagopus</i>	1590.549	1579.966	10.584	12.594	0.0004
<i>Canis aureus</i>	3744.190	3737.869	6.321	8.302	0.004
<i>Canis latrans</i>	3366.006	3361.490	4.516	6.490	0.011
<i>Canis lupus</i>	1180.250	1177.665	2.585	4.520	0.034
<i>Gulo gulo</i>	718.866	716.816	2.050	3.899	0.051
<i>Herpestes edwardsii</i>	1206.553	1205.695	0.858	2.783	0.097
<i>Lontra canadensis</i>	843.393	842.630	0.763	2.679	0.104
<i>Lutra lutra</i>	542.344	541.557	0.787	2.659	0.106
<i>Lynx canadensis</i>	590.802	590.491	0.311	2.207	0.141
<i>Martes americana</i>	895.864	895.997	-0.133	1.805	0.181
<i>Martes foina</i>	1038.512	1038.710	-0.198	1.755	0.187
<i>Martes martes</i>	793.424	793.768	-0.343	1.589	0.210
<i>Meles meles</i>	2184.635	2185.052	-0.417	1.562	0.212
<i>Mustela erminea</i> (N)	504.450	505.155	-0.705	1.227	0.271
<i>Mustela erminea</i> (P)	1244.716	1245.570	-0.854	1.110	0.294
<i>Mustela frenata</i>	2470.720	2471.825	-1.105	0.884	0.347
<i>Mustela nivalis</i> (N)	747.040	748.299	-1.259	0.712	0.400
<i>Mustela nivalis</i> (P)	1966.720	1968.238	-1.518	0.473	0.492
<i>Mustela putorius</i>	968.103	969.696	-1.593	0.394	0.531
<i>Mustela vison</i>	1299.641	1301.284	-1.643	0.343	0.559
<i>Paradoxurus hermaphroditus</i>	536.137	537.830	-1.693	0.295	0.588
<i>Procyon lotor</i>	739.345	741.067	-1.722	0.263	0.609
<i>Spilogale gracilis</i>	640.880	642.615	-1.734	0.251	0.618
<i>Urocyon cinereoargenteus</i>	5636.335	5638.174	-1.839	0.160	0.689
<i>Ursus arctos</i>	2009.156	2011.040	-1.884	0.115	0.735
<i>Viverricula indica</i>	1951.454	1953.344	-1.889	0.109	0.742
<i>Vulpes vulpes</i> (N)	1469.998	1471.969	-1.971	0.028	0.867
<i>Vulpes vulpes</i> (P)	785.874	787.871	-1.997	0.003	0.956

## Appendix 4D

### CBL as a function of sex, latitude, longitude and distance to range edge categories. Distance to range edge treated as a categorical 3-level predictor (edge, sub-edge and core)

For each species categories of edge, sub-edge and interior were based either on:

1. Equal distances. Based on the distance of the specimen furthest from the edge: specimens 0-1/3 of this distance are classified as edge specimens, those 1/3 to 2/3 of this distance are sub-edge, and the rest are interior.
2. Equal numbers of specimens. The third of the specimens closest to the edge are classified as edge, the third most distant are classified as interior specimens, and the rest are classified as sub-edge. In case of ties specimens were classified as edge or interior specimens in preference to sub-edge.

For sample sizes see Table 1

Edge specimens are compared to either 1, interior ones, or 2, sub-edge ones.

#### 1. Equal distances

Species	factor	Estimate	Std. Error	t	p
<i>Alopex lagopus</i>	edge vs. interior specimens	-1.070	1.782	-0.601	0.549
<i>Alopex lagopus</i>	edge vs. sub-edge specimens	0.870	0.798	1.090	0.277
<i>Alopex lagopus</i>	Intercept	118.396	9.464	12.510	<0.0001
<i>Alopex lagopus</i>	Latitude	0.023	0.192	0.119	0.906
<i>Alopex lagopus</i>	Longitude	0.011	0.029	0.386	0.700
<i>Alopex lagopus</i>	sex	4.462	0.608	7.338	<0.0001
<i>Canis aureus</i>	edge vs. interior specimens	-2.078	1.919	-1.083	0.281
<i>Canis aureus</i>	edge vs. sub-edge specimens	-2.111	2.056	-1.027	0.307
<i>Canis aureus</i>	Intercept	151.372	3.047	49.678	<0.0001
<i>Canis aureus</i>	Latitude	0.224	0.082	2.739	0.007
<i>Canis aureus</i>	Longitude	-0.145	0.031	-4.737	<0.0001
<i>Canis aureus</i>	sex	4.973	1.416	3.512	0.001
<i>Canis latrans</i>	edge vs. interior specimens	0.481	1.575	0.305	0.760
<i>Canis latrans</i>	edge vs. sub-edge specimens	-1.023	1.486	-0.688	0.492
<i>Canis latrans</i>	Intercept	168.505	2.836	59.423	<0.0001

<i>Canis latrans</i>	Latitude	0.431	0.049	8.889	<0.0001
<i>Canis latrans</i>	Longitude	0.098	0.026	3.788	0.0002
<i>Canis latrans</i>	sex	6.451	1.121	5.752	<0.0001
<i>Canis lupus</i>	edge vs. interior specimens	7.844	2.271	3.454	0.001
	edge vs. sub-edge				
<i>Canis lupus</i>	specimens	3.947	3.218	1.227	0.222
<i>Canis lupus</i>	Intercept	200.463	6.872	29.171	<0.0001
<i>Canis lupus</i>	Latitude	0.245	0.153	1.603	0.111
<i>Canis lupus</i>	Longitude	-0.139	0.055	-2.533	0.012
<i>Canis lupus</i>	sex	7.873	1.351	5.827	<0.0001
<i>Gulo gulo</i>	edge vs. interior specimens	0.166	1.170	0.141	0.888
	edge vs. sub-edge				
<i>Gulo gulo</i>	specimens	0.468	1.616	0.290	0.772
<i>Gulo gulo</i>	Intercept	118.904	4.945	24.047	<0.0001
<i>Gulo gulo</i>	Latitude	0.153	0.088	1.751	0.082
<i>Gulo gulo</i>	Longitude	-0.047	0.029	-1.603	0.111
<i>Gulo gulo</i>	sex	10.243	0.965	10.618	<0.0001
<i>Herpestes edwardsii</i>	edge vs. interior specimens	2.341	1.613	1.451	0.150
	edge vs. sub-edge				
<i>Herpestes edwardsii</i>	specimens	2.660	1.654	1.609	0.111
<i>Herpestes edwardsii</i>	Intercept	67.577	3.395	19.907	<0.0001
<i>Herpestes edwardsii</i>	Latitude	-0.080	0.046	-1.749	0.084
<i>Herpestes edwardsii</i>	Longitude	0.081	0.038	2.148	0.034
<i>Herpestes edwardsii</i>	sex	4.578	0.561	8.154	<0.0001
<i>Lontra canadensis</i>	edge vs. interior specimens	-3.947	0.893	-4.421	<0.0001
	edge vs. sub-edge				
<i>Lontra canadensis</i>	specimens	-0.797	0.955	-0.835	0.405
<i>Lontra canadensis</i>	Intercept	106.839	2.630	40.624	<0.0001
<i>Lontra canadensis</i>	Latitude	-0.003	0.063	-0.055	0.956
<i>Lontra canadensis</i>	Longitude	-0.042	0.016	-2.691	0.008
<i>Lontra canadensis</i>	sex	3.024	0.718	4.212	<0.0001
<i>Lutra lutra</i>	edge vs. interior specimens	-1.610	1.433	-1.123	0.264
	edge vs. sub-edge				
<i>Lutra lutra</i>	specimens	0.337	1.426	0.237	0.814
<i>Lutra lutra</i>	Intercept	108.323	3.408	31.784	<0.0001
<i>Lutra lutra</i>	Latitude	0.045	0.064	0.698	0.487
<i>Lutra lutra</i>	Longitude	-0.059	0.024	-2.489	0.014
<i>Lutra lutra</i>	sex	7.735	0.995	7.773	<0.0001
<i>Lynx canadensis</i>	edge vs. interior specimens	-0.906	0.995	-0.911	0.363
	edge vs. sub-edge				
<i>Lynx canadensis</i>	specimens	-2.346	1.578	-1.486	0.139
<i>Lynx canadensis</i>	Intercept	104.189	2.409	43.259	<0.0001
<i>Lynx canadensis</i>	Latitude	0.119	0.061	1.938	0.054
<i>Lynx canadensis</i>	Longitude	-0.033	0.015	-2.208	0.028
<i>Lynx canadensis</i>	sex	5.190	0.476	10.909	<0.0001
<i>Martes americana</i>	edge vs. interior specimens	-2.062	0.420	-4.911	<0.0001
	edge vs. sub-edge				
<i>Martes americana</i>	specimens	0.767	0.523	1.466	0.144

<i>Martes americana</i>	Intercept	52.637	1.780	29.567	<0.0001
<i>Martes americana</i>	Latitude	0.476	0.040	11.885	<0.0001
<i>Martes americana</i>	Longitude	0.030	0.008	3.673	0.0003
<i>Martes americana</i>	sex	6.010	0.360	16.674	<0.0001
<i>Martes foina</i>	edge vs. interior specimens	-0.778	0.580	-1.342	0.181
<i>Martes foina</i>	edge vs. sub-edge specimens	-1.308	0.615	-2.127	0.034
<i>Martes foina</i>	Intercept	70.926	1.628	43.565	<0.0001
<i>Martes foina</i>	Latitude	0.149	0.033	4.586	<0.0001
<i>Martes foina</i>	Longitude	0.007	0.013	0.564	0.573
<i>Martes foina</i>	sex	3.958	0.277	14.307	<0.0001
<i>Martes martes</i>	edge vs. interior specimens	-0.338	1.114	-0.303	0.762
<i>Martes martes</i>	edge vs. sub-edge specimens	-0.700	1.230	-0.569	0.570
<i>Martes martes</i>	Intercept	72.199	4.240	17.027	<0.0001
<i>Martes martes</i>	Latitude	0.167	0.077	2.179	0.031
<i>Martes martes</i>	Longitude	-0.061	0.038	-1.624	0.107
<i>Martes martes</i>	sex	5.224	0.540	9.674	<0.0001
<i>Meles meles</i>	edge vs. interior specimens	1.618	0.748	2.162	0.031
<i>Meles meles</i>	edge vs. sub-edge specimens	0.362	0.692	0.524	0.601
<i>Meles meles</i>	Intercept	108.142	2.099	51.528	<0.0001
<i>Meles meles</i>	Latitude	0.405	0.038	10.604	<0.0001
<i>Meles meles</i>	Longitude	-0.084	0.015	-5.707	<0.0001
<i>Meles meles</i>	sex	3.024	0.533	5.673	<0.0001
<i>Mustela erminea</i> (N)	edge vs. interior specimens	0.412	0.173	2.383	0.017
<i>Mustela erminea</i> (N)	edge vs. sub-edge specimens	-0.161	0.216	-0.743	0.458
<i>Mustela erminea</i> (N)	Intercept	24.162	0.519	46.539	<0.0001
<i>Mustela erminea</i> (N)	Latitude	0.304	0.013	23.622	<0.0001
<i>Mustela erminea</i> (N)	Longitude	0.031	0.003	9.313	<0.0001
<i>Mustela erminea</i> (N)	sex	5.295	0.151	35.116	<0.0001
<i>Mustela erminea</i> (P)	edge vs. interior specimens	0.171	0.352	0.484	0.628
<i>Mustela erminea</i> (P)	edge vs. sub-edge specimens	0.394	0.406	0.971	0.332
<i>Mustela erminea</i> (P)	Intercept	44.592	1.022	43.646	<0.0001
<i>Mustela erminea</i> (P)	Latitude	-0.033	0.018	-1.853	0.065
<i>Mustela erminea</i> (P)	Longitude	-0.008	0.004	-2.187	0.029
<i>Mustela erminea</i> (P)	sex	3.806	0.239	15.912	<0.0001
<i>Mustela frenata</i>	edge vs. interior specimens	-0.831	0.287	-2.896	0.004
<i>Mustela frenata</i>	edge vs. sub-edge specimens	-0.757	0.314	-2.414	0.016
<i>Mustela frenata</i>	Intercept	43.841	0.797	55.041	<0.0001
<i>Mustela frenata</i>	Latitude	-0.033	0.012	-2.707	0.007
<i>Mustela frenata</i>	Longitude	-0.009	0.006	-1.630	0.104
<i>Mustela frenata</i>	sex	5.294	0.207	25.538	<0.0001
<i>Mustela nivalis</i> (N)	edge vs. interior specimens	-1.141	0.341	-3.343	0.001
<i>Mustela nivalis</i> (N)	edge vs. sub-edge specimens	-0.827	0.418	-1.979	0.050

	specimens				
<i>Mustela nivalis</i> (N)	Intercept	30.330	0.928	32.681	<0.0001
<i>Mustela nivalis</i> (N)	Latitude	-0.053	0.030	-1.752	0.082
<i>Mustela nivalis</i> (N)	Longitude	-0.026	0.011	-2.368	0.019
<i>Mustela nivalis</i> (N)	sex	2.658	0.239	11.109	<0.0001
				-	
<i>Mustela nivalis</i> (P)	edge vs. interior specimens	-2.680	0.240	11.171	<0.0001
	edge vs. sub-edge				
<i>Mustela nivalis</i> (P)	specimens	-0.744	0.248	-2.996	0.003
<i>Mustela nivalis</i> (P)	Intercept	51.606	0.597	86.431	<0.0001
				-	
<i>Mustela nivalis</i> (P)	Latitude	-0.333	0.011	29.727	<0.0001
<i>Mustela nivalis</i> (P)	Longitude	-0.003	0.005	-0.726	0.468
<i>Mustela nivalis</i> (P)	sex	4.445	0.179	24.842	<0.0001
<i>Mustela putorius</i>	edge vs. interior specimens	2.358	0.502	4.695	<0.0001
	edge vs. sub-edge				
<i>Mustela putorius</i>	specimens	1.390	0.515	2.699	0.007
<i>Mustela putorius</i>	Intercept	55.720	2.477	22.493	<0.0001
<i>Mustela putorius</i>	Latitude	0.046	0.049	0.943	0.346
<i>Mustela putorius</i>	Longitude	-0.053	0.033	-1.607	0.109
<i>Mustela putorius</i>	sex	7.183	0.325	22.113	<0.0001
<i>Mustela vison</i>	edge vs. interior specimens	0.197	0.410	0.481	0.631
	edge vs. sub-edge				
<i>Mustela vison</i>	specimens	-0.398	0.590	-0.674	0.501
<i>Mustela vison</i>	Intercept	52.279	1.529	34.181	<0.0001
<i>Mustela vison</i>	Latitude	0.005	0.034	0.141	0.888
				-	
<i>Mustela vison</i>	Longitude	-0.074	0.007	10.706	<0.0001
<i>Mustela vison</i>	sex	5.443	0.374	14.567	<0.0001
<i>Paradoxurus hermaphroditus</i>	edge vs. interior specimens	6.404	2.042	3.136	0.002
	edge vs. sub-edge				
<i>Paradoxurus hermaphroditus</i>	specimens	2.593	1.752	1.480	0.142
<i>Paradoxurus hermaphroditus</i>	Intercept	109.181	9.194	11.875	<0.0001
<i>Paradoxurus hermaphroditus</i>	Latitude	-0.003	0.120	-0.027	0.978
<i>Paradoxurus hermaphroditus</i>	Longitude	-0.108	0.083	-1.303	0.196
<i>Paradoxurus hermaphroditus</i>	sex	4.186	1.280	3.269	0.001
<i>Procyon lotor</i>	edge vs. interior specimens	0.745	1.140	0.653	0.515
	edge vs. sub-edge				
<i>Procyon lotor</i>	specimens	1.310	0.991	1.322	0.189
<i>Procyon lotor</i>	Intercept	99.324	2.492	39.858	<0.0001
<i>Procyon lotor</i>	Latitude	-0.105	0.045	-2.350	0.020
<i>Procyon lotor</i>	Longitude	-0.120	0.029	-4.192	0.0001
<i>Procyon lotor</i>	sex	4.102	0.845	4.854	<0.0001
<i>Spilogale gracilis</i>	edge vs. interior specimens	-2.575	0.764	-3.369	0.001
	edge vs. sub-edge				
<i>Spilogale gracilis</i>	specimens	1.875	0.759	2.469	0.015
<i>Spilogale gracilis</i>	Intercept	53.139	15.981	3.325	0.001
<i>Spilogale gracilis</i>	Latitude	-0.141	0.102	-1.384	0.170
<i>Spilogale gracilis</i>	Longitude	-0.037	0.162	-0.227	0.821

<i>Spilogale gracilis</i>	sex	4.317	0.662	6.523	<0.0001
<i>Urocyon cinereoargenteus</i>	edge vs. interior specimens	-0.233	1.063	-0.219	0.827
	edge vs. sub-edge				
<i>Urocyon cinereoargenteus</i>	specimens	0.815	1.032	0.790	0.431
<i>Urocyon cinereoargenteus</i>	Intercept	105.430	2.499	42.186	<0.0001
<i>Urocyon cinereoargenteus</i>	Latitude	0.454	0.045	9.995	<0.0001
<i>Urocyon cinereoargenteus</i>	Longitude	0.051	0.017	2.903	0.004
<i>Urocyon cinereoargenteus</i>	sex	3.088	0.588	5.253	<0.0001
<i>Ursus arctos</i>	edge vs. interior specimens	-23.372	4.285	-5.454	<0.0001
	edge vs. sub-edge				
<i>Ursus arctos</i>	specimens	-6.714	3.633	-1.848	0.067
<i>Ursus arctos</i>	Intercept	273.849	23.869	11.473	<0.0001
<i>Ursus arctos</i>	Latitude	-1.045	0.333	-3.140	0.002
<i>Ursus arctos</i>	Longitude	-0.847	0.113	-7.493	<0.0001
<i>Ursus arctos</i>	sex	43.410	2.852	15.223	<0.0001
<i>Viverricula indica</i>	edge vs. interior specimens	-1.044	1.206	-0.866	0.389
	edge vs. sub-edge				
<i>Viverricula indica</i>	specimens	1.721	1.200	1.434	0.155
<i>Viverricula indica</i>	Intercept	82.590	2.765	29.868	<0.0001
<i>Viverricula indica</i>	Latitude	0.143	0.048	2.947	0.004
<i>Viverricula indica</i>	Longitude	0.101	0.025	4.077	0.0001
<i>Viverricula indica</i>	sex	2.171	0.695	3.124	0.002
<i>Vulpes vulpes</i> (N)	edge vs. interior specimens	-1.004	0.953	-1.054	0.293
	edge vs. sub-edge				
<i>Vulpes vulpes</i> (N)	specimens	-0.857	1.079	-0.794	0.428
<i>Vulpes vulpes</i> (N)	Intercept	115.289	1.914	60.229	<0.0001
<i>Vulpes vulpes</i> (N)	Latitude	0.280	0.049	5.697	<0.0001
<i>Vulpes vulpes</i> (N)	Longitude	-0.043	0.017	-2.516	0.013
<i>Vulpes vulpes</i> (N)	sex	6.935	0.722	9.603	<0.0001
<i>Vulpes vulpes</i> (P)	edge vs. interior specimens	2.132	1.219	1.749	0.081
	edge vs. sub-edge				
<i>Vulpes vulpes</i> (P)	specimens	0.942	1.195	0.788	0.431
<i>Vulpes vulpes</i> (P)	Intercept	106.782	2.152	49.629	<0.0001
<i>Vulpes vulpes</i> (P)	Latitude	0.569	0.043	13.179	<0.0001
<i>Vulpes vulpes</i> (P)	Longitude	-0.021	0.016	-1.301	0.194
<i>Vulpes vulpes</i> (P)	sex	6.696	0.737	9.090	<0.0001

## 2. Equal numbers of specimens

Species	factor	Estimate	Std. Error	t	p
<i>Alopex lagopus</i>	edge vs. interior specimens	0.504	0.821	0.614	0.540
	edge vs. sub-edge				
<i>Alopex lagopus</i>	specimens	-1.539	1.828	-0.842	0.401
<i>Alopex lagopus</i>	Intercept	120.622	9.766	12.352	<0.0001
<i>Alopex lagopus</i>	Latitude	-0.012	0.196	-0.064	0.949
<i>Alopex lagopus</i>	Longitude	0.009	0.029	0.302	0.763
<i>Alopex lagopus</i>	sex	4.367	0.608	7.187	<0.0001

<i>Canis aureus</i>	edge vs. interior specimens	-2.909	2.020	-1.440	0.153
	edge vs. sub-edge specimens				
<i>Canis aureus</i>	specimens	-1.685	1.784	-0.945	0.347
<i>Canis aureus</i>	Intercept	152.472	3.182	47.924	<0.0001
<i>Canis aureus</i>	Latitude	0.179	0.079	2.265	0.026
<i>Canis aureus</i>	Longitude	-0.149	0.031	-4.862	<0.0001
<i>Canis aureus</i>	sex	5.079	1.416	3.586	0.001
<i>Canis latrans</i>	edge vs. interior specimens	0.182	1.442	0.126	0.900
	edge vs. sub-edge specimens				
<i>Canis latrans</i>	specimens	-1.392	1.423	-0.979	0.329
<i>Canis latrans</i>	Intercept	168.431	2.788	60.417	<0.0001
<i>Canis latrans</i>	Latitude	0.442	0.051	8.734	<0.0001
<i>Canis latrans</i>	Longitude	0.100	0.026	3.862	0.0002
<i>Canis latrans</i>	sex	6.464	1.119	5.777	<0.0001
<i>Canis lupus</i>	edge vs. interior specimens	5.274	1.833	2.877	0.005
	edge vs. sub-edge specimens				
<i>Canis lupus</i>	specimens	1.668	1.752	0.952	0.342
<i>Canis lupus</i>	Intercept	207.347	6.659	31.137	<0.0001
<i>Canis lupus</i>	Latitude	0.168	0.167	1.002	0.318
<i>Canis lupus</i>	Longitude	-0.152	0.059	-2.603	0.010
<i>Canis lupus</i>	sex	8.391	1.369	6.128	<0.0001
<i>Gulo gulo</i>	edge vs. interior specimens	-0.268	1.134	-0.236	0.814
	edge vs. sub-edge specimens				
<i>Gulo gulo</i>	specimens	0.757	1.210	0.625	0.533
<i>Gulo gulo</i>	Intercept	118.790	4.955	23.975	<0.0001
<i>Gulo gulo</i>	Latitude	0.156	0.087	1.792	0.076
<i>Gulo gulo</i>	Longitude	-0.047	0.029	-1.623	0.107
<i>Gulo gulo</i>	sex	10.125	0.971	10.422	<0.0001
<i>Herpestes edwardsii</i>	edge vs. interior specimens	0.082	0.723	0.114	0.910
	edge vs. sub-edge specimens				
<i>Herpestes edwardsii</i>	specimens	-0.185	0.697	-0.266	0.791
<i>Herpestes edwardsii</i>	Intercept	70.188	3.292	21.323	<0.0001
<i>Herpestes edwardsii</i>	Latitude	-0.073	0.047	-1.577	0.118
<i>Herpestes edwardsii</i>	Longitude	0.076	0.039	1.934	0.056
<i>Herpestes edwardsii</i>	sex	4.546	0.573	7.939	<0.0001
<i>Lontra canadensis</i>	edge vs. interior specimens	-3.331	0.933	-3.571	0.0005
	edge vs. sub-edge specimens				
<i>Lontra canadensis</i>	specimens	-2.102	0.900	-2.335	0.021
<i>Lontra canadensis</i>	Intercept	108.274	2.622	41.301	<0.0001
<i>Lontra canadensis</i>	Latitude	-0.016	0.065	-0.254	0.800
<i>Lontra canadensis</i>	Longitude	-0.033	0.016	-2.140	0.034
<i>Lontra canadensis</i>	sex	3.045	0.735	4.141	0.0001
<i>Lutra lutra</i>	edge vs. interior specimens	-1.214	1.181	-1.028	0.306
	edge vs. sub-edge specimens				
<i>Lutra lutra</i>	specimens	0.583	1.266	0.461	0.646
<i>Lutra lutra</i>	Intercept	108.072	3.417	31.626	<0.0001
<i>Lutra lutra</i>	Latitude	0.043	0.066	0.655	0.514
<i>Lutra lutra</i>	Longitude	-0.059	0.024	-2.489	0.014

<i>Lutra lutra</i>	sex	7.796	1.010	7.722	<0.0001
<i>Lynx canadensis</i>	edge vs. interior specimens	0.398	0.584	0.681	0.496
	edge vs. sub-edge				
<i>Lynx canadensis</i>	specimens	0.333	0.645	0.517	0.606
<i>Lynx canadensis</i>	Intercept	102.751	2.571	39.972	<0.0001
<i>Lynx canadensis</i>	Latitude	0.128	0.064	1.990	0.048
<i>Lynx canadensis</i>	Longitude	-0.031	0.015	-2.069	0.040
<i>Lynx canadensis</i>	sex	5.231	0.478	10.943	<0.0001
<i>Martes americana</i>	edge vs. interior specimens	-1.900	0.436	-4.354	<0.0001
	edge vs. sub-edge				
<i>Martes americana</i>	specimens	-0.114	0.480	-0.238	0.812
<i>Martes americana</i>	Intercept	53.782	1.807	29.768	<0.0001
<i>Martes americana</i>	Latitude	0.433	0.040	10.833	<0.0001
<i>Martes americana</i>	Longitude	0.020	0.008	2.523	0.012
<i>Martes americana</i>	sex	5.868	0.368	15.927	<0.0001
<i>Martes foina</i>	edge vs. interior specimens	0.447	0.410	1.090	0.277
	edge vs. sub-edge				
<i>Martes foina</i>	specimens	0.180	0.375	0.480	0.632
<i>Martes foina</i>	Intercept	69.926	1.532	45.642	<0.0001
<i>Martes foina</i>	Latitude	0.149	0.033	4.490	<0.0001
<i>Martes foina</i>	Longitude	0.006	0.013	0.459	0.646
<i>Martes foina</i>	sex	3.908	0.277	14.083	<0.0001
<i>Martes martes</i>	edge vs. interior specimens	0.451	0.647	0.698	0.486
	edge vs. sub-edge				
<i>Martes martes</i>	specimens	-0.422	0.709	-0.595	0.553
<i>Martes martes</i>	Intercept	71.399	3.459	20.643	<0.0001
<i>Martes martes</i>	Latitude	0.172	0.071	2.434	0.016
<i>Martes martes</i>	Longitude	-0.060	0.037	-1.608	0.110
<i>Martes martes</i>	sex	5.320	0.538	9.897	<0.0001
<i>Meles meles</i>	edge vs. interior specimens	1.844	0.632	2.916	0.004
	edge vs. sub-edge				
<i>Meles meles</i>	specimens	0.144	0.647	0.222	0.824
<i>Meles meles</i>	Intercept	108.294	2.062	52.507	<0.0001
<i>Meles meles</i>	Latitude	0.402	0.038	10.599	<0.0001
<i>Meles meles</i>	Longitude	-0.084	0.015	-5.757	<0.0001
<i>Meles meles</i>	sex	2.984	0.529	5.638	<0.0001
<i>Mustela erminea</i> (N)	edge vs. interior specimens	0.479	0.173	2.762	0.006
	edge vs. sub-edge				
<i>Mustela erminea</i> (N)	specimens	0.438	0.171	2.557	0.011
<i>Mustela erminea</i> (N)	Intercept	23.985	0.516	46.487	<0.0001
<i>Mustela erminea</i> (N)	Latitude	0.307	0.013	23.906	<0.0001
<i>Mustela erminea</i> (N)	Longitude	0.032	0.003	9.872	<0.0001
<i>Mustela erminea</i> (N)	sex	5.294	0.151	35.016	<0.0001
<i>Mustela erminea</i> (P)	edge vs. interior specimens	0.396	0.284	1.394	0.164
	edge vs. sub-edge				
<i>Mustela erminea</i> (P)	specimens	-0.210	0.287	-0.732	0.465
<i>Mustela erminea</i> (P)	Intercept	44.039	1.037	42.474	<0.0001
<i>Mustela erminea</i> (P)	Latitude	-0.020	0.019	-1.067	0.286

<i>Mustela erminea</i> (P)	Longitude	-0.008	0.004	-2.159	0.031
<i>Mustela erminea</i> (P)	sex	3.766	0.239	15.779	<0.0001
<i>Mustela frenata</i>	edge vs. interior specimens	-0.922	0.251	-3.672	0.0003
	edge vs. sub-edge				
<i>Mustela frenata</i>	specimens	-0.573	0.235	-2.442	0.015
<i>Mustela frenata</i>	Intercept	42.990	0.672	63.932	<0.0001
<i>Mustela frenata</i>	Latitude	-0.030	0.012	-2.545	0.011
<i>Mustela frenata</i>	Longitude	-0.015	0.005	-2.912	0.004
<i>Mustela frenata</i>	sex	5.278	0.207	25.544	<0.0001
<i>Mustela nivalis</i> (N)	edge vs. interior specimens	-1.008	0.335	-3.006	0.003
	edge vs. sub-edge				
<i>Mustela nivalis</i> (N)	specimens	-0.745	0.387	-1.925	0.056
<i>Mustela nivalis</i> (N)	Intercept	29.897	0.910	32.836	<0.0001
<i>Mustela nivalis</i> (N)	Latitude	-0.042	0.031	-1.362	0.175
<i>Mustela nivalis</i> (N)	Longitude	-0.023	0.011	-2.094	0.038
<i>Mustela nivalis</i> (N)	sex	2.669	0.242	11.040	<0.0001
<i>Mustela nivalis</i> (P)	edge vs. interior specimens	-2.611	0.194	-13.445	<0.0001
	edge vs. sub-edge				
<i>Mustela nivalis</i> (P)	specimens	-1.725	0.204	-8.470	<0.0001
<i>Mustela nivalis</i> (P)	Intercept	51.884	0.593	87.498	<0.0001
<i>Mustela nivalis</i> (P)	Latitude	-0.340	0.011	-30.576	<0.0001
<i>Mustela nivalis</i> (P)	Longitude	-0.001	0.004	-0.308	0.758
<i>Mustela nivalis</i> (P)	sex	4.429	0.179	24.726	<0.0001
<i>Mustela putorius</i>	edge vs. interior specimens	2.274	0.428	5.318	<0.0001
	edge vs. sub-edge				
<i>Mustela putorius</i>	specimens	0.850	0.388	2.190	0.029
<i>Mustela putorius</i>	Intercept	54.471	2.522	21.596	<0.0001
<i>Mustela putorius</i>	Latitude	0.088	0.051	1.728	0.085
<i>Mustela putorius</i>	Longitude	-0.089	0.035	-2.556	0.011
<i>Mustela putorius</i>	sex	7.278	0.323	22.557	<0.0001
<i>Mustela vison</i>	edge vs. interior specimens	0.902	0.439	2.053	0.041
	edge vs. sub-edge				
<i>Mustela vison</i>	specimens	-0.229	0.443	-0.515	0.607
<i>Mustela vison</i>	Intercept	51.766	1.504	34.429	<0.0001
<i>Mustela vison</i>	Latitude	0.015	0.033	0.459	0.647
<i>Mustela vison</i>	Longitude	-0.072	0.007	-10.709	<0.0001
<i>Mustela vison</i>	sex	5.507	0.371	14.825	<0.0001
<i>Paradoxurus hermaphroditus</i>	edge vs. interior specimens	4.687	2.083	2.250	0.027
	edge vs. sub-edge				
<i>Paradoxurus hermaphroditus</i>	specimens	4.003	1.623	2.467	0.015
<i>Paradoxurus hermaphroditus</i>	Intercept	110.148	8.997	12.243	<0.0001
<i>Paradoxurus hermaphroditus</i>	Latitude	0.076	0.117	0.656	0.514
<i>Paradoxurus hermaphroditus</i>	Longitude	-0.123	0.084	-1.463	0.147
<i>Paradoxurus hermaphroditus</i>	sex	4.277	1.277	3.349	0.001
<i>Procyon lotor</i>	edge vs. interior specimens	0.946	1.052	0.900	0.370
	edge vs. sub-edge				
<i>Procyon lotor</i>	specimens	1.745	1.046	1.668	0.098
<i>Procyon lotor</i>	Intercept	99.163	2.569	38.593	<0.0001

<i>Procyon lotor</i>	Latitude	-0.097	0.045	-2.138	0.034
<i>Procyon lotor</i>	Longitude	-0.118	0.030	-3.978	0.0001
<i>Procyon lotor</i>	sex	4.100	0.841	4.873	<0.0001
<i>Spilogale gracilis</i>	edge vs. interior specimens	-2.479	0.763	-3.247	0.002
<i>Spilogale gracilis</i>	edge vs. sub-edge specimens	1.904	0.769	2.477	0.015
<i>Spilogale gracilis</i>	Intercept	52.035	16.064	3.239	0.002
<i>Spilogale gracilis</i>	Latitude	-0.146	0.103	-1.420	0.159
<i>Spilogale gracilis</i>	Longitude	-0.047	0.162	-0.289	0.773
<i>Spilogale gracilis</i>	sex	4.369	0.665	6.568	<0.0001
<i>Urocyon cinereoargenteus</i>	edge vs. interior specimens	-0.779	0.713	-1.093	0.276
<i>Urocyon cinereoargenteus</i>	edge vs. sub-edge specimens	0.523	0.777	0.673	0.502
<i>Urocyon cinereoargenteus</i>	Intercept	105.589	2.485	42.490	<0.0001
<i>Urocyon cinereoargenteus</i>	Latitude	0.459	0.046	9.928	<0.0001
<i>Urocyon cinereoargenteus</i>	Longitude	0.050	0.018	2.745	0.007
<i>Urocyon cinereoargenteus</i>	sex	3.120	0.588	5.307	<0.0001
<i>Ursus arctos</i>	edge vs. interior specimens	-20.920	4.369	-4.788	<0.0001
<i>Ursus arctos</i>	edge vs. sub-edge specimens	-9.028	3.540	-2.551	0.012
<i>Ursus arctos</i>	Intercept	258.706	23.457	11.029	<0.0001
<i>Ursus arctos</i>	Latitude	-0.998	0.339	-2.944	0.004
<i>Ursus arctos</i>	Longitude	-0.933	0.111	-8.436	<0.0001
<i>Ursus arctos</i>	sex	42.868	2.901	14.779	<0.0001
<i>Viverricula indica</i>	edge vs. interior specimens	-2.448	0.956	-2.561	0.012
<i>Viverricula indica</i>	edge vs. sub-edge specimens	-1.848	0.996	-1.856	0.066
<i>Viverricula indica</i>	Intercept	85.320	3.357	25.415	<0.0001
<i>Viverricula indica</i>	Latitude	0.150	0.048	3.131	0.002
<i>Viverricula indica</i>	Longitude	0.089	0.029	3.072	0.003
<i>Viverricula indica</i>	sex	2.056	0.719	2.859	0.005
<i>Vulpes vulpes</i> (N)	edge vs. interior specimens	-0.178	0.871	-0.204	0.839
<i>Vulpes vulpes</i> (N)	edge vs. sub-edge specimens	-1.502	0.876	-1.715	0.088
<i>Vulpes vulpes</i> (N)	Intercept	115.312	1.807	63.820	<0.0001
<i>Vulpes vulpes</i> (N)	Latitude	0.285	0.049	5.861	<0.0001
<i>Vulpes vulpes</i> (N)	Longitude	-0.038	0.017	-2.242	0.026
<i>Vulpes vulpes</i> (N)	sex	6.879	0.719	9.561	<0.0001
<i>Vulpes vulpes</i> (P)	edge vs. interior specimens	0.227	0.940	0.241	0.810
<i>Vulpes vulpes</i> (P)	edge vs. sub-edge specimens	-0.899	0.902	-0.996	0.320
<i>Vulpes vulpes</i> (P)	Intercept	107.587	2.035	52.873	<0.0001
<i>Vulpes vulpes</i> (P)	Latitude	0.590	0.043	13.874	<0.0001
<i>Vulpes vulpes</i> (P)	Longitude	-0.023	0.016	-1.434	0.153
<i>Vulpes vulpes</i> (P)	sex	6.626	0.737	8.989	<0.0001

#### Appendix 4E

CBL as a function of sex, latitude, longitude and distance to range edge. Distance to range edge treated as a continuous predictor. Only specimens closer to an inland rather than to a coastal range edge are used. Minimum sample size per species: n = 20. For sample sizes see Table 3.

<i>Species</i>	factor	Estimate	Std. Error	t	p
<i>Herpestes edwardsii</i>	distance to range edge	0.603	1.067	0.565	0.575
<i>Herpestes edwardsii</i>	intercept	58.860	6.116	9.623	<0.0001
<i>Herpestes edwardsii</i>	latitude	0.362	0.185	1.962	0.055
<i>Herpestes edwardsii</i>	longitude	0.043	0.060	0.711	0.480
<i>Herpestes edwardsii</i>	sex	4.695	0.767	6.123	<0.0001
<i>Martes americana</i>	distance to range edge	-1.669	2.390	-0.698	0.488
<i>Martes americana</i>	intercept	60.533	5.715	10.593	<0.0001
<i>Martes americana</i>	latitude	0.247	0.135	1.825	0.074
<i>Martes americana</i>	longitude	-0.040	0.057	-0.689	0.494
<i>Martes americana</i>	sex	4.764	0.929	5.126	<0.0001
<i>Meles meles</i>	distance to range edge	6.744	2.228	3.027	0.008
<i>Meles meles</i>	intercept	132.387	6.152	21.520	<0.0001
<i>Meles meles</i>	latitude	-0.449	0.215	-2.088	0.052
<i>Meles meles</i>	longitude	-0.161	0.043	-3.713	0.002
<i>Meles meles</i>	sex	3.111	1.343	2.317	0.033
<i>Mustela erminea</i> (N)	distance to range edge	-1.996	0.530	-3.767	0.0002
<i>Mustela erminea</i> (N)	intercept	22.177	3.745	5.922	<0.0001
<i>Mustela erminea</i> (N)	latitude	0.643	0.059	10.969	<0.0001
<i>Mustela erminea</i> (N)	longitude	0.121	0.026	4.628	<0.0001
<i>Mustela erminea</i> (N)	sex	4.445	0.417	10.670	<0.0001
<i>Mustela erminea</i> (P)	distance to range edge	5.091	2.251	2.261	0.031
<i>Mustela erminea</i> (P)	intercept	34.085	9.014	3.781	0.001
<i>Mustela erminea</i> (P)	latitude	-0.037	0.251	-0.146	0.885
<i>Mustela erminea</i> (P)	longitude	-0.074	0.042	-1.773	0.086
<i>Mustela erminea</i> (P)	sex	4.113	0.799	5.147	<0.0001
<i>Mustela frenata</i>	distance to range edge	-0.869	0.403	-2.157	0.033
<i>Mustela frenata</i>	intercept	41.795	2.275	18.369	<0.0001
<i>Mustela frenata</i>	latitude	0.054	0.025	2.147	0.034
<i>Mustela frenata</i>	longitude	-0.014	0.018	-0.792	0.430
<i>Mustela frenata</i>	sex	4.999	0.574	8.702	<0.0001

	distance to range				
<i>Mustela nivalis</i> (N)	edge	0.399	1.025	0.389	0.701
<i>Mustela nivalis</i> (N)	intercept	32.713	4.154	7.874	<0.0001
<i>Mustela nivalis</i> (N)	latitude	-0.059	0.111	-0.529	0.602
<i>Mustela nivalis</i> (N)	longitude	0.012	0.057	0.218	0.829
<i>Mustela nivalis</i> (N)	sex	2.647	0.591	4.477	0.0002
	distance to range				
<i>Mustela nivalis</i> (P)	edge	-0.644	3.369	-0.191	0.851
<i>Mustela nivalis</i> (P)	intercept	60.279	6.398	9.422	<0.0001
<i>Mustela nivalis</i> (P)	latitude	-0.508	0.400	-1.272	0.220
<i>Mustela nivalis</i> (P)	longitude	-0.052	0.092	-0.560	0.582
<i>Mustela nivalis</i> (P)	sex	5.152	1.320	3.903	0.001
	distance to range				
<i>Mustela vison</i>	edge	-11.607	2.428	-4.780	0.0001
<i>Mustela vison</i>	intercept	29.125	10.804	2.696	0.013
<i>Mustela vison</i>	latitude	0.944	0.189	4.994	<0.0001
<i>Mustela vison</i>	longitude	-0.117	0.055	-2.129	0.044
<i>Mustela vison</i>	sex	6.560	1.115	5.883	<0.0001
	distance to range				
<i>Viverricula indica</i>	edge	2.435	2.488	0.979	0.337
<i>Viverricula indica</i>	intercept	55.524	12.536	4.429	0.0002
<i>Viverricula indica</i>	latitude	1.063	0.340	3.124	0.004
<i>Viverricula indica</i>	longitude	0.037	0.062	0.587	0.562
<i>Viverricula indica</i>	sex	2.727	1.495	1.824	0.080
	distance to range				
<i>Vulpes vulpes</i> (N)	edge	-3.145	1.982	-1.587	0.117
<i>Vulpes vulpes</i> (N)	intercept	127.226	6.280	20.258	<0.0001
<i>Vulpes vulpes</i> (N)	latitude	0.631	0.121	5.220	<0.0001
<i>Vulpes vulpes</i> (N)	longitude	0.153	0.069	2.209	0.030
<i>Vulpes vulpes</i> (N)	sex	8.129	1.126	7.216	<0.0001

## Appendix 5

### Species level data

<i>species</i>	Mean CBL (mm)	standard deviation of CBL (mm)	mean distance (log km)	standard deviation of distance (log km)	slope	standardized slope	log mass (g)	CBL CV, females	CBL CV, males	log range size (maps)
<i>Alopex lagopus</i>	121.20	4.31	0.60	0.44	-0.039	-0.004	3.48	2.82	3.24	6.70
<i>Canis aureus</i>	150.83	9.37	1.72	0.86	-1.411	-0.129	3.96	6.52	5.35	7.39
<i>Canis latrans</i>	178.46	9.68	1.61	0.73	-0.154	-0.012	4.03	5.36	4.65	7.16
<i>Canis lupus</i>	244.79	10.31	2.17	0.68	4.319	0.286	4.54	3.73	4.13	7.13
<i>Gulo gulo</i>	141.21	7.36	1.84	0.89	-0.240	-0.029	3.96	3.08	4.16	7.02
<i>Herpestes edwardsii</i>	76.89	3.66	1.93	0.52	0.747	0.106	3.13	3.62	3.66	6.49
<i>Lontra canadensis</i>	110.63	4.93	1.43	0.79	-2.038	-0.329	3.92	3.98	4.39	7.13
<i>Lutra lutra</i>	112.36	6.66	1.70	0.67	-1.166	-0.117	3.92	4.61	4.96	7.56
<i>Lynx canadensis</i>	116.38	4.57	2.16	0.52	-0.127	-0.014	3.94	3.62	2.65	7.03
<i>Martes americana</i>	77.08	4.77	1.42	0.87	-0.825	-0.150	3.00	5.68	4.65	6.92
<i>Martes foina</i>	79.42	3.08	1.94	0.55	-0.177	-0.031	3.1	3.16	2.91	6.88
<i>Martes martes</i>	82.51	4.04	2.05	0.55	0.255	0.035	3.11	4.07	3.66	6.86
<i>Meles meles</i>	128.71	6.97	1.55	0.64	0.783	0.072	3.98	5.43	5.22	7.36
<i>Mustela erminea</i> (N)	40.73	3.92	1.73	0.83	0.218	0.046	2.35	7.43	7.49	7.06
<i>Mustela erminea</i> (P)	45.16	3.03	1.80	0.63	0.264	0.055	2.35	6.55	4.63	7.34
<i>Mustela frenata</i>	46.34	3.56	1.79	0.67	-0.653	-0.123	2.38	6.56	5.17	7.06
<i>Mustela nivalis</i> (N)	31.24	1.98	1.54	0.94	-0.521	-0.247	1.91	3.81	5.57	6.98
<i>Mustela nivalis</i> (P)	35.98	4.18	1.74	0.64	-1.646	-0.252	1.91	9.05	10.33	7.44
<i>Mustela putorius</i>	63.80	4.98	1.73	0.61	1.521	0.187	3.01	6.01	5.13	6.80
<i>Mustela vison</i>	63.69	5.06	1.57	0.87	0.205	0.035	3.00	5.40	7.29	7.11
<i>Paradoxurus hermaphroditus</i>	104.52	7.38	1.47	0.76	3.527	0.363	3.54	6.51	6.97	6.77
<i>Procyon lotor</i>	110.47	5.47	1.22	0.68	1.033	0.129	3.95	4.20	4.97	6.99
<i>Spilogale gracilis</i>	55.24	4.18	1.12	0.55	-2.212	-0.290	2.68	5.25	6.86	6.47
<i>Urocyon cinereoargenteus</i>	116.86	5.06	1.64	0.52	-0.081	-0.008	3.57	4.20	4.02	6.86

<i>Ursus arctos</i>	345.75	33.81	1.42	0.90	-10.173	-0.270	5.51	7.49	8.71	7.01
<i>Viverricula indica</i>	97.31	4.37	1.62	0.69	-1.372	-0.217	3.34	4.67	4.17	6.86
<i>Vulpes vulpes</i> (N)	137.61	7.75	1.73	0.73	-0.380	-0.036	3.74	4.78	5.16	7.15
<i>Vulpes vulpes</i> (P)	135.90	9.53	1.82	0.60	0.803	0.051	3.74	6.39	6.62	7.62

mean distance is the mean of the log transformed distances from range edge (km) for all specimens.  
Slope is the slope of the distance from range edge/CBL relationship (from table 1 and Appendix 4A)  
Log masses (in grams) are from Meiri et al. (2005e)  
CV is the coefficient of variation in CBL  
Log range size (km<sup>2</sup>) is from the range maps in Appendix 1.