



# Global change and carnivore body size: data are stasis

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## ABSTRACT

**Aim** Global warming and other anthropogenic changes to the environment affect many aspects of biology and have often been invoked as causing body size changes in vertebrates. Here we examine a diverse set of carnivore populations in search of patterns in body size change that could reflect global warming (in accord with Bergmann's rule).

**Location** Global.

**Methods** We used > 4400 specimens representing 22 carnivore species in 52 populations collected over the last few decades to examine whether size changed with collection date when geography and sex are accounted for. We then examined several factors related to global warming, body mass, diet, and the attributes of the different datasets, to see whether they affect the standardized slope ( $\beta$ ) of the size versus time regression.

**Results** Six of 52 populations we examined show a significant effect of year of collection on body size at the 0.05 probability level. The response of size to global warming does not reflect spatial patterns of size variation, nor do diet or body mass affect tendency of populations to change in body size. Size changes are no more pronounced in populations that have been sampled more recently. However, change, where it occurs, is rapid.

**Main conclusions** There may be a tendency in the literature to report only cases where recent changes are prevalent. Although in our data only a minority of populations show body size changes, we may see changes accelerating in the future in response to more drastic climatic changes and other anthropogenic changes.

## Keywords

**Bergmann's rule, body size evolution, Carnivora, evolutionary rates, global change, global warming, publication bias.**

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## INTRODUCTION

Body size is one of the most fundamental traits affecting animal form, life history, physiology and ecology (Peters, 1983; Schmidt-Nielsen, 1984). Within species, body size often varies considerably over the geographic range in response to factors such as climate, competition and predation regimes, and food availability (Dayan & Simberloff, 1998; Raia & Meiri, 2006; Meiri *et al.*, 2007). It is therefore unsurprising that body size is also highly labile temporally, and many examples of rapid size change in response to climatic changes (Dayan *et al.*, 1991) and insularization (Lister, 1989) are known. Members of the mammalian order

Carnivora often vary greatly in size across their geographic range, usually in accordance with Bergmann's Rule (Klein, 1986; Meiri & Dayan, 2003; Meiri *et al.*, 2004, 2005d, 2007). Carnivores likewise often evolve smaller sizes during interglacials relative to their sizes in colder, glacial periods (Dayan *et al.*, 1991).

Indeed size changes can be so rapid that they can be observed over a period of just a few decades, often following anthropogenic introductions (Johnston & Selander, 1964; Baker & Moeed, 1979; Yom-Tov *et al.*, 1986; Simberloff *et al.*, 2000; Phillips & Shine, 2005). Recently, it has become apparent that size can also change with time within decades, within the natural range of species, following climatic and various anthropogenic changes (e.g.

Oschadleus, 2004; Chamaillé-Jammes *et al.*, 2006). Global warming features prominently as a suggested cause of size decreases. It is often claimed (e.g. Smith *et al.*, 1998; Yom-Tov, 2001) that homeotherm size decreases, in accordance with Bergmann's rule, whereby body size is negatively correlated with temperature. Recent size increases, however, also appear common (Järvinen, 1994; Nowakowski, 2002; Kanuscak *et al.*, 2004). It is therefore likely that climate change is not the sole, or even the primary, driver of size changes, and that other recent environmental changes cause size evolution. In a series of recent works, Yom-Tov and co-workers (e.g. Yom-Tov, 2003; Yom-Tov *et al.*, 2003, 2006, 2007, 2008) have shown that body sizes of various Holarctic birds and mammals have changed during the 20th century, changes they ascribe to changes in food availability. Yom-Tov (2003) suggested that large carnivorous taxa increase more in size than smaller species because their higher position in the feeding hierarchy allows them better access to anthropogenic food sources. Conversely, Schmidt & Jensen (2003) argued that large species have recently decreased in size (including two species that Yom-Tov *et al.*, 2003, claimed increased in size in the same area) while small species have increased. They argued that natural habitats are increasingly fragmented, and are, in fact, insularized. Thus, as expected by the island rule, large mammals grow smaller because of resource limitation, whereas small mammals increase in size because of reduced competition and predation pressures (Lomolino, 2005, but see Meiri *et al.*, 2006, 2008).

Here we use a large (> 4400 specimens) database of sizes of members of the mammalian order Carnivora to examine whether recent temporal size changes occur more frequently than expected by chance, and we test the following predictions about size change:

1. All species decrease in size through time, following Bergmann's rule, because of global warming.
2. Global warming will cause species to show similar size variation through time to the variation they show in space. Thus species showing Bergmann's rule across space will decrease in size through time, species showing spatial patterns opposite to Bergmann's rule will increase, and those that do not change directionally across space will show no tendency to change size with time.
3. Larger species are more likely to decrease in size because of habitat fragmentation and smaller ones should grow larger because of reduced competition and predation pressures (Schmidt & Jensen, 2003).
4. Larger species are more likely to increase in size because they can garner more resources through interspecific aggression (Yom-Tov, 2003).
5. Omnivorous species are likely to have access to human refuse and should increase in size more than strictly carnivorous species.
6. Anthropogenic changes have been accelerating, and rates of body size change are therefore more pronounced in species that have been sampled longer and more recently.

## METHODS

We measured carnivore skulls in the following natural history museums: American Museum of Natural History; Ann Arbor

Museum of Zoology; Bell Museum of Natural History; Canadian Museum of Nature; Carnegie Museum; Field Museum; 'Giacomo Doria', Genoa; Harrison Zoological Institute; Institut royal des Sciences naturelles de Belgique; Museum für Naturkunde, Berlin; Museum of Comparative Zoology; Museum of Vertebrate Zoology; National Museum of Ireland; National Science Museum, Tokyo; National Wildlife Institute, Bologna; Natural History Collections, Hebrew University; Natural History Museum, LA County; Natural History Museum, London; New Walk Museum; Oxford University Museum of Natural History; Primate Research Institute, Kyoto University; Royal British Columbia Museum; Royal Ontario Museum; San Diego Natural History Museum; Smithsonian Institution; Staatliche Naturhistorische Sammlungen, Dresden; Tel-Aviv University Zoological Museum; Ulster Museum; University of Alaska, Museum of Natural History; University of Amsterdam, Museum of Natural History; University of Kansas Museum of Natural History; Wildlife Disease Ecology Team, Woodchester Park; Zoological Museum, University of Copenhagen.

Condylal-basal length (CBL, log-transformed in all analyses) was chosen as an index of size. We used only wild-caught, sexed adult specimens. Data were collected to study biogeographic variation in size and morphological variability (e.g. Meiri *et al.*, 2005a,b) and are therefore unbiased with respect to the questions we study here. The year of collection was recorded from the specimen labels or museum databases. Where collection dates were given as two years (e.g. 'winter 1913–1914', season '1954–1955') we arbitrarily used the earlier year. We divide species geographically into assemblages ranging from small countries and single USA states (e.g. Israel, Florida) to larger countries and states or regions (e.g. Alaska, Germany, New England). Within each of these areas (henceforth, areas) we regressed CBL against year of collection. We controlled for effects of sex and geographic variation within countries by adding sex, latitude and longitude as additional predictors in a multiple regression test. We used data only from populations from areas where we have a minimum sample size of 40 specimens (mean = 85) spanning at least 40 years (mean = 87, 1900 to 1987). Because some geographic size variation could remain unaccounted for, we used a sensitivity analysis, in which only populations spanning < 1 degree of latitude and longitude were used. In this analysis we used a minimum of 20 specimens (mean = 34) spanning at least 40 years (mean = 64) and regressed CBL against year of collection, controlling for sex.

To examine whether we could predict the direction and degree of size change through time, we used the standardized slope  $\beta$  of the regression of CBL on collection year as a response variable. The six hypotheses outlined above lead, respectively, to the following predictions.

1. All slopes (for each species/population) should be negative.
2. Slopes of size versus year of collection ( $\beta$ ) would be positively correlated with the slope values for size regressed on latitude for each species. The expectation was that species with a positive size-latitude relationship decrease in size because of global warming, species with a negative size-latitude relationship increase in size, and those that show no geographic variation in size also show no temporal variation.

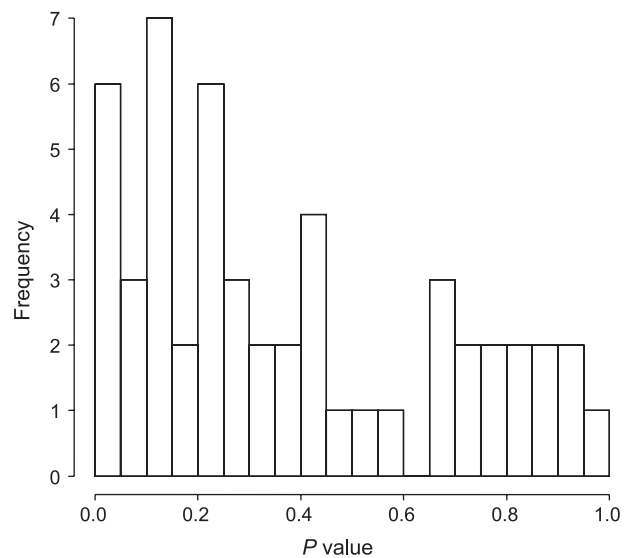
3. Body mass (values from Meiri *et al.*, 2005c) would be negatively correlated with  $\beta$  (Schmidt & Jensen, 2003).
4. Body mass would be positively correlated with  $\beta$  (Yom-Tov, 2003).
5. Omnivorous species would have higher values of  $\beta$  than more carnivorous species. Dietary categories were derived from the literature (e.g. Nowak, 1999).
6. Body size change should be more pronounced in species that have been sampled longer and more recently. Thus absolute values of  $\beta$  (regardless of whether slopes are positive or negative) were predicted to be steeper where populations were sampled more recently and longer.

Using the slope of the  $\ln(\text{CBL})$  versus time relationship, we calculated evolutionary rates in darwins (one darwin is a change in the character by a factor of  $e$  in one million years, Haldane, 1949) by multiplying slopes by one million. We avoided correcting for multiple tests using, e.g. sequential Bonferroni correction (Cabin & Mitchell, 2000), because such methods are unable to detect many significant results if  $P$  values are close to 0.05 (Moran, 2003). Instead we tested whether more significant results were obtained than would be expected by chance using a chi-square test.

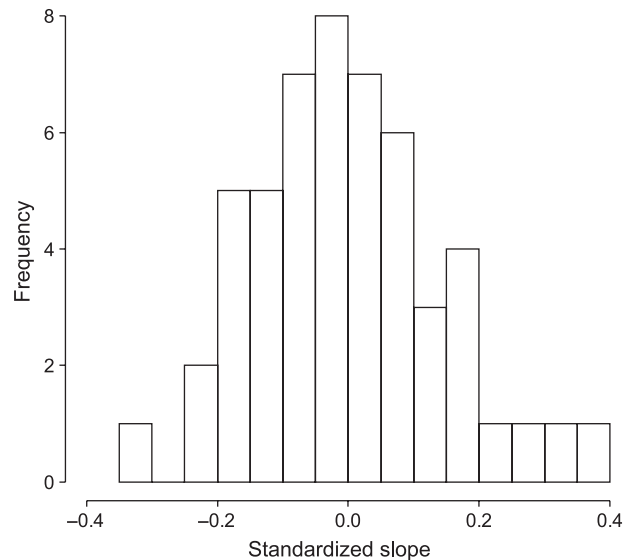
## RESULTS

Data on the 52 populations (22 species in 7 families, 23 areas) studied are shown in Table 1. Size in six populations changed significantly (at  $P < 0.05$ ) through time. British and Irish stoats (*Mustela erminea*) and Alaskan mink (*M. vison*) increased in size through time, whereas size in the former species declined through time in Benelux and Minnesota. Long-tailed weasels (*M. frenata*) decreased in size in New England. There were more significant changes than the 5% expected by chance ( $\chi^2 = 4.68$ ,  $P = 0.03$ ), but these still represent only *c.* 12% of the populations (Fig. 1). Size in three more populations showed change through time at the  $0.05 < P < 0.1$  level: Michigan *M. frenata* and French red foxes, *Vulpes vulpes*, decreasing in size, the latter species increasing in size in Israel. The slopes, standardized slopes and probabilities for all explanatory variables are listed in Appendix S1 in the Supporting Information. Mean CBL values for all populations are listed in Appendix S2. The mean standardized slope for all populations,  $-0.003 \pm 1_{\text{SE}} 0.102$ , did not significantly differ from zero, and the frequency distribution of standardized slopes was roughly symmetrical about a slope of zero (Fig. 2). Furthermore, most individual slopes did not differ from zero, and when they did they seemed just as likely to be positive as to be negative. Thus there was no overall tendency for size either to decrease or to increase, negating hypothesis 1.

The models for the sensitivity analysis, using only populations spanning  $< 1$  degree of latitude and longitude, are presented in Appendix S3. Only two of 19 populations showed size change through time: *Mustela putorius* in Belgium and the Netherlands at  $51^\circ \text{N}$ ,  $6^\circ \text{E}$  decreased in size between 1920 and 1974, whereas *M. erminea* in Maine at  $45^\circ \text{N}$ ,  $69^\circ \text{W}$  increased in size between 1874 and 1940. However adjacent populations (*M. putorius* at  $51^\circ \text{N}$ ,  $5^\circ \text{E}$ , and *M. erminea* in Maine at  $46^\circ \text{N}$ ,  $69^\circ \text{W}$ ) showed no correlation between sampling year and CBL (Appendix S3).



**Figure 1** Frequency distribution of the  $P$ -values for an effect of year of collection on skull length (corrected for sex, latitude and longitude). Frequency is the number of populations associated with any  $P$  value.



**Figure 2** Frequency distribution of the standardized slopes of size change through time in different populations (corrected for sex, latitude and longitude). Frequency is the number of populations associated with different values of  $\beta$ .

When size did change it changed very fast: for the six populations for which  $P < 0.05$ , the mean rate was 671 darwins (range: 315–896), comparable to the fastest rates reported for size change in the literature (Millien, 2006), and for the three populations for which  $0.05 < P < 0.1$  the average rate was 719 darwins (440–884). Such high rates are expected because of the well known negative relationship between sampling duration and evolutionary rates (Gingerich, 1983; Gould, 1984).

**Table 1** Populations of carnivores used, with areas in which specimens originated, sample sizes, and periods over which specimens were collected.  $\beta$  is the standardized slope of the regression of (log) Condylo-basal length (CBL) on collection year, and  $P$  is the probability that this slope does not differ from zero.

Species	Area	$n$	Earliest date	Latest date	Span (years)	$\beta$	$P$
<i>Alopex lagopus</i>	Alaska	82	1897	1993	96	-0.077	0.435
<i>Canis latrans</i>	Baja California	41	1884	1979	95	0.217	0.118
<i>Canis lupus</i>	Alaska	89	1901	1994	93	-0.082	0.427
<i>Canis lupus</i>	British Columbia	45	1891	1982	91	0.313	0.110
<i>Canis lupus</i>	Vancouver Island	58	1937	1985	48	-0.035	0.801
<i>Lynx canadensis</i>	Alaska	68	1905	1992	87	-0.117	0.258
<i>Lynx canadensis</i>	British Columbia	45	1889	1983	94	-0.098	0.361
<i>Gulo gulo</i>	Alaska	52	1891	1993	102	-0.057	0.661
<i>Martes americana</i>	Alaska	54	1860	1996	136	-0.187	0.488
<i>Martes americana</i>	British Columbia	98	1889	1996	107	0.075	0.221
<i>Martes americana</i>	Vancouver Island	194	1904	1988	84	-0.010	0.672
<i>Martes foina</i>	Germany	64	1876	1999	123	0.019	0.860
<i>Martes martes</i>	Benelux	42	1947	2004	57	0.163	0.317
<i>Martes melampus</i>	Honshu	104	1944	1991	47	0.060	0.247
<i>Meles meles</i>	Benelux	66	1918	2000	82	0.185	0.143
<i>Meles meles</i>	Britain	42	1911	1989	78	-0.163	0.300
<i>Mustela erminea</i>	Alaska	226	1879	1998	119	0.045	0.211
<i>Mustela erminea</i>	Benelux	126	1926	1988	62	-0.192	0.015
<i>Mustela erminea</i>	Britain	139	1890	1984	94	0.171	0.00006
<i>Mustela erminea</i>	British Columbia	211	1891	1999	108	-0.011	0.794
<i>Mustela erminea</i>	Germany	42	1887	1994	107	0.065	0.536
<i>Mustela erminea</i>	Ireland	72	1895	1982	87	0.124	0.028
<i>Mustela erminea</i>	Labrador	62	1898	1990	92	0.008	0.963
<i>Mustela erminea</i>	Minnesota	71	1890	1980	90	-0.239	0.0001
<i>Mustela erminea</i>	New England	178	1874	1997	123	0.072	0.143
<i>Mustela erminea</i>	Ontario	53	1893	1981	88	-0.142	0.258
<i>Mustela erminea</i>	Washington	55	1894	1974	80	0.140	0.243
<i>Mustela frenata</i>	British Columbia	49	1894	1999	105	-0.011	0.921
<i>Mustela frenata</i>	California	151	1885	1974	89	0.041	0.445
<i>Mustela frenata</i>	Michigan	52	1903	1971	68	-0.092	0.058
<i>Mustela frenata</i>	New England	110	1864	1979	115	-0.171	0.003
<i>Mustela frenata</i>	Oregon	62	1883	1990	107	0.086	0.190
<i>Mustela frenata</i>	Washington	68	1891	1960	69	0.162	0.138
<i>Mustela nivalis</i>	Alaska	56	1900	1987	87	-0.110	0.235
<i>Mustela nivalis</i>	Benelux	266	1928	1990	62	0.075	0.137
<i>Mustela nivalis</i>	Britain	123	1895	1987	92	-0.005	0.895
<i>Mustela nivalis</i>	Italy	52	1883	1972	89	0.032	0.740
<i>Mustela putorius</i>	Benelux	263	1912	2004	92	0.005	0.906
<i>Mustela vison</i>	Alaska	84	1904	1999	95	0.361	0.00003
<i>Mustela vison</i>	Ontario	46	1912	1955	43	0.045	0.722
<i>Mustela vison</i>	Vancouver Island	40	1886	1975	89	-0.109	0.224
<i>Nyctereutes procyonoides</i>	Honshu	66	1949	1989	40	-0.125	0.421
<i>Procyon lotor</i>	Florida	42	1891	1999	108	0.127	0.375
<i>Spilogale gracilis</i>	California	60	1887	1954	67	-0.051	0.579
<i>Urocyon cinereoargenteus</i>	California	72	1891	1987	96	-0.049	0.657
<i>Ursus arctos</i>	Admiralty Island	58	1905	1979	74	-0.023	0.824
<i>Ursus arctos</i>	Alaska	92	1894	1975	81	-0.096	0.103
<i>Viverra zibetha</i>	Borneo	53	1887	1962	75	-0.032	0.800
<i>Vulpes vulpes</i>	Alaska	47	1903	1996	93	-0.186	0.263
<i>Vulpes vulpes</i>	Benelux	62	1932	2001	69	-0.219	0.187
<i>Vulpes vulpes</i>	France	47	1909	1992	83	-0.308	0.052
<i>Vulpes vulpes</i>	Israel	42	1945	2000	55	0.265	0.079



show significant or marginally significant size change: *Mustela vison* increases in size in Alaska but not in Ontario or Vancouver Island; *Mustela frenata* decrease in size in New England and perhaps also in Michigan ( $P = 0.058$ ) but not in the other three populations we examined. Similarly, *Vulpes vulpes* may be decreasing in size in France ( $P = 0.052$ ) but shows no trends in adjacent Benelux or in Alaska and may be increasing in size Israel ( $P = 0.079$ ). Furthermore, no groupings of similar responses were found in different areas: in no area did more than one species change in size through time.

While size has sometimes changed, we hesitate to say it has actually evolved over that time span because we have no evidence for genetic changes. However Johnston & Selander (1964) and Clegg *et al.* (2002) have shown that some recent size changes are indeed adaptive and thus probably correspond to evolutionary changes, rather than being mere phenotypic responses. When change occurs, however, rates can be extremely fast, comparable with the fastest rates reported by Millien (2006), which were measured over similar time spans. The fastest rates we found, however, were not restricted to islands (cf. Millien, 2006).

Neither body mass nor food habits predict the degree and direction of size changes. There is no evidence that global warming is causing most species to decline in size. Further, the spatial patterns of size variation were poor predictors of temporal size change, implying, perhaps, that global warming has not reached a level at which it exerts strong selective pressure on body size. There was no tendency for large and small carnivores to respond differently to year of collection, even though our sample covers the entire range of carnivore sizes, from least weasels (*Mustela nivalis*) to brown bears (*Ursus arctos*). Thus there is little evidence from size measurements that, on average, large species either experience more resource shortage than small species because of habitat fragmentation (Schmidt & Jensen, 2003) or have better access than small species to human refuse through interspecific aggression (Yom-Tov, 2003). That slopes for populations of omnivorous species do not differ from those of more carnivorous ones further supports the conclusion that food habits play little role in shaping size response to environmental change.

It therefore seems that carnivore size change through time is rare and idiosyncratic, changing between taxa and localities. Most of the populations we analyzed show no size change at all. This result seems at odds with those of published studies, where size changes are almost always reported. Even when multiple populations were studied, the majority showed significant changes of body size through time (Yom-Tov, 2001, 2003). The only studies we are aware of that show no relationship between size and year (or other climatic variable) are those of Koontz *et al.* (2001) and Blois *et al.* (2008).

Some of the geographical groupings we used incorporate large areas. We tried to control for the effects of geographic variation within samples by correcting for latitude and longitude. Much variation, however, is invariably left even with such corrections, in response to specific ecological and anthropogenic influences not accounted for by such linear trends (Meiri *et al.*, 2007). Thus there will invariably be much noise in our data, which will lower

the power of detecting significant trends. However, we do not find any obvious tendency for patterns in smaller areas, or in more isolated ones (islands), and the result of our sensitivity analysis, in which specimens were grouped only over much smaller areas actually identified an even weaker response of size to collection date. In fact, significant trends alongside little evidence for change are often detected for different species in the same areas. Furthermore, significant size changes through time were previously reported for areas that are as large as the largest ones we study here (e.g. Alaska) and using similar methods (Yom-Tov *et al.*, 2008).

It is possible that case studies are selected for research or for submission for publication if they show what look like interesting patterns. Global warming drastically affects many organisms (Root *et al.*, 2003). Ecologists therefore invest a great deal of effort in studying effects of warming, and this effort is reflected in the actions of policymakers and research-funding agencies. There are good ecological reasons to expect ecological changes to take place and good moral reasons to want to publicize these effects. Failing to find that global warming has consistent and drastic consequences is likely to be perceived as uninteresting by journal editors and even by the researchers themselves (Rosenthal, 1979; Palmer, 1999). It may even be perceived as undermining conservation efforts. Only unbiased presentation of the whole picture, however, is likely to yield a good understanding of the real ecological consequences of global change. Our sample was collected for purposes other than the identification of current size changes (e.g. Meiri *et al.*, 2005a,b) and is therefore unbiased with respect to the populations we study. We show that size does change through time in some populations but that this pattern is not predominant.

## CONCLUSIONS

Our results have some implication for studies of size evolution that use specimens collected over long periods. Time can probably not be ignored when one examines patterns related to, for example, geographic variation or sexual size dimorphism. It must be shown to have no effect, or else it should be included in the models as an additional covariate.

Although only a minority of carnivore populations exhibited size change over time, in some instances body size changed significantly over a few decades, and these cases deserve further study to see if they are associated with anthropogenic environmental change.

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## SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

**Appendix S1** Statistics for the 52 multiple regression tests of size (condylo-basal length) versus year of collection, sex, latitude and longitude.

**Appendix S2** Mean skull lengths (Condylo-basal length = CBL, in mm) of populations inhabiting the regions studied.

**Appendix S3** Models for an analysis using only populations spanning 1 < degree of latitude and longitude.

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## BIOSKETCH

Shai Meiri is interested in the evolution of body size and its implications, biogeographic correlates of morphology and the morphological signatures of speciation and community composition.

Editor: Brian McGill

## Appendix S1

Statistics for the 52 multiple regression tests of size (condylo-basal length) vs. year of collection, sex, latitude and longitude.

species	place	Factor	Beta	Std.Err. of Beta	B	Std.Err. of B	p-level	darwins
<i>Alopex lagopus</i>	Alaska	Intercept	na	na	1.071	0.936	0.256	na
		Latitude	0.045	0.102	0.002	0.005	0.659	na
		Longitude	0.052	0.095	0.000	0.001	0.581	na
		sex	0.597	0.093	0.039	0.006	0.000000	na
		year	-0.077	0.098	0.000	0.000	0.435	153.55
<i>Canis latrans</i>	Baja California	Intercept	na	na	2.057	1.695	0.233	na
		Latitude	0.650	0.232	0.010	0.004	0.008	na
		Longitude	0.398	0.230	0.009	0.005	0.093	na
		sex	0.267	0.137	0.028	0.014	0.059	na
		year	0.217	0.135	0.001	0.000	0.118	517.89
<i>Canis lupus</i>	Alaska	Intercept	na	na	1.598	0.843	0.062	na
		Latitude	0.089	0.117	0.001	0.001	0.449	na
		Longitude	-0.037	0.123	0.000	0.001	0.766	na
		sex	0.530	0.091	0.040	0.007	0.000000	na
		year	-0.082	0.103	0.000	0.000	0.427	147.46
<i>Canis lupus</i>	British Columbia	Intercept	na	na	1.653	1.205	0.178	na
		Latitude	0.216	0.242	0.002	0.003	0.376	na
		Longitude	0.099	0.229	0.001	0.003	0.669	na
		sex	0.402	0.143	0.030	0.010	0.007	na
		year	0.313	0.191	0.000	0.000	0.110	439.63
<i>Canis lupus</i>	Vancouver Island	Intercept	na	na	1.223	1.197	0.312	na
		Latitude	-0.372	0.342	-0.022	0.020	0.282	na
		Longitude	-0.307	0.327	-0.009	0.010	0.351	na
		sex	0.549	0.114	0.044	0.009	0.00001	na
		year	-0.035	0.138	0.000	0.000	0.801	114.09
<i>Gulo gulo</i>	Alaska	Intercept	na	na	-3.875	1.064	0.0007	na
		Latitude	0.069	0.100	0.001	0.001	0.497	na
		Longitude	-0.072	0.090	-0.001	0.001	0.427	na
		sex	0.788	0.090	0.090	0.010	0.000000	na
		year	-0.117	0.102	0.000	0.000	0.258	245.89
<i>Lynx canadensis</i>	Alaska	Intercept	na	na	1.237	0.863	0.157	na
		Latitude	0.076	0.115	0.001	0.002	0.508	na
		Longitude	-0.084	0.116	-0.001	0.001	0.470	na
		sex	0.515	0.106	0.037	0.008	0.000008	na
		year	-0.098	0.107	0.000	0.000	0.361	170.02
<i>Lynx canadensis</i>	British Columbia	Intercept	na	na	-0.221	1.166	0.851	na
		Latitude	0.067	0.220	0.001	0.005	0.763	na
		Longitude	0.141	0.213	0.003	0.004	0.513	na
		sex	0.621	0.122	0.053	0.010	0.000009	na
		year	-0.057	0.130	0.000	0.000	0.661	64.91

species	place	Factor	Beta	Std.Err. of Beta	B	Std.Err. of B	p-level	darwins
<i>Martes americana</i>	Alaska	Intercept	na	na	-1.496	1.672	0.375	na
		Latitude	-0.002	0.163	0.000	0.003	0.989	na
		Longitude	-0.139	0.251	-0.001	0.002	0.581	na
		sex	0.524	0.110	0.061	0.013	0.00002	na
		year	-0.187	0.268	0.000	0.000	0.488	246.82
<i>Martes americana</i>	British Columbia	Intercept	na	na	-4.239	0.546	0.000000	na
		Latitude	0.357	0.062	0.007	0.001	0.000000	na
		Longitude	0.107	0.071	0.001	0.001	0.138	na
		sex	0.794	0.051	0.081	0.005	0.000000	na
		year	0.075	0.061	0.000	0.000	0.221	87.11
<i>Martes americana</i>	Vancouver Island	Intercept	na	na	-5.495	0.295	0.000000	na
		Latitude	0.086	0.061	0.006	0.004	0.165	na
		Longitude	0.131	0.061	0.004	0.002	0.034	na
		sex	0.950	0.023	0.100	0.002	0.000000	na
		year	-0.010	0.024	0.000	0.000	0.672	24.90
<i>Martes foina</i>	Germany	Intercept	na	na	-0.002	0.795	0.998	na
		Latitude	-0.142	0.102	-0.005	0.004	0.169	na
		Longitude	-0.052	0.107	-0.001	0.002	0.631	na
		sex	0.640	0.100	0.046	0.007	0.000000	na
		year	0.019	0.109	0.000	0.000	0.860	21.36
<i>Martes martes</i>	Benelux	Intercept	na	na	-3.187	1.602	0.054	na
		Latitude	-0.176	0.183	-0.007	0.008	0.341	na
		Longitude	0.123	0.139	0.014	0.016	0.383	na
		sex	0.729	0.127	0.067	0.012	0.000001	na
		year	0.163	0.160	0.001	0.001	0.317	534.57
<i>Martes melampus</i>	Honshu	Intercept	na	na	-5.693	1.005	0.000000	na
		Latitude	0.082	0.078	0.018	0.017	0.297	na
		Longitude	-0.006	0.079	0.000	0.005	0.937	na
		sex	0.854	0.051	0.086	0.005	0.000000	na
		year	0.060	0.051	0.000	0.000	0.247	391.08
<i>Meles meles</i>	Benelux	Intercept	na	na	2.614	1.034	0.014	na
		Latitude	-0.328	0.133	-0.017	0.007	0.016	na
		Longitude	0.117	0.126	0.008	0.009	0.358	na
		sex	0.333	0.118	0.024	0.008	0.007	na
		year	0.185	0.125	0.000	0.000	0.143	355.57
<i>Meles meles</i>	Britain	Intercept	na	na	2.655	1.429	0.071	na
		Latitude	0.192	0.155	0.006	0.005	0.224	na
		Longitude	0.090	0.155	0.003	0.005	0.566	na
		sex	0.311	0.152	0.025	0.012	0.048	na
		year	-0.163	0.155	0.000	0.000	0.300	315.63
<i>Mustela erminea</i>	Alaska	Intercept	na	na	-	11.719	0.682	0.000000
		Latitude	0.137	0.040	0.003	0.001	0.0007	na
		Longitude	-0.262	0.039	-0.003	0.000	0.000000	na
		sex	0.788	0.035	0.144	0.006	0.000000	na
		year	0.045	0.036	0.000	0.000	0.211	125.90
<i>Mustela erminea</i>	Benelux	Intercept	na	na	-4.539	0.850	0.000000	na
		Latitude	0.331	0.074	0.025	0.005	0.00002	na
		Longitude	-0.007	0.065	0.000	0.005	0.919	na
		sex	0.714	0.063	0.086	0.008	0.000000	na
		year	-0.192	0.078	-0.001	0.000	0.015	851.32

<b>species</b>	<b>place</b>	<b>Factor</b>	<b>Beta</b>	<b>Std.Err. of Beta</b>	<b>B</b>	<b>Std.Err. of B</b>	<b>p-level</b>	<b>darwins</b>
<i>Mustela erminea</i>	Britain	Intercept	na	na	-5.794	0.565	0.000000	na
		Latitude	-0.275	0.081	-0.007	0.002	0.0009	na

species	place	Factor	Beta	Std.Err. of Beta	B	Std.Err. of B	p-level	darwins	
<i>Mustela frenata</i>	California	year	-0.011	0.106	0.000	0.000	0.921	25.61	
		Intercept	na	na	-7.841	0.822	0.000000	na	
		Latitude	-0.474	0.083	-0.012	0.002	0.000000	na	
		Longitude	-0.388	0.082	-0.012	0.003	0.000005	na	
		sex	0.734	0.051	0.103	0.007	0.000000	na	
<i>Mustela frenata</i>	Michigan	year	0.041	0.053	0.000	0.000	0.445	140.92	
		Intercept	na	na	-	13.000	1.017	0.000000	na
		Latitude	0.100	0.067	0.007	0.004	0.143	na	
		Longitude	-0.163	0.067	-0.008	0.003	0.018	na	
		sex	0.930	0.048	0.164	0.008	0.000000	na	
<i>Mustela frenata</i>	New England	year	-0.092	0.047	0.000	0.000	0.058	440.16	
		Intercept	na	na	-	12.399	1.164	0.000000	na
		Latitude	-0.008	0.056	0.000	0.003	0.882	na	
		Longitude	-0.064	0.052	0.000	0.000	0.221	na	
		sex	0.823	0.051	0.171	0.011	0.000000	na	
<i>Mustela frenata</i>	Oregon	year	-0.171	0.056	-0.001	0.000	0.003	615.41	
		Intercept	na	na	-	12.944	1.141	0.000000	na
		Latitude	0.028	0.065	0.002	0.004	0.671	na	
		Longitude	-0.374	0.062	-0.013	0.002	0.000000	na	
		sex	0.910	0.062	0.143	0.010	0.000000	na	
<i>Mustela frenata</i>	Washington	year	0.086	0.065	0.000	0.000	0.190	333.51	
		Intercept	na	na	-7.556	1.676	0.00003	na	
		Latitude	-0.147	0.107	-0.012	0.009	0.177	na	
		Longitude	-0.112	0.096	-0.005	0.004	0.248	na	
		sex	0.670	0.093	0.100	0.014	0.000000	na	
<i>Mustela nivalis</i>	Alaska	year	0.162	0.107	0.001	0.000	0.138	569.55	
		Intercept	na	na	-7.276	1.610	0.00004	na	
		Latitude	0.129	0.095	0.003	0.002	0.181	na	
		Longitude	0.033	0.097	0.001	0.002	0.737	na	
		sex	0.748	0.091	0.114	0.014	0.000000	na	
<i>Mustela nivalis</i>	Benelux	year	-0.110	0.091	-0.001	0.000	0.235	500.47	
		Intercept	na	na	-9.761	0.762	0.000000	na	
		Latitude	0.389	0.051	0.048	0.006	0.000000	na	
		Longitude	-0.084	0.041	-0.007	0.004	0.043	na	
		sex	0.601	0.038	0.098	0.006	0.000000	na	
<i>Mustela nivalis</i>	Britain	year	0.075	0.050	0.001	0.000	0.137	514.23	
		Intercept	na	na	-	11.852	0.752	0.000000	na
		Latitude	0.081	0.063	0.003	0.002	0.203	na	
		Longitude	0.014	0.062	0.001	0.004	0.818	na	
		sex	0.882	0.041	0.151	0.007	0.000000	na	
<i>Mustela nivalis</i>	Italy	year	-0.005	0.040	0.000	0.000	0.895	17.96	
		Intercept	na	na	-	10.960	1.902	0.000001	na
		Latitude	-0.257	0.119	-0.024	0.011	0.035	na	
		Longitude	-0.353	0.128	-0.014	0.005	0.008	na	
		sex	0.789	0.088	0.154	0.017	0.000000	na	
<i>Mustela putorius</i>	Benelux	year	0.032	0.096	0.000	0.000	0.740	117.14	
		Intercept	na	na	-7.008	0.846	0.000000	na	
		Latitude	-0.202	0.045	-0.020	0.004	0.00001	na	

species	place	Factor	Beta	Std.Err. of Beta	B	Std.Err. of B	p-level	darwins
<i>Mustela vison</i>	Alaska	Longitude	0.169	0.044	0.016	0.004	0.0002	na
		sex	0.686	0.041	0.118	0.007	0.000000	na
		year	0.005	0.045	0.000	0.000	0.906	28.51
		Intercept	na	na	-6.289	1.520	0.00009	na
		Latitude	-0.225	0.097	-0.007	0.003	0.023	na
		Longitude	-0.121	0.100	-0.001	0.001	0.230	na
<i>Mustela vison</i>	Ontario	sex	0.502	0.084	0.089	0.015	0.000000	na
		year	0.361	0.082	0.001	0.000	0.00003	896.00
		Intercept	na	na	-6.563	1.868	0.001	na
		Latitude	0.529	0.133	0.015	0.004	0.0003	na
		Longitude	-0.253	0.131	-0.004	0.002	0.060	na
		sex	0.753	0.118	0.090	0.014	0.000000	na
<i>Mustela vison</i>	Vancouver Island	year	0.045	0.125	0.000	0.001	0.722	223.43
		Intercept	na	na	-5.853	1.462	0.0003	na
		Latitude	-0.405	0.350	-0.030	0.026	0.255	na
		Longitude	-0.251	0.350	-0.010	0.014	0.478	na
		sex	0.797	0.089	0.109	0.012	0.000000	na
		year	-0.109	0.089	0.000	0.000	0.224	407.95
<i>Nyctereutes procyonoides</i>	Honshu	Intercept	na	na	5.100	1.633	0.003	na
		Latitude	0.204	0.185	0.008	0.007	0.275	na
		Longitude	-0.278	0.175	-0.008	0.005	0.117	na
		sex	0.228	0.123	0.013	0.007	0.069	na
		year	-0.125	0.154	0.000	0.001	0.421	432.17
		Intercept	na	na	1.752	1.425	0.226	na
<i>Procyon lotor</i>	Florida	Latitude	-0.240	0.216	-0.006	0.005	0.273	na
		Longitude	0.268	0.222	0.009	0.007	0.234	na
		sex	0.345	0.134	0.033	0.013	0.014	na
		year	0.127	0.142	0.000	0.000	0.375	216.87
		Intercept	na	na	-8.440	1.313	0.000000	na
		Latitude	-0.760	0.223	-0.022	0.006	0.001	na
<i>Spilogale gracilis</i>	California	Longitude	-1.248	0.223	-0.032	0.006	0.000001	na
		sex	0.683	0.086	0.097	0.012	0.000000	na
		year	-0.051	0.091	0.000	0.000	0.579	198.44
		Intercept	na	na	1.871	0.734	0.013	na
		Latitude	0.077	0.106	0.001	0.001	0.473	na
		Longitude	0.013	0.109	0.000	0.000	0.904	na
<i>Urocyon cinereoargenteus</i>	California	sex	0.487	0.106	0.030	0.006	0.00002	na
		year	-0.049	0.109	0.000	0.000	0.657	72.85
		Intercept	na	na	-7.477	5.760	0.200	na
		Latitude	0.075	0.103	0.025	0.034	0.470	na
		Longitude	-0.002	0.105	-0.001	0.039	0.988	na
		sex	0.712	0.100	0.117	0.016	0.000000	na
<i>Ursus arctos</i>	Admiralty Island	year	-0.023	0.101	0.000	0.000	0.824	86.21
		Intercept	na	na	-4.982	1.206	0.00008	na
		Latitude	-0.372	0.072	-0.012	0.002	0.000002	na
		Longitude	-0.160	0.073	-0.002	0.001	0.031	na
		sex	0.663	0.059	0.117	0.010	0.000000	na
		year	-0.096	0.058	0.000	0.000	0.103	349.38
<i>Viverra</i>	Borneo	Intercept	na	na	2.150	0.726	0.005	na

species	place	Factor	Beta	Std.Err. of Beta	B	Std.Err. of B	p-level	darwins
<i>tangalunga</i>		Latitude	0.174	0.152	0.002	0.002	0.256	na
		Longitude	-0.126	0.155	-0.001	0.001	0.420	na
		sex	0.518	0.136	0.027	0.007	0.0004	na
		year	-0.032	0.126	0.000	0.000	0.800	35.16
<i>Vulpes vulpes</i>	Alaska	Intercept	na	na	0.131	1.300	0.920	na
		Latitude	0.142	0.159	0.002	0.002	0.377	na
		Longitude	-0.223	0.122	-0.001	0.001	0.074	na
		sex	0.566	0.126	0.050	0.011	0.00006	na
		year	-0.186	0.164	0.000	0.000	0.263	268.40
<i>Vulpes vulpes</i>	Benelux	Intercept	na	na	1.360	1.057	0.203	na
		Latitude	-0.019	0.157	-0.001	0.006	0.903	na
		Longitude	-0.065	0.119	-0.005	0.009	0.588	na
		sex	0.559	0.108	0.045	0.009	0.000003	na
		year	-0.219	0.164	0.000	0.000	0.187	462.77
<i>Vulpes vulpes</i>	France	Intercept	na	na	1.272	1.388	0.365	na
		Latitude	0.023	0.134	0.001	0.003	0.863	na
		Longitude	0.221	0.145	0.010	0.007	0.136	na
		sex	0.544	0.129	0.051	0.012	0.0001	na
		year	-0.308	0.154	-0.001	0.000	0.052	833.31
<i>Vulpes vulpes</i>	Israel	Intercept	na	na	-2.458	1.799	0.180	na
		Latitude	-0.006	0.145	0.000	0.006	0.968	na
		Longitude	0.313	0.140	0.051	0.023	0.032	na
		sex	0.359	0.135	0.037	0.014	0.012	na
		year	0.265	0.147	0.001	0.000	0.079	884.15

## Appendix S2

Mean skull lengths (CBL, in mm) of populations inhabiting the regions studied.

<b>Species</b>	<b>region</b>	<b>sex</b>	<b>CBL (mm)</b>
<i>Alopex lagopus</i>	Alaska	female	118.43
<i>Alopex lagopus</i>	Alaska	male	123.13
<i>Canis latrans</i>	Baja California	female	166.92
<i>Canis latrans</i>	Baja California	male	174.66
<i>Canis lupus</i>	Alaska	female	240.49
<i>Canis lupus</i>	Alaska	male	250.70
<i>Canis lupus</i>	British Columbia	female	244.13
<i>Canis lupus</i>	British Columbia	male	249.85
<i>Canis lupus</i>	Israel	female	200.43
<i>Canis lupus</i>	Israel	male	210.72
<i>Canis lupus</i>	Vancouver Island	female	227.91
<i>Canis lupus</i>	Vancouver Island	male	237.89
<i>Lynx canadensis</i>	Alaska	female	116.34
<i>Lynx canadensis</i>	Alaska	male	120.61
<i>Lynx canadensis</i>	British Columbia	female	112.66
<i>Lynx canadensis</i>	British Columbia	male	118.78
<i>Gulo gulo</i>	Alaska	female	134.31
<i>Gulo gulo</i>	Alaska	male	146.24
<i>Martes americana</i>	Alaska	female	76.56
<i>Martes americana</i>	Alaska	male	82.15
<i>Martes americana</i>	British Columbia	female	72.51
<i>Martes americana</i>	British Columbia	male	78.15
<i>Martes americana</i>	Vancouver Island	female	72.62
<i>Martes americana</i>	Vancouver Island	male	80.07
<i>Martes foina</i>	Germany	female	78.17
<i>Martes foina</i>	Germany	male	81.49
<i>Martes martes</i>	Benelux	female	79.95
<i>Martes martes</i>	Benelux	male	84.71
<i>Martes melampus</i>	Honshu	female	78.37
<i>Martes melampus</i>	Honshu	male	85.18
<i>Meles meles</i>	Benelux	female	131.33
<i>Meles meles</i>	Benelux	male	134.33
<i>Meles meles</i>	Britain	female	126.26
<i>Meles meles</i>	Britain	male	129.18
<i>Mustela erminea</i>	Alaska	female	39.61
<i>Mustela erminea</i>	Alaska	male	45.32
<i>Mustela erminea</i>	Benelux	female	43.29
<i>Mustela erminea</i>	Benelux	male	46.75
<i>Mustela erminea</i>	Britain	female	45.46

<b>Species</b>	<b>region</b>	<b>sex</b>	<b>CBL (mm)</b>
<i>Mustela erminea</i>	Britain	male	49.41
<i>Mustela erminea</i>	British Columbia	female	36.86
<i>Mustela erminea</i>	British Columbia	male	42.47
<i>Mustela erminea</i>	Germany	female	44.35
<i>Mustela erminea</i>	Germany	male	47.67
<i>Mustela erminea</i>	Ireland	female	40.21
<i>Mustela erminea</i>	Ireland	male	46.24
<i>Mustela erminea</i>	Labrador	female	37.01
<i>Mustela erminea</i>	Labrador	male	42.49
<i>Mustela erminea</i>	Minnesota	female	36.04
<i>Mustela erminea</i>	Minnesota	male	41.65
<i>Mustela erminea</i>	New England	female	36.51
<i>Mustela erminea</i>	New England	male	41.56
<i>Mustela erminea</i>	North Western Teritorries	female	38.85
<i>Mustela erminea</i>	North Western Teritorries	male	43.40
<i>Mustela erminea</i>	Ontario	female	36.92
<i>Mustela erminea</i>	Ontario	male	42.27
<i>Mustela erminea</i>	Washington	female	34.35
<i>Mustela erminea</i>	Washington	male	36.28
<i>Mustela frenata</i>	British Columbia	female	45.07
<i>Mustela frenata</i>	British Columbia	male	48.11
<i>Mustela frenata</i>	California	female	44.09
<i>Mustela frenata</i>	California	male	48.67
<i>Mustela frenata</i>	Michigan	female	40.35
<i>Mustela frenata</i>	Michigan	male	47.37
<i>Mustela frenata</i>	New England	female	40.97
<i>Mustela frenata</i>	New England	male	48.28
<i>Mustela frenata</i>	Oregon	female	41.32
<i>Mustela frenata</i>	Oregon	male	46.62
<i>Mustela frenata</i>	Washington	female	42.70
<i>Mustela frenata</i>	Washington	male	47.16
<i>Mustela nivalis</i>	Alaska	female	29.88
<i>Mustela nivalis</i>	Alaska	male	33.61
<i>Mustela nivalis</i>	Benelux	female	32.57
<i>Mustela nivalis</i>	Benelux	male	36.27
<i>Mustela nivalis</i>	Britain	female	33.55
<i>Mustela nivalis</i>	Britain	male	39.14
<i>Mustela nivalis</i>	Italy	female	37.88
<i>Mustela nivalis</i>	Italy	male	43.95
<i>Mustela putorius</i>	Benelux	female	58.62
<i>Mustela putorius</i>	Benelux	male	66.36

<b>Species</b>	<b>region</b>	<b>sex</b>	<b>CBL (mm)</b>
<i>Mustela vison</i>	Alaska	female	63.20
<i>Mustela vison</i>	Alaska	male	69.70
<i>Mustela vison</i>	Ontario	female	62.11
<i>Mustela vison</i>	Ontario	male	66.29
<i>Mustela vison</i>	Vancouver Island	female	61.87
<i>Mustela vison</i>	Vancouver Island	male	69.30
<i>Nyctereutes procyonoides</i>	Honshu	female	109.13
<i>Nyctereutes procyonoides</i>	Honshu	male	110.30
<i>Procyon lotor</i>	Florida	female	105.11
<i>Procyon lotor</i>	Florida	male	108.96
<i>Spilogale gracilis</i>	California	female	51.67
<i>Spilogale gracilis</i>	California	male	55.96
<i>Urocyon cinereoargenteus</i>	California	female	116.16
<i>Urocyon cinereoargenteus</i>	California	male	119.91
<i>Ursus arctos</i>	Admiralty	female	309.28
<i>Ursus arctos</i>	Admiralty	male	347.83
<i>Ursus arctos</i>	Alaska	female	337.84
<i>Ursus arctos</i>	Alaska	male	382.42
<i>Viverra zibetha</i>	Borneo	female	110.80
<i>Viverra zibetha</i>	Borneo	male	113.55
<i>Vulpes vulpes</i>	Alaska	female	139.16
<i>Vulpes vulpes</i>	Alaska	male	146.43
<i>Vulpes vulpes</i>	Benelux	female	137.74
<i>Vulpes vulpes</i>	Benelux	male	144.32
<i>Vulpes vulpes</i>	France	female	134.22
<i>Vulpes vulpes</i>	France	male	140.63
<i>Vulpes vulpes</i>	Israel	female	122.34
<i>Vulpes vulpes</i>	Israel	male	127.55

**Appendix S3 - Models for an analysis using only populations spanning < 1 degree of latitude and longitude.**

Species	country	longitude	latitude	n	earliest date	latest date	factor	Estimate	Std. Error	t	P
<i>Alopex lagopus</i>	Alaska	-157	71	29	1897	1962	Intercept	4.999	0.474	10.557	0.0000
<i>Alopex lagopus</i>							sex	0.042	0.010	4.081	0.0004
<i>Alopex lagopus</i>							year	0.000	0.000	-0.471	0.6414
<i>Martes foina</i>	Germany	14	51	39	1879	1999	Intercept	4.274	0.343	12.472	0.0000
<i>Martes foina</i>							sex	0.053	0.008	6.215	0.0000
<i>Martes foina</i>							year	0.000	0.000	0.233	0.8170
<i>Meles meles</i>	Israel	35	32	24	1911	1986	Intercept	3.420	1.031	3.318	0.0033
<i>Meles meles</i>							sex	0.049	0.016	2.948	0.0077
<i>Meles meles</i>							year	0.001	0.001	1.299	0.2079
<i>Melogale orientalis</i>	Java	107	-7	23	1881	1970	Intercept	4.477	0.491	9.111	0.0000
<i>Melogale orientalis</i>							sex	0.041	0.010	4.144	0.0005
<i>Melogale orientalis</i>							year	0.000	0.000	-0.407	0.6886
<i>Mustela erminea</i>	Vermont	-73	44	30	1912	1977	Intercept	1.849	0.959	1.927	0.0645
<i>Mustela erminea</i>							sex	0.080	0.017	4.821	0.0000
<i>Mustela erminea</i>							year	0.001	0.000	1.808	0.0818
<i>Mustela erminea</i> *	Maine	-69	45	62	1874	1940	Intercept	1.933	0.812	2.380	0.0244
<i>Mustela erminea</i> *							year	0.001	0.000	2.233	0.0337
<i>Mustela erminea</i>	Maine	-69	46	28	1902	1950	Intercept	2.852	1.582	1.803	0.0835
<i>Mustela erminea</i>							sex	0.140	0.046	3.033	0.0056
<i>Mustela erminea</i>							year	0.000	0.001	0.489	0.6293
<i>Mustela erminea</i>	British Columbia & Washington	-122	49	39	1895	1939	Intercept	2.945	0.943	3.123	0.0035
<i>Mustela erminea</i>							sex	0.155	0.018	8.653	0.0000
<i>Mustela erminea</i>							year	0.000	0.000	0.622	0.5380
<i>Mustela erminea</i>	Minnesota	-93	45	32	1931	1979	Intercept	5.110	1.314	3.888	0.0005
<i>Mustela erminea</i>							sex	0.134	0.024	5.628	0.0000

<i>Mustela erminea</i>							year	-0.001	0.001	-1.150	0.2596
<i>Mustela frenata</i>	California	-117	33	24	1899	1964	Intercept	3.111	0.670	4.644	0.0001
<i>Mustela frenata</i>							sex	0.080	0.012	6.518	0.0000
<i>Mustela frenata</i>							year	0.000	0.000	1.051	0.3054
<i>Mustela frenata</i>	Michigan	-84	42	42	1903	1971	Intercept	4.435	0.626	7.091	0.0000
<i>Mustela frenata</i>							sex	0.162	0.012	13.097	0.0000
<i>Mustela frenata</i>							year	0.000	0.000	-1.195	0.2390
<i>Mustela nivalis</i>	Italy	8	44	28	1907	1954	Intercept	4.661	1.651	2.823	0.0092
<i>Mustela nivalis</i>							sex	0.126	0.019	6.646	0.0000
<i>Mustela nivalis</i>							year	-0.001	0.001	-0.606	0.5498
<i>Mustela nivalis</i>	Belgium & the Netherlands	5	51	46	1928	1990	Intercept	2.545	1.742	1.461	0.1510
<i>Mustela nivalis</i>							sex	0.086	0.019	4.460	0.0001
<i>Mustela nivalis</i>							year	0.000	0.001	0.552	0.5840
<i>Mustela nivalis</i>	Alaska	-157	71	34	1928	1969	Intercept	2.698	1.239	2.177	0.0372
<i>Mustela nivalis</i>							sex	0.117	0.014	8.550	0.0000
<i>Mustela nivalis</i>							year	0.000	0.001	0.579	0.5667
<i>Mustela putorius</i>	Belgium & the Netherlands	5	51	50	1939	2000	Intercept	2.793	1.952	1.431	0.1590
<i>Mustela putorius</i>							sex	0.106	0.017	6.077	0.0000
<i>Mustela putorius</i>							year	0.001	0.001	0.653	0.5170
<i>Mustela putorius</i>	Belgium & the Netherlands	6	51	26	1920	1974	Intercept	7.713	1.421	5.427	0.0000
<i>Mustela putorius</i>							sex	0.094	0.025	3.804	0.0009
<i>Mustela putorius</i>							year	-0.002	0.001	-2.523	0.0190
<i>Mustela putorius</i>	Netherlands	5	52	33	1921	1986	Intercept	2.258	1.131	1.997	0.0549
<i>Mustela putorius</i>							sex	0.120	0.020	6.072	0.0000
<i>Mustela putorius</i>							year	0.001	0.001	1.585	0.1234
<i>Ursus arctos</i>	Admiralty	-134	57	22	1907	1979	Intercept	5.888	0.963	6.115	0.0000
<i>Ursus arctos</i>							sex	0.133	0.029	4.573	0.0002
<i>Ursus arctos</i>							year	0.000	0.000	-0.181	0.8580

<i>Ursus arctos</i>	Admiralty	-134	58	31	1905	1970	Intercept	4.894	1.608	3.044	0.0050
<i>Ursus arctos</i>							sex	0.114	0.024	4.697	0.0001
<i>Ursus arctos</i>							year	0.000	0.001	0.523	0.6048

CBL (ln transformed) in each population is regressed against sex and year of collection.

\* we have no measurement of females from this region

0.000 is  $< 0.0005$

0.0000 is  $< 0.00005$

sex is the difference between male and female ln CBL

slope is the slope of ln CBL on year of collection