*Global Ecology and Biogeography, (Global Ecol. Biogeogr.)* (2007) **16**, 788–794

**RESEARCH PAPER**

# What determines conformity to Bergmann's rule?

Shai Meiri[1]*, Yoram Yom-Tov[2] and Eli Geffen[2]

[1]*NERC Centre for Population Biology, Imperial College London, Silwood Park Campus, Ascot, Berkshire SL5 7PY, UK. E-mail: s.meiri@imperial.ac.uk,* [2]*Department of Zoology, Tel Aviv University, Tel Aviv 69978, Israel. E-mails: yomtov@post.tau.ac.il; geffene@post.tau.ac.il*

*Correspondence: Shai Meiri, NERC Centre for Population Biology, Imperial College London, Silwood Park Campus, Ascot, Berkshire SL5 7PY, UK.
E-mail: s.meiri@imperial.ac.uk

## ABSTRACT

**Aim** Bergmann's rule, the tendency of body size within species in bird and mammal populations to be positively correlated with latitude, is among the best known biogeographical generalizations. The factors behind such clines, however, are not well understood. Here we use a large data base of 79 mammalian carnivore species to examine the factors affecting latitudinal size clines.

**Location** Worldwide.

**Methods** We measured the skulls and teeth of carnivores in natural history museums, and calculated the amount of variation in size explained by latitude, supplementing our measurements with published data. We examined the effects of a number of variables on the tendency to show latitudinal clines.

**Results** We found that geographical range and latitudinal extent are strongly related to size clines. Minimum temperatures across the range, net primary productivity and habitat diversity also have some, albeit much less, influence.

**Main conclusions** We suggest that species with large geographical ranges are likely to encounter significant heterogeneity in those factors that influence body size, and are thus likely to exhibit size clines. However, the key factors that determine body size may not always operate along a latitudinal (or other geographical) cline, but be spatially linked to patches in the species range. One such important factor is likely to be food availability, which we show is a strong predictor of size in the brown bear (*Ursus arctos*) but is not associated with a latitudinal cline. We argue that the spatial distribution of key resources within the species range constitutes a significant predictor of carnivore body size.

**Keywords**

**Body size, carnivores, clines, food availability, geographical variation, latitude, primary productivity, rainfall, range size, temperature.**

## INTRODUCTION

Bergmann's rule is the best known ecogeographical rule. It states that within species of homeotherms, body size is larger in cold regions than in warm ones (Mayr, 1963). This rule is usually interpreted as an adaptation to thermal conditions: a higher body surface-to-volume ratio in warm areas enables effective heat dissipation and a lower surface-to-volume ratio reduces heat loss in cold areas (Mayr, 1956). Since temperature and other environmental variables are highly correlated with latitude, Bergmann's rule has often been portrayed as a positive relation between latitude and body size. Such a relationship has been widely documented among both homeotherms and ectotherms (Ray, 1960; Atkinson, 1994; Ashton & Feldman, 2003; Meiri & Dayan, 2003).

The thermal explanation for Bergmann's rule has often been questioned. Scholander (1955) argued that vascular control and fur insulation are more effective mechanisms for heat dissipation and conservation than are changes in body size. Other authors have suggested that the geographical trends interpreted as conforming to Bergmann's rule can be explained by factors other than temperature. Rosenzweig (1968) suggested that body size is better correlated with primary productivity or food availability. This latter claim is supported by studies of body-size variation in Australian and Israeli mammals, which demonstrated that both moisture and precipitation were often better correlated with

DOI: 10.1111/j.1466-8238.2007.00330.x

body size than temperature (Yom-Tov & Nix, 1986; Yom-Tov & Geffen, 2006). Furthermore, in several ectotherm species that conform to Bergmann's rule, factors other than heat conversion and dissipation may better explain body-size gradients (Ray, 1960; Arnett & Gotelli, 1999). The interpretation of the correlations between body size on the one hand and latitude, temperature and precipitation on the other is difficult because these environmental factors often covary, and other climatic and ecological factors are key predictors of body size (e.g. Angilletta & Dunham, 2003; Millien *et al.*, 2006; Yom-Tov & Geffen, 2006).

In all studies where multiple mammalian species have been tested for correlation between latitude and morphometric variables, some species did not show any association, and many homeotherms do not conform to Bergmann's rule. Meiri & Dayan (2003) tested for an association between latitude and size in 94 bird species and 149 mammal species, and concluded that 72% of the birds and 65% of the mammals follow Bergmann's rule. However, further examination of these data showed that only 26% of the bird species and 30% of the mammal species had over 50% of the variance in body size explained by latitude (mean variation explained by latitude: 35% for birds, 37% for mammals). Ashton (2004) reported similar patterns for 77 mammal species (21% of species with over 50% of the variance in body size explained by latitude; mean 28%). In an independent analysis of 44 carnivore species by Meiri *et al.* (2004a), no species had over 50% of the variance in body size explained by latitude (mean variance in body size explained by latitude = 13%). Thus, although many species showed a correlation between latitude and morphology, only in a small portion of these does latitude account for much of the variation in body size.

Why is latitude a strong predictor of body size in so few species? To answer this question we examined 79 carnivore species for which correlation coefficients between latitude and body size were available. In this study we aimed to explain differences in the amount of variance in body size accounted for by latitude (i.e. $r^2$) among species. We considered seven alternative predictors, and tested their relative contribution using multiple regression. Our primary hypothesis was that body size is modulated by food availability. Consequently, species that show a larger range in net primary production (NPP) and the amount of rainfall should have a larger span in body size (Yom-Tov & Geffen, 2006). Thus, high variability in productivity is likely to be associated with the evolution of size clines. Body size is a likely predictor, because the tendency for size to vary with latitude is predicted to increase with increasing body size (Freckleton *et al.*, 2003; Meiri & Dayan, 2003). We hypothesized that the tendency to vary in size would also be related to the latitudinal range, the distribution area occupied by a species, and the temperature range and habitat diversity encountered by a species. The rationale for this is that body size variation within a species reflects the environmental conditions to which it is exposed, and the greater the variability, the greater the opportunity to change in size. While this relationship may seem trivial (Meiri & Dayan, 2003; Meiri *et al.*, 2004a), it has never been explicitly quantified. Consequently, species with a range that has steep gradients for these variables should vary more in size than species facing shallower gradients.

## METHODS

We measured carnivore skulls and teeth in natural history collections (see Acknowledgements), and used two size indices: condylobasal length of the skull (CBL) and the length of the first lower molar ($M_1$). These are the most common measurements of cranial and dental size indices in mammals, and were chosen to facilitate comparisons with published accounts of size clines in carnivores (Klein, 1986; Meiri *et al.*, 2004a). Both CBL and $M_1$ are highly precise measurements, and in adults are not affected by body condition (Gittleman & Van Valkenburgh, 1997; Meiri *et al.*, 2005a). Measurements were taken with digital callipers to 0.01-mm precision or Vernier callipers to 0.02-mm precision (for measurements exceeding 300 mm). We used only adult specimens. As insular mammals often diverge markedly in size from their mainland counterparts (Meiri *et al.*, 2004b, 2006), we analysed only mainland specimens. We recorded latitude for each specimen and used only specimens for which reasonably accurate locality data were available (error of less than 2° of latitude, although for the vast majority of specimens latitude was known with much greater accuracy). We analysed data with sex as an additional explanatory variable, and for all specimens pooled, regardless of sex. We pooled all specimens of each species regardless of continent, and did not distinguish between latitude south and north of the equator. Size was then regressed on latitude for each species. We used the coefficients of determination, $r^2$, obtained to compare the tendency of different species to vary in size with latitude, supplementing our own data with comparable data from the literature. The correlation coefficient $r$ may be a more fitting response variable to test for the prevalence of Bergmann's rule, because negative correlations between size and latitude depart from the rule. Here, however, we were more interested in the forces leading to the evolution of size clines in general, regardless of their direction.

For each species we obtained the following data: body mass, latitude range, area of distribution range, habitat diversity within distribution range, the lowest mean winter temperature for the species range, annual precipitation range and net primary productivity range. Data on the body weight of each species were obtained from the museum data of the specimens we measured, supplemented with data from the literature. Because mass often varies considerably across the geographical range, and sampling is usually not equal, we used the midpoint of the mass range as an estimate (Meiri *et al.*, 2005b). We used distribution maps of all species from carnivore action plans (IUCN publications), 'Mammalian Species' accounts (American Society of Mammalogists) and from Long (2003). From these maps we calculated the total distribution area using the program IMAGE (version 1.63; W. Rasband, National Institutes of Health, USA) and the latitudinal range of each species. We estimated habitat composition by superimposing each species' range on a detailed global map of biomes (Natural Resources Conservation Service, US Department of Agriculture), and calculating the proportion of each of 13 distinct habitats within the range using the program MULTISPEC (version 5; D. Landgrebe and L. Biehl, Purdue University, West Lafayette, IN, USA). Habitat diversity for each species' range was calculated from habitat proportions using the Shannon–Wiener index (Pielou, 1966). Temperature data were obtained from Institut Geografii (1998) and converted to degrees centigrade. We used maps of mean January and July temperatures, assuming that these are the coldest months of the year in the Northern and Southern Hemispheres, respectively, and recorded the lowest mean temperature across the geographical range of each species. The ranges of annual precipitation for the entire range of each species were obtained from the same source (Institut Geografii, 1998). Net primary production (NPP; g C $m^{-2}$ $year^{-1}$) data were kindly provided by Dr Mark Lomas (University of Sheffield). These are annual NPP for 1° cells and we used the calculated mean for the 20th century (1901–2000). Distribution maps usually represent the extent of occurrence rather than the area of occupancy, and as such may overestimate the range of climatic variables that populations within species are exposed to. This is an issue for all the species we examine, and should therefore not bias our results.

Our analysis aimed to explain the variance in $r^2$ of CBL and $M_1$ as a function of latitude by a series of independent variables (body mass, latitude range, geographical range size, habitat diversity, mean winter temperature, annual precipitation range and net primary productivity range), using multiple regression. To select the best regression model (i.e. subset of predictors) we used Akaike's information criterion (AIC; Burnham & Anderson, 2002; Johnson & Omland, 2004; Sullivan & Joyce, 2005). This approach weighs different models by the amount of the variance explained and model complexity (i.e. the number of explanatory variables, $K$). Because $n/K < 40$ for our data set the AIC values were corrected for small sample size ($AIC_c$) using the equation in Burnham & Anderson (2001). The level of support for an $AIC_c$ value was evaluated by $\Delta AIC_c$ (i.e. $AIC_c = AIC_i - AIC_{min}$) and Akaike weights (Burnham & Anderson, 2001). An Akaike weight is the relative likelihood of the model given the data. Models with $\Delta AIC_c$ values of 0–2 provide similar support (Burnham & Anderson, 2001).

To address any possible dependency between taxa due to phylogeny we conducted independent contrasts analysis using CAIC (version 2.6; Purvis & Rambaut, 1995) and a published phylogeny for the carnivores (Ortolani, 1999).

For illustration purposes, we regressed brown bear (*Ursus arctos*) CBL as a function of geographical distance from the nearest salmon spawning area (calculated using ArcView, ESRI). Data on salmon spawning areas were obtained from Augerot (2005), the Wild Salmon Center (X. Augerot and G. Robillard, pers. comm.) and the Ocean Biogeographic Information System (OBIS; http://www.iobis.org/).

## RESULTS

Data on the coefficient of determination for CBL and $M_1$ as a function of latitude ($r^2_{CBL}$ or $r^2_{M_1}$), along with the values of the different predictor variables for each species, are shown in Appendix S1 in Supplementary Material. The tolerance of a variable ($1 - r^2$) is a measure of its collinearity with all other independent variables in the model. The higher the intercorrelation between the independent variables, the lower the tolerance will be. In general, only a tolerance of 0.2 or lower creates an inflationary impact on the standard error of the regression coefficient (Keith, 2006). Mean tolerance (± SD) for each of the independent variables in our study was high, indicating low correlation between them (log body weight [BW] = 0.84 ± 0.02, area = 0.59 ± 0.03, latitude = 0.36 ± 0.04, temperature = 0.62 ± 0.06, rain = 0.73 ± 0.08, NPP = 0.62 ± 0.05 and habitat = 0.52 ± 0.05).

Model selection using the AIC showed that for $r^2_{CBL}$ the best model included only the latitudinal range (Table 1). This pattern was also true after controlling for sex (Table 1). However, accounting for phylogeny, the best model was composed of area, rain range and temperature range. The best model for $r^2_{CBL}$ after controlling for sex and accounting for phylogeny was composed of area, temperature range and NPP range. Other combinations of these variables and rain range were equally probable (Table 2). The best model for $r^2_{M_1}$ was composed of area, latitudinal range and temperature. However, $\Delta AIC_c$ between the best model and the next three models in Table 1 was lower than 2, indicating that the alternative models are equally supported. Accounting for phylogeny and sex revealed that all five best models are equally supported, and all include area and NPP range (Table 2). All the explanatory variables were always positively related to $r^2$ scores. For all models, $r^2$ was low; the highest variance explained by these best models was about 28% and 33% for CBL and $M_1$, respectively (Table 2). Hence, the size of the geographical range is always a significant predictor of size change for latitude. Latitudinal span also usually had a significant effect, except in the case of $M_1$ where NPP and temperature appeared as key predictors.

We used the Wald test to evaluate significant effects in a particular regression model. Latitudinal range was the only significant effect on CBL ($\chi^2 = 10.3$, $P = 0.001$) and CBL controlled for sex ($\chi^2 = 7.4$, $P = 0.006$). Area was the only significant effect on CBL contrasts ($\chi^2 = 11.3$, $P < 0.001$) and CBL contrasts controlled for sex ($\chi^2 = 12.6$, $P < 0.001$). Latitudinal range ($\chi^2 = 8.8$, $P = 0.003$), area ($\chi^2 = 8.5$, $P = 0.004$) and temperature range ($\chi^2 = 4.4$, $P = 0.04$) had a significant effect on $M_1$, and latitudinal range ($\chi^2 = 6.9$, $P = 0.008$) and area ($\chi^2 = 5.3$, $P = 0.02$) had a significant effect on $M_1$ controlled for sex. A similar pattern was observed for $M_1$ after accounting for phylogeny. Latitudinal range ($\chi^2 = 4.9$, $P = 0.03$), area ($\chi^2 = 12.2$, $P < 0.001$), temperature range ($\chi^2 = 3.9$, $P = 0.047$) and NPP range ($\chi^2 = 13.9$, $P < 0.001$) were significant for $M_1$, and area ($\chi^2 = 7.1$, $P = 0.008$) and NPP range ($\chi^2 = 18.2$, $P < 0.001$) were significant for $M_1$ controlled for sex.

## DISCUSSION

Although these variables explain some of the tendency of species to change in size with latitude, over 65% of the variation remains unexplained. Why do some species show a tight fit between body size and latitude, while others show no such trend? We argue that almost any species will show a geographical variation in body size if the key factor that influences its size varies to a large extent across its range, and this was supported in all tests. Distribution area, latitudinal extent and habitat diversity do not affect body size directly. However, these parameters are likely to correlate

Table 1 The five best models in multiple regression of $r^2$ as the dependent and seven independent environmental and spatial variables. $K$ is the number of parameters in the model, $\mathrm{AIC_c}$ is Akaike's information criterion (AIC) corrected for small sample size, $\Delta\mathrm{AIC_c}$ is the difference in $\mathrm{AIC_c}$ values between each model and the best model (i.e. lowest $\mathrm{AIC_c}$), and $W_{\mathrm{AIC}}$ is the Akaike weight.

| Variables selected | $K$ | $R^2$ | $\mathrm{AIC_c}$ | $\Delta\mathrm{AIC_c}$ | $W_{\mathrm{AIC}}$ |
|---|---|---|---|---|---|
| CBL | | | | | |
| 1. Latitude | 1 | 0.165 | −51.9 | 0.00 | 0.28 |
| 2. Latitude, temperature | 2 | 0.188 | −51.3 | 0.67 | 0.20 |
| 3. Latitude, temperature, area | 3 | 0.202 | −51.0 | 0.95 | 0.18 |
| 4. Latitude, NPP | 2 | 0.170 | −50.9 | 1.00 | 0.17 |
| 5. Latitude, temperature, NPP | 3 | 0.199 | −50.8 | 1.11 | 0.16 |
| CBL controlled for sex | | | | | |
| 1. Latitude | 1 | 0.177 | −48.1 | 0.00 | 0.28 |
| 2. Latitude, temperature, area | 3 | 0.212 | −47.3 | 0.73 | 0.19 |
| 3. Latitude, temperature | 2 | 0.198 | −47.3 | 0.75 | 0.19 |
| 4. Latitude, area | 2 | 0.183 | −47.1 | 0.95 | 0.17 |
| 5. Latitude, log BW | 2 | 0.179 | −46.9 | 1.13 | 0.16 |
| $\mathrm{M_1}$ | | | | | |
| 1. Latitude, area, temperature | 3 | 0.113 | −81.8 | 0.00 | 0.35 |
| 2. Latitude, area, temperature, NPP | 4 | 0.118 | −81.0 | 0.79 | 0.24 |
| 3. Latitude, area, temperature, rain | 4 | 0.123 | −80.2 | 1.55 | 0.16 |
| 4. Latitude, area, temperature, log BW | 4 | 0.113 | −79.8 | 1.95 | 0.13 |
| 5. Latitude, area, temperature, rain, NPP | 5 | 0.131 | −79.7 | 2.09 | 0.12 |
| $\mathrm{M_1}$ controlled for sex | | | | | |
| 1. Latitude, area, temperature | 3 | 0.114 | −49.9 | 0.00 | 0.31 |
| 2. Latitude, area | 2 | 0.083 | −49.2 | 0.66 | 0.22 |
| 3. Area | 1 | 0.072 | −48.7 | 1.16 | 0.17 |
| 4. Latitude, area, habitat | 3 | 0.094 | −48.5 | 1.38 | 0.15 |
| 5. Latitude, area, temperature, habitat | 4 | 0.116 | −48.3 | 1.54 | 0.14 |

CBL, condylo-basal length of the skull; $\mathrm{M_1}$, anterior–posterior length of the first lower molar; NPP, net primary productivity; BW, body weight.

with body size clines, simply because they encompass several factors that affect body size. Range size and latitudinal range are expected to explain a major portion of the variance among species because species with a small range may span a limited range of factors such as food availability that generates selection on body size (Meiri *et al.*, 2004a; cf. Ashton, 2004). The range maps we used represent the extent of occurrence of species rather than areas of occupancy, which may be a better predictor of the actual environmental variability encountered by a species. Thus it is reasonable to expect an even stronger relationship between body size and areas of occupancy or habitat diversity.

For many species, food availability during the growth period is the key factor that determines adult size (e.g. Arnett & Gotelli, 1999). Recent increases in body size of several species of mammals have been attributed to improved diet (Yom-Tov, 2003; Yom-Tov *et al.*, 2003; Yom-Tov & Yom-Tov, 2005), and prey size and availability were shown to be strong predictors of geographical variation in carnivore size (Raia & Meiri, 2006). Here we find that NPP influences tooth size, which may be more closely regulated by food in carnivores than skull size (Dayan *et al.*, 1992). We hypothesize that a north–south trend in body size will appear in those species where food availability is correlated with latitude (and thus temperature), but not if such key factors do not vary on a south–north cline. Geist (1987), for example, has shown that in North America the body size trend in the grey wolf (*Canis lupus*) conforms to Bergmann's rule up to latitudes 60–65° N, but reverses its direction at higher latitudes. Geist (1987) argued that these trends are related to duration of the annual food productivity pulse, and that body size is a function of food availability.

To demonstrate our hypothesis that a body size trend may be affected by food availability, and not as predicted by Bergmann's rule, we draw attention to the case of the brown bear. The brown bear has a huge range size (106.9 million $\mathrm{km^2}$; Appendix 1) which spans a wide latitudinal range (40°), nearly equalling that of the grey wolf (127 million $\mathrm{km^2}$ and 60°; Appendix 1). However, the body size in the brown bear is practically independent of latitude ($r^2 = 0.08$), whereas wolf body size is tightly correlated with latitude ($r^2 = 0.69$). Indeed, body size in the brown bear is much better explained by distance to the nearest salmon spawning area, a rich resource commonly used by bears whenever available (females: $r^2 = 0.404$, $F_{(1,79)} = 53.6$, $P < 0.0001$; males: $r^2 = 0.403$, $F_{(1,83)} = 56.0$, $P < 0.0001$; Fig. 1). Hilderbrand *et al.* (1999) showed that a marine meat source (i.e. salmon) explains 86% of the variance in female body mass ($F_{(1,11)} = 67.6$, $P < 0.0001$; original data modified by adding relevant mass data from Schwartz *et al.*, 2003). In contrast to salmon availability, latitude is a very poor predictor of body size in brown bears. Salmon availability is not distributed along north–south or east–west clines, but patchily.

Table 2 The five best models in multiple regression of $r^2$ as the dependent and seven independent environmental and spatial variables, controlled for phylogeny. $K$ is the number of parameters in the model, $\mathrm{AIC_c}$ is Akaike's information criterion (AIC) corrected for small sample size, $\Delta\mathrm{AIC_c}$ is the difference in $\mathrm{AIC_c}$ values between each model and the best model (i.e. lowest $\mathrm{AIC_c}$), and $W_{\mathrm{AIC}}$ is the Akaike weight. Regressions on contrasts were forced through the origin.

| Variables selected | $K$ | $R^2$ | $\mathrm{AIC_c}$ | $\Delta\mathrm{AIC_c}$ | $W_{\mathrm{AIC}}$ |
|---|---|---|---|---|---|
| CBL | | | | | |
| 1. Area, rain, temperature | 3 | 0.281 | −276.1 | 0.00 | 0.35 |
| 2. Area, rain | 2 | 0.252 | −275.8 | 0.31 | 0.30 |
| 3. Area, rain, temperature, latitude | 4 | 0.284 | −274.1 | 2.02 | 0.13 |
| 4. Area, rain, temperature, habitat | 4 | 0.281 | −273.8 | 2.27 | 0.11 |
| 5. Area, rain, temperature, NPP | 4 | 0.281 | −273.8 | 2.27 | 0.11 |
| CBL controlled for sex | | | | | |
| 1. Area, temperature, NPP | 3 | 0.285 | −263.6 | 0.00 | 0.30 |
| 2. Area, temperature, NPP, rain | 4 | 0.305 | −263.0 | 0.53 | 0.23 |
| 3. Area, temperature, rain | 3 | 0.277 | −262.8 | 0.72 | 0.21 |
| 4. Area, NPP | 2 | 0.241 | −261.9 | 1.63 | 0.13 |
| 5. Area, rain | 2 | 0.240 | −261.8 | 1.73 | 0.13 |
| $\mathrm{M_1}$ | | | | | |
| 1. Area, latitude, temperature, NPP, habitat | 5 | 0.324 | −301.0 | 0.00 | 0.28 |
| 2. Area, temperature, NPP | 3 | 0.277 | −300.4 | 0.61 | 0.21 |
| 3. Area, latitude, NPP | 3 | 0.275 | −300.2 | 0.83 | 0.18 |
| 4. Area, latitude, temperature, NPP | 4 | 0.294 | −300.0 | 1.02 | 0.17 |
| 5. Area, latitude, temperature, rain, NPP, habitat | 6 | 0.336 | −299.9 | 1.05 | 0.16 |
| $\mathrm{M_1}$ controlled for sex | | | | | |
| 1. Area, NPP | 2 | 0.330 | −217.3 | 0.00 | 0.28 |
| 2. Area, NPP, latitude | 3 | 0.351 | −217.0 | 0.34 | 0.23 |
| 3. Area, NPP, temperature | 3 | 0.347 | −216.6 | 0.73 | 0.19 |
| 4. Area, NPP, latitude, habitat | 4 | 0.369 | −216.3 | 1.06 | 0.16 |
| 5. Area, NPP, log BW | 3 | 0.340 | −216.0 | 1.37 | 0.14 |

CBL, condylo-basal length of the skull; $\mathrm{M_1}$, anterior–posterior length of the first lower molar; NPP, net primary productivity; BW, body weight.

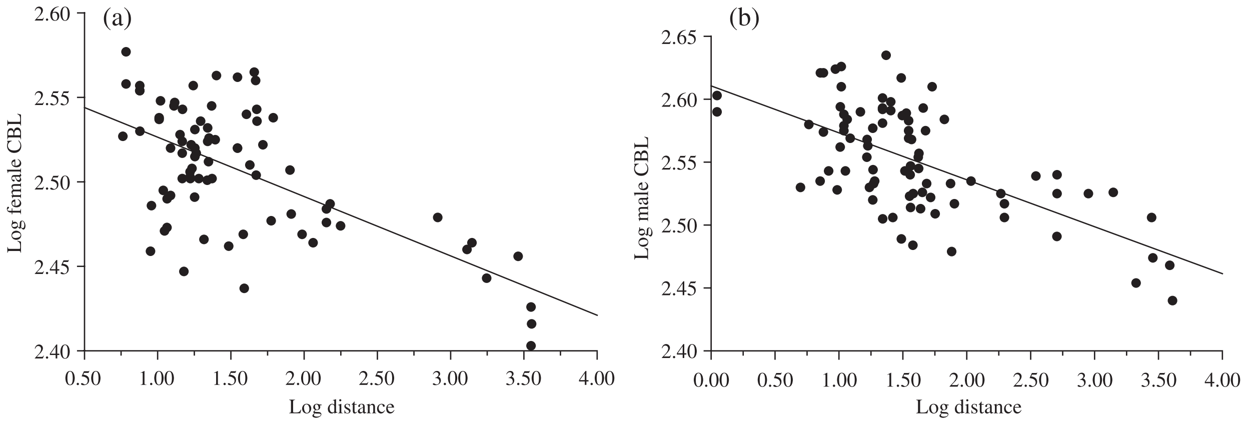

Figure 1 Bear skull size vs. distance to the nearest salmon spawning area. Regression of (a) female ($y = -0.035x + 2.56$) and (b) male ($y = -0.037 + 2.61$) condylo-basal length of brown bear skull (CBL, in mm) as a function of geographical distance to the nearest salmon spawning area (in km). Distance to the nearest salmon spawning area accounted for 40.4% ($F_{(1,79)} = 53.6$, $P < 0.0001$) and 40.3% ($F_{(1,83)} = 56.0$, $P < 0.0001$) of the variance in female and male skull length.

Thus, while for some carnivores, like the wolf, food resources presumably increase along a south–north cline, at least up to a point, for others, like the brown bear, resources may not change along such a cline. Salmon distribution may also explain body size in other piscivorous carnivores (e.g. the otter, *Lontra canadensis*), but for many other carnivores where latitude is a poor predictor of body size, the factors that influence body size are unknown. Many of these factors may be species specific. For example, although the body size of Arctic foxes is not related to latitude (this study), the body size of Arctic foxes living on Mednyi Island is significantly larger than in other populations, and this phenomenon has been attributed to an unusual abundance of carcasses washed ashore (Goltsman *et al*., 2005). We suggest that the factors influencing body size are related to key components in the species' diet and to the spatial distribution of these key components over the species' range.

We have referred above mostly to the availability of food as a key factor accounting for variation in body size. However, the same argument could also apply to other candidate factors, such as interspecific competition (e.g. Dayan & Simberloff, 1998). Selection on body size due to competition may also be affected by the patchy distribution of the competitors.

We suggest that the main message of the present study is that it is unrealistic to explain variation in a species' morphology solely on the basis of latitudinal clines. In species where size changes across the range but not according to Bergmann's rule, the specific distribution of key dietary components or other key factors may be better predictors. To adequately model geographical variation in size requires detailed autecological information on the diet and natural history of the species under study throughout its geographical range. At present such highly species-specific data cannot be readily integrated into a comparative framework.

## ACKNOWLEDGEMENTS

We would like to thank Mark Lomas for providing NPP data. We thank Tamar Dayan and Daniel Simberloff for valuable discussion, and for permission to use data they measured. We thank R. Asher (Museum für Naturkunde, Humboldt, Berlin), H. Baagøe (Zoological Museum, University of Copenhagen), D. Balkwill and M. Gosselin (Canadian Museum of Nature), Y. C. Man (Raffles Museum), J. Chupasko (MCZ, Harvard), J. Dawson (New-Walk Museum), H. Endo (National Science Museum, Tokyo), J. Eger (ROM, Toronto), D. Harrison and M. Perch (HZM), D. Hills (NHM, London), T. Holmes (University of Kansas Museum of Natural History), G. Jarrell (University of Alaska, Museum of Natural History), L. Kenness and D. Nagorsen (Royal British Columbia Museum), R. Kraft (Zoologische Staatssammlung, München), Y. Kunimatsu (Primate Research Institute, Kyoto University), E. Lacey (MVZ, Berkeley), G. Lenglet (Institut Royal des Sciences Naturelles de Belgique), S. B. McLaren (Carnegie Museum), M. Nowak-Kemp (Oxford University Museum of Natural History), B. Randall and E. Westwig (AMNH), A. Rol (University of Amsterdam, Zoological Museum), A. Ross (Ulster Museum), T. Shariv (Tel-Aviv University Zoological Museum), B. Shepherd (Smithsonian Institution), C. Smeenk ('Naturalis', Leiden), W. Stanley (Field Museum), C. Stefen (Staatliche Naturhistorische Sammlungen, Dresden), R. Symonds (Zoology Museum, Cambridge), S. M. Woodward and G. Véron (MNHN, Paris) for their invaluable help during data collecting. We thank Love Dalen, Brad Hawkins, Gavin Thomas and Robert Reed for enlightening comments on the manuscript, to Naomi Paz for editing the paper, and to Uri Roll for his dedicated help with the GIS analysis.

## REFERENCES

Angilletta, M.J. & Dunham, A.E. (2003) The temperature-size rule in ectotherms: simple evolutionary explanations may not be general. *The American Naturalist*, **162**, 332–342.

Arnett, A.E. & Gotelli, N.J. (1999) Geographic variation in life-history traits of the ant lion, *Myrmeleon immaculatus*: evolutionary implications of Bergmann's rule. *Evolution*, **53**, 1180–1188.

Ashton, K.G. (2004) Sensitivity of intraspecific latitudinal clines of body size for tetrapods to sampling, latitude and body size. *Integrative and Comparative Biology*, **44**, 403–412.

Ashton, K.G. & Feldman, C.R. (2003) Bergmann's rule in nonavian reptiles: turtles follow it, lizards and snakes reverse it. *Evolution*, **57**, 1151–1163.

Atkinson, D. (1994) Temperature and organism size — a biological law for ectotherms? *Advances in Ecological Research*, **25**, 1–58.

Augerot, X. (2005) *Atlas of Pacific salmon: the first map-based status assessment of salmon in the north Pacific*. University of California Press, Berkeley.

Burnham, K.P. & Anderson, D.R. (2001) Kullback–Leibler information as a basis for strong inference in ecological studies. *Wildlife Research*, **28**, 111–119.

Burnham, K.P. & Anderson, D.R. (2002) *Model selection and multi-model inference*, 2nd edn. Springer, New York.

Dayan, T. & Simberloff, D. (1998) Size patterns among competitors: ecological character displacement and character release in mammals, with special reference to island populations. *Mammal Review*, **28**, 99–124.

Dayan, T., Simberloff, D., Tchernov, E. & Yom-Tov, Y. (1992) Canine carnassials: Character displacement in the wolves, jackals and foxes of Israel. *Biological Journal of the Linnean Society*, **45**, 315–331.

Freckleton, R.P., Harvey, P.H. & Pagel, M. (2003) Bergmann's rule and body size in mammals. *The American Naturalist*, **161**, 821–825.

Geist, V. (1987) Bergmann's rule is invalid. *Canadian Journal of Zoology*, **65**, 1035–1038.

Gittleman, J.L. & Van Valkenburgh, B. (1997) Sexual dimorphism in the canines and skulls of carnivores: effects of size, phylogeny and behavioural ecology. *Journal of Zoology*, **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. *Journal of Zoology*, **267**, 405–418.

Hilderbrand, G.V., Schwartz, C.C., Robbins, C.T., Jacoby, M.E., Hanley, T.A., Arthur, S.M. & Servheen, C. (1999) The importance of meat, particularly salmon, to body size, population productivity, and conservation of North American brown bears. *Canadian Journal of Zoology*, **77**, 132–138.

Institut Geografii (1998) *Resources and environment: world atlas*. Holzel, Vienna.

Johnson, J.B. & Omland, K.S. (2004) Model selection in ecology and evolution. *Trends in Ecology & Evolution*, **19**, 101–108.

Keith, T.Z. (2006) *Multiple regression and beyond*. Pearson, Allyn & Bacon, Boston.

Klein, R.G. (1986) Carnivore size and Quaternary climatic change in Southern Africa. *Quaternary Research*, **26**, 153–170.

Long, J.L. (2003) *Introduced mammals of the world*. CSIRO Publications, Collingwood, Victoria.

Mayr, E. (1956) Geographical character gradients and climatic adaptation. *Evolution*, **10**, 105–108.

Mayr, E. (1963) *Animal species and evolution*. Belknap Press, Cambridge, MA.

Meiri, S. & Dayan, T. (2003) On the validity of Bergmann's rule. *Journal of Biogeography*, **30**, 331–351.

Meiri, S., Dayan, T., & Simberloff, D. (2004a) Carnivores, biases and Bergmann's rule. *Biological Journal of the Linnean Society*, **81**, 579–588.

Meiri, S., Dayan, T., & Simberloff, D. (2004b) Body size of insular carnivores: little support for the island rule. *The American Naturalist*, **163**, 469–479.

Meiri, S., Dayan, T. & Simberloff, D. (2005a) Variability and correlations in carnivore crania and dentition. *Functional Ecology*, **19**, 337–343.

Meiri, S., Simberloff, D. & Dayan, T. (2005b) Insular carnivore biogeography: island area and mammalian optimal body size. *The American Naturalist*, **165**, 505–514.

Meiri, S., Dayan, T. & Simberloff, D. (2006) The generality of the island rule reexamined. *Journal of Biogeography*, **33**, 1571–1577.

Millien, V., Lyons, S.K., Olson, L., Smith, F.A., Wilson, A.B. & Yom-Tov, Y. (2006) Ecotypic variation in the context of global climate change: revisiting the rules. *Ecology Letters*, **9**, 853–869.

Ortolani, A. (1999) Spots, stripes, tail tips and dark eyes: predicting the function of carnivore colour patterns using the comparative method. *Biological Journal of the Linnean Society*, **67**, 433–476.

Pielou, E.C. (1966) The measurement of diversity in different types of biological collections. *Journal of Theoretical Biology*, **13**, 131–144.

Purvis, A. & Rambaut, A. (1995) Comparative analysis by independent contrasts (CAIC): an Apple Macintosh application for analyzing comparative data. *Computer Applications for the Biosciences*, **11**, 247–251.

Raia, P. & Meiri, S. (2006) The island rule in large mammals. Paleontology meets ecology. *Evolution*, **60**, 1731–1742.

Ray, C. (1960) The application of Bergmann's and Allen's rules to the poikilotherms. *Journal of Morphology*, **106**, 85–108.

Rosenzweig, M.L. (1968) The strategy of body size in mammalian carnivores. *American Midland Naturalist*, **80**, 299–315.

Scholander, P.F. (1955) Evolution of climatic adaptation in homeotherms. *Evolution*, **9**, 15–26.

Schwartz, C.C., Miller, S.D. & Haroldson, M.A. (2003) Grizzly bear. *Wild mammals of North America: biology, management, and conservation* (ed. by G.A. Feldhamer, B.C. Thompson and J.A. Chapman), pp. 556–586. Johns Hopkins University Press, Baltimore.

Sullivan, J. & Joyce, P. (2005) Model selection in phylogenetics. *Annual Review of Ecology, Evolution, & Systematics*, **36**, 445–466.

Yom-Tov, Y. (2003) Body sizes of carnivores commensal with humans have increased over the past 50 years. *Functional Ecology*, **17**, 323–327.

Yom-Tov, Y. & Geffen, E. (2006) The determination of mammal body size: ambient temperature or food? *Oecologia*, **148**, 213–218.

Yom-Tov, Y. & Nix, H. (1986) Climatological correlates for body size of five species of Australian mammals. *Biological Journal of the Linnean Society*, **29**, 245–262.

Yom-Tov, Y. & Yom-Tov, J. (2005) Global warming, Bergmann's rule and body size in the masked shrew *Sorex cinereus* in Alaska. *Journal of Animal Ecology*, **74**, 803–808.

Yom-Tov, Y., Yom-Tov, S. & Baagøe, H. J. (2003) Increase of skull size in the red fox (*Vulpes vulpes*) and Eurasian badger (*Meles meles*) in Denmark during the 20th century: an effect of improved diet? *Evolutionary Ecology Research*, **5**, 1037–1048.

## BIOSKETCHES

**Shai Meiri** is studying macroecological patterns in diverse vertebrate groups. He is interested in the evolution of body size and its implications, and in the biogeographical and morphological implications of predation. His other fields of interest include biogeographical correlates of morphology and the morphological signature of speciation.

**Eli Geffen** is an ecologist interested primarily in the evolutionary biology of mammals and birds.

**Yoram Yom-Tov** is a professor in the Department of Zoology, and curator of reptiles, birds and mammals at the Zoological Museum, Tel Aviv University. His main research interests are biogeography, bird migration, behavioural ecology and the factors affecting the body size of birds and mammals.

Editor: Tim Blackburn

## SUPPLEMENTARY MATERIAL

The following supplementary material is available for this article:

**Appendix S1** Carnivore species analysed, response of their condylo-basal length (CBL) and first lower molar ($M_1$) to latitude, and attributes of their geographical range.

This material is available as part of the online article from:
http://www.blackwell-synergy.com/doi/abs/10.1111/j.1466-8238.2007.00330.x
(This link will take you to the article abstract).

**Appendix S1.** Carnivore species analysed, response of their condylo-basal length (CBL) and first lower molar (M1) to latitude, and attributes of their geographic range

| Species | $r^2_{CBL}$ | Slope (CBL) | $r^2_{M1}$ | Slope ($M_1$) | Body mass kg |
|---|---|---|---|---|---|
| *Acinonyx jubatus* [1] | na | na | 0.126 | 0.046 | 45.5 |
| *Alopex lagopus* [3] | 0.004 | -0.050 | 0.001 | 0.004 | 3.0 |
| *Aonyx capensis* [1] | na | na | 0.335 | 0.335 | 12.5 |
| *Arctogalidia trivirgata* [3] | 0.009 | -0.094 | 0.323 | 0.037 | 2.2 |
| *Atilax paludinosus* [1] | na | na | 0.022 | 0.008 | 3.6 |
| *Bassariscus astutus* [3] | 0.034 | -0.128 | 0.020 | 0.011 | 1.0 |
| *Canis aureus* [3] | 0.168 | 0.363 | 0.191 | 0.063 | 9.0 |
| *Canis latrans* [3] | 0.287 | 0.393 | 0.234 | 0.046 | 10.8 |
| *Canis lupus* [3] | 0.692 | 1.237 | 0.642 | 0.140 | 32.7 |
| *Canis mesomelas* [1] | na | na | 0.397 | 0.063 | 7.9 |
| *Crocuta crocuta* [1] | na | na | 0.257 | 0.144 | 64.7 |
| *Cuon alpinus* [3] | 0.705 | 0.385 | 0.098 | 0.029 | 15.9 |
| *Eira barbara* [3] | 0.048 | 0.339 | 0.140 | 0.061 | 5.3 |
| *Felis bengalensis* [3] | 0.082 | 0.178 | 0.074 | 0.017 | 3.2 |
| *Felis canadensis* [3] | 0.158 | 0.280 | 0.014 | 0.010 | 8.5 |
| *Felis caracal* [1,3] | 0.626 | 6.045 | 0.127 | 0.034 | 9.1 |
| *Felis chaus* [3] | 0.225 | 0.730 | 0.148 | 0.056 | 7.9 |
| *Felis concolor* [3] | 0.204 | 0.368 | 0.019 | 0.009 | 49.7 |
| *Felis pardalis* [3] | 0.015 | -0.300 | 0.030 | -0.045 | 10.0 |
| *Felis rufus* [3] | 0.088 | 0.280 | 0.103 | 0.027 | 10.5 |
| *Felis serval* [3] | na | na | 0.025 | 0.017 | 11.5 |
| *Felis silvestris* [1,3] | 0.052 | 0.130 | 0.071 | 0.019 | 3.2 |
| *Felis wiedii* [3] | 0.004 | -0.409 | 0.159 | -0.028 | 3.2 |
| *Galerella pulverulenta* [1] | na | na | 0.251 | 0.048 | 0.8 |
| *Galerella sanguinea* [3] | 0.263 | -0.305 | 0.093 | -0.020 | 0.7 |
| *Genetta genetta* [3] | 0.124 | 0.196 | 0.185 | 0.009 | 2.0 |

| | | | | | |
|---|---|---|---|---|---|
| *Ictonyx striatus* [1] | na | na | 0.148 | -0.220 | 0.8 |
| *Lontra canadensis* [3] | 0.002 | 0.028 | 0.079 | -0.027 | 9.1 |
| *Lontra longicaudis* [3] | 0.165 | -0.350 | 0.012 | -0.014 | 8.3 |
| *Lutra lutra* [3] | 0.267 | 0.287 | 0.000 | 0.001 | 8.3 |
| *Lycaon pictus* [1] | na | na | 0.045 | 0.027 | 26.4 |
| *Martes americana* [3] | 0.183 | 0.324 | 0.017 | 0.015 | 1.0 |
| *Martes flavigula* [3] | 0.458 | 0.446 | 0.436 | 0.058 | 1.8 |
| *Martes foina* [3] | 0.092 | 0.160 | 0.035 | 0.017 | 1.3 |
| *Martes martes* [3] | 0.008 | 0.105 | 0.007 | 0.014 | 1.2 |
| *Martes pennanti* [3] | 0.000 | 0.020 | 0.005 | 0.017 | 3.4 |
| *Meles meles* [3] | 0.462 | 0.526 | 0.169 | 0.041 | 9.5 |
| *Mellivora capensis* [1,3] | 0.043 | -0.222 | 0.096 | -0.029 | 8.1 |
| *Melogale moschata* [3] | 0.299 | 0.629 | 0.282 | 0.063 | 0.8 |
| *Melogale personata* [3] | 0.016 | -0.230 | 0.028 | -0.039 | 1.9 |
| *Mephitis mephitis* [2,3] | 0.048 | 0.154 | 0.180 | 0.008 | 1.9 |
| *Mustela erminea* [3] | 0.159 | 0.221 | 0.217 | 0.036 | 0.2 |
| *Mustela frenata* [3] | 0.000 | -0.009 | 0.004 | 0.005 | 0.2 |
| *Mustela nigripes* [3] | 0.001 | -0.016 | 0.027 | 0.016 | 0.9 |
| *Mustela nivalis* [3] | 0.178 | -0.244 | 0.171 | -0.025 | 0.1 |
| *Mustela putorius* [3] | 0.004 | 0.076 | 0.007 | 0.008 | 1.0 |
| *Mustela sibirica* [3] | 0.007 | 0.052 | 0.041 | 0.015 | 0.5 |
| *Mustela vison* [3] | 0.075 | 0.208 | 0.000 | -0.001 | 1.0 |
| *Nasua narica* [3] | 0.078 | -0.373 | 0.204 | -0.039 | 4.0 |
| *Paguma larvata* [3] | 0.604 | -0.596 | 0.566 | -0.069 | 2.8 |
| *Panthera leo* [1] | na | na | 0.017 | 0.030 | 157.8 |
| *Panthera pardus* [1,3] | 0.017 | 0.302 | 0.003 | -0.012 | 36.7 |
| *Panthera tigris* [3] | 0.086 | 0.653 | 0.003 | -0.009 | 157.0 |
| *Paradoxurus hermaphroditus* [3] | 0.038 | 0.186 | 0.002 | -0.003 | 2.3 |
| *Potos flavus* [3] | 0.063 | 0.230 | 0.041 | 0.015 | 3.0 |
| *Procyon cancrivorus* [3] | 0.052 | 0.200 | 0.008 | 0.010 | 5.0 |
| *Procyon lotor* [3] | 0.004 | 0.029 | 0.010 | -0.005 | 6.9 |
| *Pseudalopex culpaeus* [3] | 0.168 | 0.187 | 0.039 | -0.011 | 9.6 |

| | | | | | |
|---|---|---|---|---|---|
| *Ursus arctos*[3] | 0.081 | 1.528 | 0.216 | 0.094 | 186.5 |
| *Viverra zibetha*[3] | 0.012 | 0.071 | 0.054 | -0.021 | 8.2 |
| *Viverricula indica*[3] | 0.060 | 0.147 | 0.013 | -0.007 | 2.2 |
| *Vormela peregusna*[3] | 0.011 | 0.061 | 0.010 | 0.008 | 0.3 |
| *Vulpes chama*[1] | na | na | 0.131 | 0.032 | 3.1 |
| *Vulpes rueppellii*[3] | 0.057 | -0.188 | 0.005 | -0.009 | 1.9 |
| *Vulpes velox*[3] | 0.130 | 0.279 | 0.336 | 0.057 | 2.4 |
| *Vulpes vulpes*[3] | 0.383 | 0.477 | 0.478 | 0.063 | 5.2 |

[1]Klein 1986, [2]Koch 1986, [3]this study.

| Range size (million km$^2$) | Minimum latitude | Maximum latitude | Latitude range | Latitude range (total) | Mean winter temperature ($^o$C) | Rainfall range (mm) | NPP range | Habitat diversity |
|---|---|---|---|---|---|---|---|---|
| 31.5 | -35 | 40 | 40 | 75 | 4.4 | 800 | 826 | 0.66 |
| 12.3 | 51 | 80 | 29 | 29 | -34.5 | 400 | 278 | 0.45 |
| 18.0 | -35 | 15 | 35 | 50 | 15.6 | 1500 | 591 | 0.60 |
| 0.8 | 2 | 27 | 25 | 25 | 4.5 | 3300 | 95 | 0.61 |
| 13.4 | -35 | 15 | 35 | 50 | 15.6 | 1750 | 735 | 0.52 |
| 4.0 | 12 | 40 | 28 | 28 | -7.0 | 700 | 253 | 0.75 |
| 33.7 | -5 | 45 | 45 | 50 | -1.1 | 975 | 402 | 0.69 |
| 28.4 | 5 | 71 | 66 | 66 | -34.5 | 3750 | 608 | 0.99 |
| 127.0 | 10 | 85 | 75 | 75 | -34.5 | 1975 | 650 | 0.91 |
| 4.4 | -35 | 15 | 35 | 50 | 15.6 | 1400 | 558 | 0.75 |
| 14.2 | -35 | 20 | 35 | 55 | 15.6 | 900 | 558 | 0.63 |
| 15.8 | -9 | 50 | 50 | 59 | -23.5 | 3700 | 862 | 0.98 |
| 18.2 | -30 | 20 | 30 | 50 | 10.0 | 3750 | 658 | 0.56 |
| 19.5 | 0 | 50 | 50 | 50 | -28.9 | 3500 | 1018 | 0.90 |
| 22.8 | 45 | 70 | 25 | 25 | -34.5 | 1750 | 145 | 0.85 |
| 19.0 | -35 | 45 | 45 | 80 | -1.1 | 475 | 305 | 0.70 |
| 11.8 | 10 | 50 | 40 | 40 | -1.1 | 2200 | 700 | 0.81 |
| 49.4 | -51 | 60 | 60 | 111 | -34.5 | 3900 | 950 | 0.95 |
| 12.5 | -30 | 35 | 35 | 65 | 4.4 | 4500 | 250 | 0.71 |
| 18.5 | 20 | 60 | 40 | 40 | -34.5 | 1700 | 497 | 0.90 |
| 8.2 | -30 | 15 | 30 | 45 | 15.6 | 900 | 558 | 0.46 |
| 35.3 | -35 | 55 | 55 | 90 | -6.7 | 900 | 640 | 0.79 |
| 14.8 | -35 | 17 | 35 | 52 | 4.5 | 1750 | 464 | 0.60 |
| 1.0 | -35 | -18 | 17 | 17 | 4.5 | 900 | 180 | 0.61 |
| 20.5 | -25 | 0 | 25 | 25 | 21.0 | 3500 | 383 | 0.66 |
| 14.0 | -31 | 47 | 47 | 78 | 4.4 | 1000 | 300 | 0.74 |

| | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| 20.2 | -35 | 20 | 35 | 55 | 15.6 | 900 | 365 | 0.62 |
| 17.5 | 25 | 65 | 40 | 40 | -34.5 | 750 | 712 | 0.89 |
| 13.4 | -35 | 20 | 35 | 55 | 4.5 | 1700 | 500 | 0.62 |
| 65.0 | 6 | 65 | 59 | 59 | -34.5 | 1600 | 726 | 0.98 |
| 20.9 | -30 | 20 | 30 | 50 | 21.1 | 900 | 474 | 0.62 |
| 12.3 | 35 | 68 | 33 | 33 | -34.5 | 1750 | 430 | 0.80 |
| 8.3 | 0 | 50 | 50 | 50 | 4.4 | 3500 | 554 | 0.62 |
| 14.6 | 28 | 68 | 40 | 40 | -34.5 | 1250 | 47 | 0.89 |
| 19.5 | 40 | 70 | 30 | 30 | -28.9 | 1000 | 441 | 0.78 |
| 3.8 | 30 | 60 | 30 | 30 | -17.8 | 1500 | 58 | 0.82 |
| 47.4 | 20 | 68 | 48 | 48 | -34.5 | 1100 | 547 | 0.92 |
| 36.9 | -35 | 32 | 35 | 67 | 10.0 | 1475 | 567 | 0.74 |
| 4.0 | 18 | 37 | 19 | 19 | -1.0 | 3500 | 70 | 0.50 |
| 3.1 | 10 | 30 | 20 | 20 | 15.6 | 2000 | 203 | 0.66 |
| 7.1 | 25 | 60 | 35 | 35 | -17.8 | 1300 | 541 | 0.92 |
| 111.5 | 35 | 80 | 45 | 45 | -34.5 | 1500 | 484 | 0.77 |
| 19.6 | -18 | 55 | 55 | 73 | -18.0 | 3800 | 804 | 0.97 |
| 9.7 | 31 | 52 | 21 | 21 | -12.2 | 800 | 333 | 0.64 |
| 104.2 | 30 | 75 | 45 | 45 | -28.9 | 1400 | 460 | 0.86 |
| 26.6 | 35 | 65 | 30 | 30 | -12.2 | 1000 | 185 | 0.90 |
| 28.6 | 6 | 60 | 54 | 54 | -34.5 | 1500 | 769 | 0.68 |
| 13.0 | 25 | 70 | 45 | 45 | -28.9 | 1800 | 625 | 0.91 |
| 2.3 | 7 | 30 | 23 | 23 | 4.4 | 3900 | 916 | 0.71 |
| 7.8 | -5 | 35 | 35 | 40 | -1.0 | 3500 | 654 | 0.69 |
| 37.2 | -35 | 35 | 35 | 70 | 4.4 | 1400 | 510 | 0.66 |
| 35.6 | -35 | 50 | 50 | 85 | -6.7 | 1475 | 925 | 0.83 |
| 26.5 | -9 | 50 | 50 | 59 | -34.5 | 3500 | 674 | 0.99 |
| 7.7 | -10 | 33 | 33 | 43 | 10.0 | 3500 | 835 | 0.77 |
| 14.7 | -17 | 20 | 20 | 37 | 10.0 | 2000 | 328 | 0.41 |
| 16.6 | -25 | 10 | 25 | 35 | 15.5 | 1000 | 414 | 0.58 |
| 13.6 | 8 | 60 | 52 | 52 | -6.7 | 3800 | 800 | 0.88 |
| 3.9 | -55 | 0 | 55 | 55 | -1.1 | 1900 | 806 | 0.97 |

| | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| 106.9 | 30 | 70 | 40 | 40 | -12.2 | 1500 | 200 | 0.92 |
| 5.1 | 0 | 36 | 36 | 36 | -1.1 | 2000 | 396 | 0.63 |
| 8.9 | -5 | 35 | 35 | 40 | -1.1 | 1500 | 776 | 0.73 |
| 8.6 | 27 | 45 | 18 | 18 | -17.8 | 500 | 300 | 0.70 |
| 2.6 | -35 | -15 | 20 | 20 | 15.6 | 200 | 446 | 0.63 |
| 18.2 | 10 | 35 | 25 | 25 | -1.0 | 250 | 255 | 0.26 |
| 0.8 | 25 | 50 | 25 | 25 | -7.0 | 600 | 217 | 0.74 |
| 129.1 | 10 | 72 | 62 | 62 | -34.5 | 1475 | 742 | 0.93 |