ORIGINAL ARTICLE

Body size clines in the European badger and the abundant centre hypothesis

Emilio Virgós[1]*, Rafal Kowalczyk[2], Atalya Trua[3], Anna de Marinis[4], Julián G. Mangas[1], Jose M. Barea-Azcón[5] and Eli Geffen[3]

[1]Department of Biology and Geology, ESCET, Universidad Rey Juan Carlos, C/Tulipán s/n, E-28933 Móstoles, Madrid, Spain, [2]Mammal Research Institute, Polish Academy of Sciences, 17-230 Białowieża, Poland, [3]Department of Zoology, Tel Aviv University, Tel Aviv 69978, Israel, [4]Istituto Nazionale Fauna Selvatica, Via Ca' Fornacetta 9, I-40064 Ozzano dell'Emilia, Italy, [5]C/ Ángel Casas, Urbanización Cortijo Bartodano, Jun (Granada), E-18213, Spain

ABSTRACT

Aim To test the abundant centre hypothesis by analysing the physical and climatic factors that influence body size variation in the European badger (*Meles meles*).

Location Data were compiled from 35 locations across Europe.

Methods We used body mass, body length and condylo-basal length (CBL) as surrogates of size. We also compiled data on latitude, several climatic variables, habitat type and site position relative to the range edge. We collapsed all continuous climatic variables into independent vectors using principal components analysis (PCA), and used a general linear model to explain the morphometric variation in badger populations across the species' range.

Results Body mass and body length were nonlinearly and significantly related to latitude. In contrast, CBL was linearly related to latitude. Body mass changed nonlinearly along the temperature (PC1) gradient, with the highest values observed at mid-range. Furthermore, body mass, body length and CBL differed significantly among habitats, with badgers showing larger size in temperate habitats and core areas relative to peripheral zones.

Main conclusions Our analysis supports the nonlinear pattern predicted by the abundant centre hypothesis only for body mass and body length. These results imply that individuals are largest and heaviest at the centre of the climatic range of badger distribution. Variation of CBL with latitude follows a linear trend, consistent with Bergmann's rule. Our results provide mixed support for the abundant centre hypothesis, and suggest food availability/quality to be the main mechanism underlying body size clines in this species.

Keywords

Bergmann's rule, Europe, macroecology, *Meles meles*, niche, range position, resource availability, seasonality.

*Correspondence: Emilio Virgós, Department of Biology and Geology, ESCET, Universidad Rey Juan Carlos, C/Tulipán s/n E-28933 Móstoles, Madrid, Spain.
E-mail: emilio.virgos@urjc.es

INTRODUCTION

Body size has been a prominent property in research into the underlying mechanisms and patterns of geographic variation in phenotype, and is linked to other fitness-related traits such as survival, age at maturity and breeding performance (Peters, 1983; Calder, 1984; Clutton-Brock, 1991; Gaillard *et al.*, 1992). Bergmann's rule is a long-established pattern, which suggests that homeothermic animals occupying cooler environments tend to have a larger body size than their close relatives inhabiting warmer climes (e.g. Bergmann, 1847; Mayr, 1956;

Blackburn *et al.*, 1999). The support for this trend is strong for mammals (e.g. Mayr, 1956; Ashton *et al.*, 2000; Meiri & Dayan, 2003) but less so for birds (Zink & Remsen, 1986; Meiri & Dayan, 2003). Moreover, several concerns have been raised regarding the validity of Bergmann's rule, especially from the physiological perspective (McNab, 1971; Geist, 1987; Dayan *et al.*, 1991). In this study we refer to Bergmann's rule in respect of intra-specific variation in body size with latitude.

Several mechanisms have been proposed to explain the above pattern. Large size should be advantageous in cold environments because it decreases the surface/mass ratio,

allowing better heat conservation, whereas small size allows more efficient heat dissipation in warm environments (Mayr, 1956). In numerous studies, Bergmann's rule has been tested by regressing body size against latitude, assuming a direct relationship between this variable and temperature (Ashton et al., 2000). However, ambient temperature may not be related solely to latitude, but also varies longitudinally and with elevation. Alternatively, body size may be a response to changes in the primary productivity of a particular environment, affecting resource availability and renewal (Rosenzweig, 1968a,b; Geist, 1987). The productivity hypothesis predicts a significant positive correlation between body size and net primary productivity (NPP) or other climatic variables related to precipitation (e.g. annual rainfall). Examination of these two alternative explanations (i.e. Bergmann's rule and the productivity hypothesis) is possible because temperature and NPP are often statistically independent (Rosenzweig, 1968a).

In addition, several studies have suggested that body size and other life-history traits respond to seasonal variability (Calder, 1974; Boyce, 1978; Lindstedt & Boyce, 1985; Ferguson & McLoughlin, 2000; McLoughlin et al., 2000) and that larger body size might be adaptive for longer periods of food shortage, which are typical in seasonal environments (the starvation resistance hypothesis; Calder, 1974; Boyce, 1978). Body size may also depend on the level of environmental variability (e.g. Carlson et al., 2008). Large body size allows a lower weight-specific metabolism and higher absolute levels of fat reserves (Lindstedt & Boyce, 1985; Millar & Hickling, 1990). These traits enable large animals to survive during periods of food scarcity (Boyce, 1978). Although this hypothesis is appealing, no supporting evidence for it has been found in carnivores (Meiri et al., 2004).

Nevertheless, a large body of evidence has indicated that changes in body size may be related to the variation in quality, distribution and quantity of food, both spatially and temporally (e.g. the resource availability hypothesis, Blackburn et al., 1999; see also Rosenzweig, 1968a; McNab, 1971; Yom-Tov & Nix, 1986; Yom-Tov & Geffen, 2006; Yom-Tov et al., 2007).

The next development in the attempt to model intraspecific size variation was the abundant centre hypothesis (ACH), which proposed that species are more abundant and show higher fitness in the centre of their distribution range than at the periphery (Brown, 1984; Hoffman & Blows, 1994; Brown et al., 1996; but see Sagarin & Gaines, 2002). The rationale behind the ACH is that species track the distribution and abundance of key resources, which are more abundant and/or of higher quality at the centre of a range (Hengeveld & Haeck, 1982; Brown, 1984; Brown et al., 1996; Pérez-Trís et al., 2000). Individuals at the core may attain a larger size than those at the periphery because during the breeding period, when resources are abundant, the young accumulate more energy and can allocate more of it to growth. In contrast, animals at the periphery have fewer resources, even at the peak of breeding, and the young in these regions have access to less food, which may result in restricted growth and smaller adult size.

It has been argued that higher population densities at the core relative to the periphery may lead to greater intraspecific competition for resources and eventually to selection for smaller body size (e.g. Fowler, 1987; Clutton-Brock & Albon, 1989; Macdonald et al., 2002). However, according to the proponents of the ACH, core areas harbour more resources than do peripheral areas. Consequently, after taking differences in population density into account, body size may either remain constant across the range or increase if resources at the core are still higher than at the periphery. Surprisingly, the relationship between body size and the ACH has not been robustly tested (Pérez-Trís et al., 2000; Hallas et al., 2002; Fukui et al., 2005). Only recently, Meiri et al. (2009) showed that the relationship between body size variation and position within the range (i.e. niche optimality) is case-specific, and called for more research into this topic.

We selected the facultatively social European badger (Meles meles Linnaeus, 1758; Kruuk, 1989; Woodroffe & Macdonald, 1993; Johnson et al., 2002) as a test case for the above hypotheses because it demonstrates a large variation in body size across a wide range (Neal & Cheeseman, 1996). Badgers feed on a diverse array of resources, from earthworms in temperate forests to insects and fruits in Mediterranean habitats (Roper, 1994; Goszczyński et al., 2000). The species shows slight sexual dimorphism, which may alter with ecological conditions (Johnson & Macdonald, 2001; Abramov & Puzachenko, 2005). Badgers maintain exclusive pair or group territories (Kruuk, 1989; Woodroffe & Macdonald, 1993). Territory size, group size and badger density appear to be largely determined by the ecological conditions. While badger territories can reach 1800 ha in Poland (Kowalczyk et al., 2003b), they may be as small as 50 ha in wooded pastureland in the United Kingdom (e.g. Johnson et al., 2001). Similar trends have been found for population density and social grouping (Johnson et al., 2002; Kowalczyk et al., 2003b). European badger females compete for reproductive success (Woodroffe & Macdonald, 1995; Dugdale et al., 2010). In this system, larger females breed, have more access to exclusive resources and are less subject to reproductive suppression compared with smaller females. If resources permit, selection in this species should thus favour large individuals, which are the more successful breeders. Furthermore, previous studies have shown a positive fit between body size variation and latitude in badgers (Meiri & Dayan, 2003; Meiri et al., 2004), although Meiri et al. (2009) found some support for the ACH. However, the above studies only considered latitude or position in the range, which are not biologically interpretable. Here, we report the results of a study that includes climatic and biological variables in an attempt to clarify the factors and mechanisms influencing body size variation across the range of this well-studied species. We tested the hypothesis that body size in the European badger should be higher at the centre of the range relative to the periphery, because of higher resource availability.

MATERIALS AND METHODS

Data collection and recording of predictors

We used three common measures as surrogates of badger size: body mass, body length and condylo-basal length (CBL). Because badger body mass can fluctuate between seasons (Kruuk & Parish, 1983; Neal & Cheeseman, 1996), we used both spring and winter body masses as response variables. Although body mass is often used to estimate the sizes of species, it may not be the best means of estimating structural size owing to its fluctuations (Piersma & Davidson, 1991; Schulte-Hostedde *et al.*, 2005). Body mass reflects concomitantly seasonal nutritional constraints and the genetic component of size (Piersma & Davidson, 1991; Dobson, 1992). Thus, CBL and other skeletal traits are considered better correlates of structural size (Atchley *et al.*, 1981; Gittleman & Van Valkenburgh, 1997; Dayan *et al.*, 2002; Meiri *et al.*, 2005; see Lynch *et al.*, 1993 for badgers), as they do not appear to be affected by body condition (Gittleman & Van Valkenburgh, 1997).

We used a large sample of body and skull data from 35 locations across the range of the European badger (Fig. 1 and Appendix S1 in the Supporting Information). The global population of *M. meles* has been recently partitioned into three subpopulations, considered by some researchers as separate species (Abramov & Puzachenko, 2005; Marmi *et al.*, 2006). Owing to this status controversy, we analysed only the European populations (west of 40° E longitude). Only adult badgers were measured. Measurement precision was to within 50 g for body mass, 0.1 mm for CBL and 0.5 cm for body length. Sex was recorded when known. We used latitude as a predictor because it is the key predictor for Bergmann's rule,
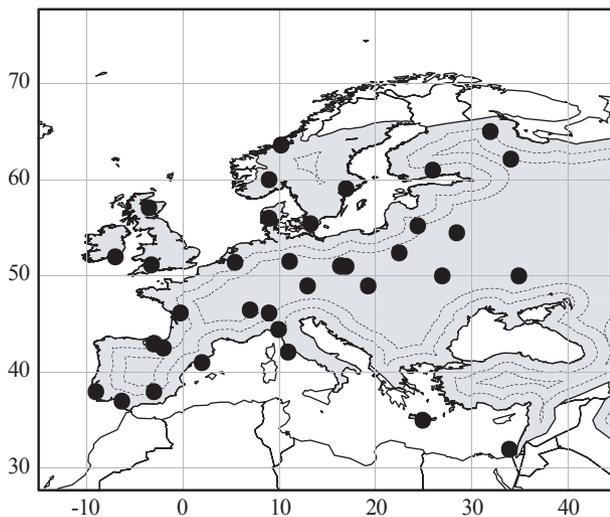

Figure 1 Distribution map (grey area; plotted onto the Fuller Dymaxion projection following Meiri *et al.*, 2009) for European badgers (*Meles meles*). The dashed lines indicate 100 and 200 km contours from the range boundary. The filled circles designate populations sampled in this study. Axis labels indicate longitude and latitude (in degrees).

despite having no clear biological meaning (Hawkins & Diniz-Filho, 2004). In addition to latitude, we compiled the following key climatic variables: average annual, winter (January) and summer (July) temperatures, annual rainfall, and coefficient of variation (CV) for average temperature and rainfall. We obtained these variables from WorldClimate web (http://www.worldclimate.com/, accessed in May and June 2008). Data were recorded from weather stations close to our locations by using time series of different length (10–30 years). We calculated NPP from monthly values, using the following expression (Lieth, 1976; Ferguson & McLoughlin, 2000)

$$NPP = 3000(1 - e^{-0.0009695(AET-20)}),$$

where AET is the actual evapotranspiration value at each location. AET values were obtained from the Phytosociological Research Center [Rivas-Martínez & Rivas y Sáenz, 2007; http://www.globalbioclimatics.org/; based on Thornthwaite & Mather's (1957) formula]. Data for each location were averaged from a time series (period variable depending on location: 13–50 years). We recorded habitat type as boreal, temperate or Mediterranean, based on a biome classification system for world ecosystems (USDA, 1999). Finally, we classified localities as either core or peripheral areas following the distribution map in Meiri *et al.* (2009). Because the distinction between core and periphery is subjective, we selected two cut-off values: locations situated ≤ 100 or 200 km away from the edge of the distribution were classified as peripheral, and those located further from the edge (> 100 or 200 km) were defined as core positions.

Finally, in order to explain morphological differences on the core–edge gradient we re-examined the analysis provided by Goszczyński *et al.* (2000; see Appendix S2) on diet shift as a function of latitude by expanding their data set from 17 to 29 locations. These locations span the entire latitudinal range occupied by the European badger, and all studies in this data set were conducted in Europe or western Asia (see Appendix S2). We used only data expressed as volume or biomass consumed. Volumes of garbage and unidentified remains were excluded from the analysis.

Statistical analyses

To eliminate any distortion due to the large variation in sample size between populations, we used the population mean for each variable in all analyses. Each population was thereby given an equal weight regardless of sample size.

In order to avoid multicollinearity, we collapsed all continuous climatic variables into independent vectors using principal components analysis (PCA). We retained the factors with an eigenvalue ≥ 1. The retained components were then used as independent variables in a general linear model (GLM; distribution = normal, and link function = identity) aimed at explaining the morphometric variation across the species' range. Finally, to accommodate the possibility of parabolic relationships between body size variables and latitude or the climatic variables, we fitted these data to the above model

using a quadratic function. To assess whether a specific set of variables were associated nonlinearly, we compared the fit between linear and nonlinear models using the Akaike information criterion (AIC). Correction of AIC values for small sample size (AIC_c) was implemented when $n/K < 40$, and ΔAIC_c and Akaike weights were used for selecting the model with best fit (Johnson & Omland, 2004). This approach weights all the possible subsets (i.e. models) by the amount of variance explained and model complexity (i.e. the number of model parameters, K). Models with ΔAIC_c values of 0–2 are similarly supported by the data, whereas those with $\Delta AIC_c > 2$ are less supported (Johnson & Omland, 2004). All statistical procedures were calculated using STATISTICA v. 8 (StatSoft Inc., Tulsa, OK, USA).

Niche breadth for each population was calculated using Levins' (1968) measure.

RESULTS

Body mass was nonlinearly and significantly related to latitude (quadratic function; Table 1, Fig. 2a). The best model showed a significant effect of the quadratic latitude term on body mass (GLM; $\chi^2_1 = 17.0$, $P < 0.001$; Table 1). The quadratic term for

Table 1 Model selection, using Akaike's information criterion corrected for small sample size (AIC_c), for the effects of latitude (Lat) and sex on body mass, body length and condylo-basal length in the European badger (*Meles meles*). Both linear and quadratic models were considered. Lat^2 stands for the quadratic term. Models are sorted by ΔAIC_c. The number of populations is given in parentheses.

Model	R^2	AIC_c	ΔAIC_c	AIC_c weight
Body mass (18)				
Lat^2, Sex	0.437	121.8		0.536
Lat, Lat^2, Sex	0.460	123.0	1.190	0.295
Lat^2	0.340	125.0	3.173	0.110
Lat, Lat^2	0.364	126.2	4.421	0.059
Sex	0.097	136.3	14.490	0.000
Lat, Sex	0.112	138.2	16.430	0.000
Lat	0.015	139.4	17.613	0.000
Body length (12)				
Lat^2	0.214	265.6		0.341
Lat^2, Sex	0.301	265.7	0.079	0.328
Lat, Lat^2	0.242	267.7	2.027	0.124
Lat, Lat^2, Sex	0.329	268.0	2.318	0.107
Sex	0.087	269.2	3.570	0.057
Lat	0.020	270.9	5.275	0.024
Lat, Sex	0.108	271.6	5.939	0.018
Condylo-basal length (13)				
Lat, Lat^2, Sex	0.628	137.6		0.766
Lat, Sex	0.524	140.9	3.320	0.146
Lat, Lat^2	0.493	142.6	4.957	0.064
Lat	0.389	144.6	6.999	0.023
Lat^2, Sex	0.293	151.2	13.609	0.001
Lat^2	0.158	152.9	15.338	0.000
Sex	0.135	153.6	16.048	0.000

latitude alone accounted for *c.* 34% of the variance in body mass (Table 1). The effect of sex on body mass (mean ± SD = 9.5 ± 1.6 and 8.6 ± 1.4 kg for males and females, respectively) was also significant for that model (GLM; $\chi^2_1 = 5.7$, $P = 0.017$; Table 1). Body mass was significantly higher during winter relative to spring (Table 2, Fig. 2b). Consequently, we averaged the seasonal body mass values and used the mean body mass in the subsequent analyses.

Body length also showed a quadratic relationship with latitude (Fig. 3). The best model, selected by AIC_c, showed a significant effect of the quadratic latitude term on body length (GLM; $\chi^2_1 = 5.8$, $P = 0.016$; Table 1). The quadratic term for
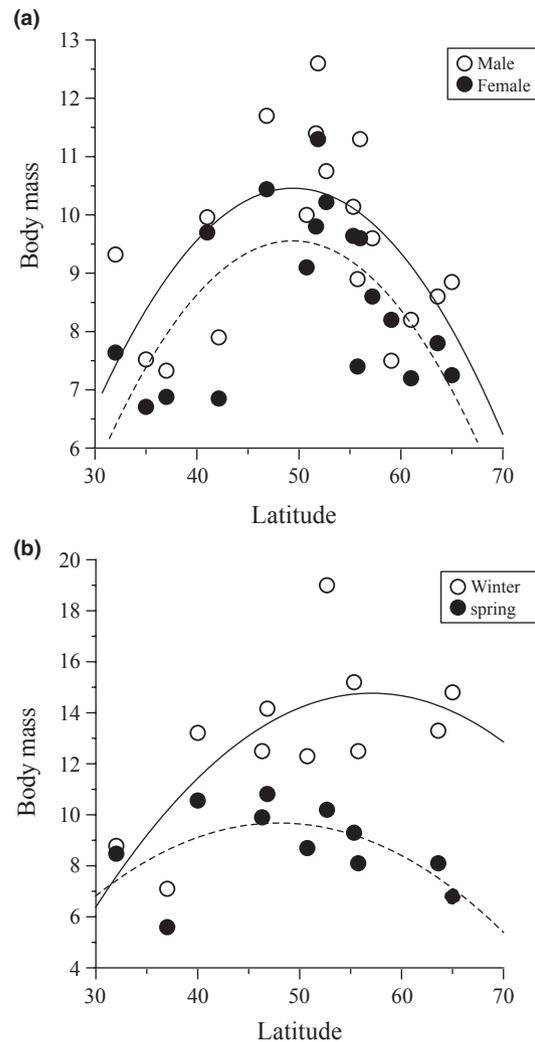

Figure 2 Variation in body mass of the European badger (*Meles meles*). (a) Body mass (kg) as a function of latitude in males (empty circles; $n = 18$) and females (filled circles; $n = 18$). Quadratic fits for the male and female data are indicated by solid and dashed lines, respectively. (b) Body mass as a function of latitude in winter (empty circles; $n = 11$) and spring (filled circles; $n = 11$). Quadratic fits for the winter and spring data are indicated by solid and dashed lines, respectively.

Table 2 Effect (using a general linear model; likelihood ratio χ^2) of latitude (Lat) and season on body mass in the European badger (*Meles meles*). Lat^2 stands for the quadratic term. The number of populations is given in parentheses.

Effects	d.f.	χ^2	*P*-value
Body mass (22)			
Lat	1	3.6	0.058
Lat^2	1	7.1	0.008
Season	1	14.2	< 0.001
Lat × Season	1	6.5	0.011
Lat^2 × Season	1	0.1	0.711

Season: coded as spring or winter body masses.

Figure 4 Contour plot for body mass of the European badger (*Meles meles*). PC1 and PC2 are principal components comprising the latitude/temperature and rainfall/net primary productivity (NPP) variables, respectively. Darker fills correspond to higher means of body mass. The following sites are indicated: Br, Britain; Dn, Denmark; Fi, Finland; Fr, France; Ge, Germany; Gr, Greece; Ir, Ireland; Is, Israel; It, Italy; Li, Lithuania; Ne, The Netherlands; No, Norway; Po, Poland; Pr, Portugal; Ru, Russia; Sp, Spain; Sw, Sweden; Sz, Switzerland. The contour plot was created using JMP v. 8.0 (SAS Institute Inc., Cary, NC, USA).

PCA collapsed latitude and the continuous climatic variables into two factors (PC1: eigenvalue = 3.2 and 45.3% of variance explained; PC2: eigenvalue = 2.3 and 33.0% of variance explained). All other factors extracted had eigenvalues considerably smaller than 1. The highest loadings for PC1 were latitude (−0.90), average winter temperature (0.90) and temperature CV (0.93), and for PC2 they were mean annual rainfall (0.82) and NPP (0.85). In other words, PC1 compounded the information on temperature and PC2 compounded that on rainfall and productivity. The PCA showed that, for our dataset, latitude is a proxy for variables associated with temperature.

A contour plot of body mass as a function of PC1 and PC2 showed that the heaviest individuals were found in populations located mid-range in the climatic envelope characterizing the species' distribution (Fig. 4). These populations were often located in core areas. Populations comprising the lightest individuals, by contrast, were often located at the periphery (Fig. 4). The quadratic model was identified by ΔAIC_c as the most probable fit for the effects of climatic components on body mass (Table 3). This model, composed of a single-effect PC1^2 (proxy for latitude and temperature, model coefficient = −0.23, $\chi^2_1 = 12.7$, $P < 0.001$), accounted for *c.* 43% of the variance in body mass (Table 3). A linear model was the most probable model for the effect of climatic components on body length, with PC2 being the only significant effect (model coefficient = 21.4, $\chi^2_1 = 4.2$, $P = 0.04$). The second most probable model was insignificant ($P = 0.126$; Table 3). The
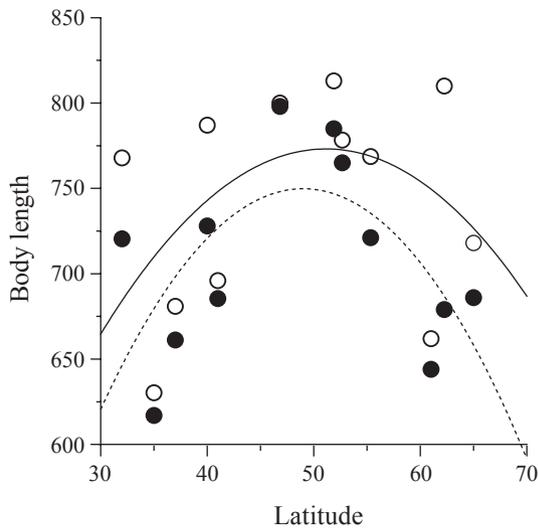

Figure 3 Body length (cm) as a function of latitude in males (empty circles; $n = 12$) and females (filled circles; $n = 12$) of the European badger (*Meles meles*). Quadratic fits for the male and female data are indicated by solid and dashed lines, respectively.

latitude alone accounted for 21.3% of the variance in body length. Overall, the body length of males was greater than that of females (mean ± SD = 73.6 ± 5.5 and 69.9 ± 5.2 cm for males and females, respectively) but this sexual difference was not significant in the second best model (GLM; $\chi^2_1 = 2.8$, $P = 0.093$) or in the other models we tested ($P > 0.05$; Table 1). In contrast, the best AIC model showed that CBL increased with latitude largely in a linear fashion (GLM; linear latitude term: $\chi^2_1 = 16.7$, $P < 0.001$; quadratic latitude term: $\chi^2_1 = 6.4$, $P = 0.011$; Table 1). Further, the linear latitude term alone accounted for 38.9% of the variance, while the quadratic term for latitude explained only 15.8% (Table 1). CBL of males was significantly greater than that of females (mean ± SD = 12.8 ± 0.5 and 12.4 ± 0.6 cm for males and females, respectively; $\chi^2_1 = 8.1$, $P = 0.004$). Interactions with sex were not included in our models because all were insignificant ($P > 0.28$ in all tests).
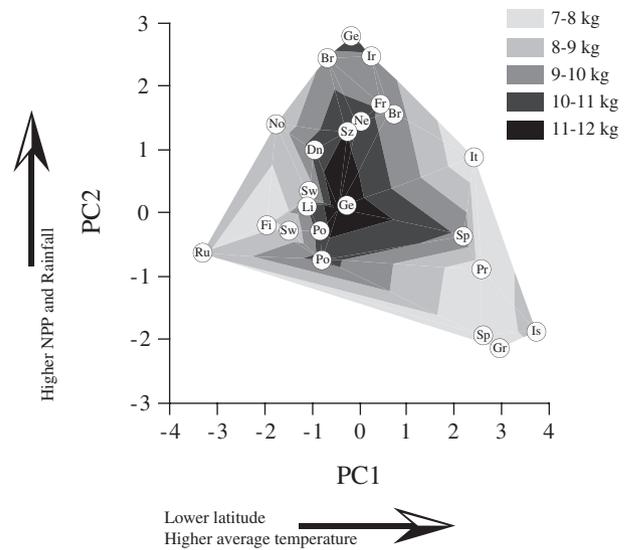
Table 3 Model selection, using Akaike's information criterion corrected for small sample size (AIC$_c$), for the effects of climatic principal components analysis (PCA) vectors (PC1, PC2) and sex on body mass, body length and condylo-basal length in the European badger (*Meles meles*). Both linear and quadratic models were considered. PC1^2 and PC2^2 stand for the quadratic terms. Models are sorted by ΔAIC$_c$. The number of populations is given in parentheses.

Model	R^2	AIC$_c$	ΔAIC$_c$	AIC$_c$ weight
Body mass (23)				
PC1^2	0.426	78.0		0.510
PC1^2, PC2	0.431	80.8	2.758	0.128
PC1, PC1^2	0.429	80.9	2.826	0.124
PC1^2, PC2^2	0.427	81.0	2.911	0.119
PC2	0.258	84.0	5.920	0.026
PC1, PC1^2, PC2^2	0.434	84.0	5.948	0.026
PC1, PC1^2, PC2	0.433	84.0	5.981	0.026
PC1^2, PC2, PC2^2	0.432	84.1	6.048	0.025
PC2, PC2^2	0.271	86.5	8.472	0.007
PC1, PC1^2, PC2, PC2^2	0.436	87.6	9.598	0.004
Body length (12)				
PC2	0.297	135.0		0.493
PC1^2	0.177	136.9	1.891	0.192
PC1	0.037	138.8	3.776	0.075
PC2^2	0.002	139.2	4.202	0.060
PC2, PC2^2	0.313	139.4	4.447	0.053
PC1, PC2	0.305	139.6	4.585	0.050
PC1^2, PC2	0.301	139.7	4.655	0.048
PC1, PC1^2	0.193	141.4	6.373	0.020
PC1, PC2, PC2^2	0.356	144.9	9.943	0.003
PC1^2, PC2, PC2^2	0.314	145.7	10.709	0.002
Condylo-basal length (25)				
PC1, PC1^2	0.544	139.0		0.520
PC1, PC1^2, PC2^2	0.565	140.9	1.967	0.194
PC1, PC1^2, PC2	0.544	142.1	3.134	0.108
PC1	0.391	143.3	4.351	0.059
PC1, PC1^2, PC2, PC2^2	0.565	144.4	5.473	0.034
PC1, PC2^2	0.426	144.7	5.720	0.030
PC1, PC2	0.421	144.9	5.951	0.027
PC1, PC2, PC2^2	0.464	146.1	7.168	0.014
PC1^2, PC2^2	0.357	147.5	8.559	0.007
PC1^2	0.209	149.8	10.874	0.002

best model for CBL was composed of linear and quadratic terms (Table 3). CBL was negatively associated with both PC1 terms, the proxy for latitude and temperature (linear: PC1, model coefficient = −1.65, $\chi^2_1 = 17.7$, $P < 0.001$; quadratic: PC1^2, model coefficient = −0.55, $\chi^2_1 = 7.2$, $P = 0.007$; Table 3). Both terms accounted for *c.* 54% of the variance in CBL, whereas PC1 alone explained *c.* 39% (Table 3). To evaluate the contribution of sex, we added this term to the best model selected. In none of the morphological variables examined was the two-way interaction between linear and/or quadratic PC terms and sex significant ($P > 0.30$ in all comparisons).

Finally, we examined whether morphology differs significantly among habitats and between core and peripheral localities. Body mass significantly differed among habitats

($F_{(2,20)} = 16.8$, $P < 0.001$). Badgers in the temperate zone were significantly heavier (mean ± SD: 10.2 ± 1.0 kg) than individuals from the Mediterranean (7.8 ± 1.1 kg) or boreal (7.9 ± 0.2 kg) zones [Tukey's honestly significant difference (HSD) test, $P < 0.05$]. The sexes showed similar trends in body mass ($F_{(2,15)} = 10.9$, $P = 0.001$ and $F_{(2,15)} = 7.8$, $P = 0.005$ for males and females, respectively). Furthermore, body mass differed profoundly between core (11.1 ± 0.7 kg) and peripheral (8.7 ± 1.2 kg) locations ($F_{(1,21)} = 11.1$, $P = 0.003$ and $F_{(1,21)} = 18.7$, $P < 0.001$ for 100 and 200 km edge buffers, respectively). No interaction was detected between the core–edge factor and sex ($P > 0.9$ in both tests).

Body length and CBL were also significantly different among habitats ($F_{(2,11)} = 6.6$, $P = 0.013$ and $F_{(2,27)} = 8.8$, $P = 0.001$, respectively). For both variables, badgers in the temperate zone were longer than in the Mediterranean zone (Tukey's HSD, $P < 0.05$). The sexes showed similar trends in body length ($F_{(2,9)} = 4.2$, $P = 0.042$ and $F_{(2,9)} = 9.2$, $P = 0.007$ for males and females, respectively). However, only females showed a significant difference in CBL among habitats ($F_{(2,11)} = 0.8$, $P = 0.487$ and $F_{(2,10)} = 7.3$, $P = 0.011$ for males and females, respectively). Core individuals had a significantly greater body length (76.6 ± 3.3 cm) than those from the range periphery (69.0 ± 5.3 cm; $F_{(1,12)} = 10.6$, $P = 0.007$ and $F_{(1,12)} = 14.0$, $P = 0.003$ for 100 and 200 km edge buffers, respectively), and had a significantly larger CBL (129.6 ± 2.2 mm) relative to individuals at the edge (125.5 ± 5.3 mm; $F_{(1,28)} = 7.5$, $P = 0.011$ and $F_{(1,28)} = 10.4$, $P = 0.003$ for 100 and 200 km edge buffers, respectively). No interaction was detected between the core–edge factor and sex ($P > 0.5$ in both tests).

The volume of animal material in the badgers' diet was significantly and positively correlated with latitude (linear regression by permutations; slope = 1.20, $r^2 = 0.21$, $F_{(1,27)} = 7.1$, $P = 0.014$; Fig. 5). However, when considered separately, earthworm, insect and vertebrate volumes in the diet were not significantly associated with latitude ($F_{(1,27)} = 3.6$, $P = 0.067$; $F_{(1,27)} = 0.2$, $P = 0.689$ and $F_{(1,27)} = 0.4$, $P = 0.526$; respectively). The volume of vegetable material in the diet, complementing the animal portion, was negatively correlated with latitude (slope = −1.25, $r^2 = 0.22$, $F_{(1,27)} = 7.6$, $P = 0.010$; Fig. 5). Niche breadth, calculated from volumes of earthworms, insects, vertebrates and vegetation in the diet, was independent of latitude ($F_{(2,27)} = 0.8$, $P = 0.382$).

DISCUSSION

Our analysis of badger body mass and body length supports the pattern predicted by the ACH, and conflicts with the trend suggested by Bergmann's rule, while the pattern of variation in CBL with latitude supports the linear trend predicted by Bergmann's rule. The curvature of body mass data appears as a function of climatic variables (Fig. 4, Table 3). These results imply that European badger individuals are heaviest in the middle of their climate range. Furthermore, their mass decreases as a function of distance from the core of the
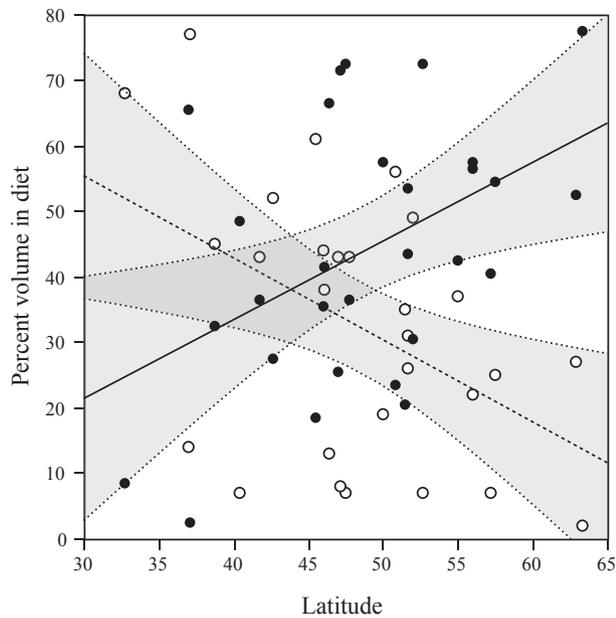
Figure 5 Relative volume (%) of animal (solid line) and vegetable (dashed line) matter in the diet of the European badger (*Meles meles*) as a function of latitude. Regression lines and their 95% confidence intervals (shaded regions) are indicated (*n* = 29; see Results for details). Filled circles represent animal matter data and open circles represent vegetable matter.

distribution. A nonlinear cline in mammalian body mass was first reported by Geist (1987), who noted that body mass in grey wolves (*Canis lupus*) is lowest at low and high latitudes, and highest in the mid-latitudinal range. Geist also showed that a positive correlation of body mass with latitude in reindeer (*Rangifer tarandus*) is only evident up to 60° N, reversing to a negative trend further north. His study provided one of the first papers to contest Bergmann's rule.

The distribution of body mass along a latitudinal cline may even be multimodal. For example, body mass of the leopard (*Panthera pardus*) is higher in central/southern Africa, India and central Asia and lowest in North Africa, the Arabian Peninsula and the Middle East (Mills & Harvey, 2001; Harrison & Bates, 1992). On a latitudinal cline, leopard body mass seems to be bimodal. The above example suggests that body mass variation in leopards across their distribution is probably regulated by prey size and availability (Raia & Meiri, 2006). In arid regions the density of ungulates, the principal prey of leopards, is clearly low, as a consequence of low productivity and scarcity of water. In these regions individuals encounter prey less often. Small individuals in xeric environments have an important advantage over larger ones, as they require lower daily energy expenditure for general maintenance (Hayward *et al.*, 2006). As ungulates in arid regions are also generally smaller, the smaller size of leopards in these regions may not impose limitations on prey type. The hypothesis behind this illustration (e.g. the resource availability hypothesis) is that abundance and availability of food resources are the key components influencing body mass and

size. The ACH extends the above principle and suggests that resources are more abundant or/and of higher quality at the centre of a species' range (Brown, 1984; Brown *et al.*, 1996).

How can we use the above ideas to explain the body mass variation observed in the European badger? In Europe and western Asia, where this species has been most studied, it is bounded in the north by the tundra (*c.* 60–70° N) and in the south by the arid lands of the Arabian and Irano-Turanian deserts (*c.* 30–45° N; Neal & Cheeseman, 1996). This elongated distribution is composed of three parallel ecozones: Mediterranean/Irano-Turanian, temperate and boreal. Our analysis of dietary shift along the latitudinal cline clearly indicates that further north badgers tend to have a more carnivorous diet (Fig. 5). This is also true for the contribution of earthworms to the diet. In contrast, southern populations have a diet rich in vegetable matter. In the mid-latitudinal range, 40–50° N, the badgers' diet is a mix of animal and vegetable products. Individuals at latitude 40° N have a diet of 40–60% and 35–55% animal and vegetable matter, respectively, while at latitude 50° N these proportions change to 55–65% and 25–40%, respectively. In contrast, animals at latitude 60° N have an almost entirely carnivorous diet (*c.* 75%). These shifts suggest that animals living at the core of their range have a greater dietary breadth (Fig. 5), which may also mean greater food security during lean times because there are more food types from which to select. Goszczyński *et al.* (2000) showed a parabolic association between dietary niche breadth and latitude, which suggests that animals at the core had more dietary diversity. Our analysis, which extends the study of Goszczyński *et al.* (2000), has failed to support such a trend. Consequently, the hypothesis of greater food security at the core due to greater dietary breadth is unsupported and insufficient to explain the curvilinear variation in body size of badgers.

Food abundance may have an important influence on body size. In southern areas, where productivity is low, overall food abundance for badgers is probably reduced throughout the year, and under such conditions selection would favour smaller individuals, which require less food in order to attain adulthood (Stearns, 1976; Lindstrom, 1999; Arnett & Gotelli, 1999). In northern populations food is abundant during spring and summer. However, when vertebrate prey numbers drop, badgers in northern populations have little else to substitute for a meal, which is why badgers in these regions have evolved the capacity to store extra fat (Kowalczyk *et al.*, 2003a). This finding fits the prediction of the starvation resistance hypothesis that larger individuals are expected in locations where food shortage may exist for long periods (Boyce, 1978). However, this prediction does not support our finding that individuals at the extreme northern edge of the distribution are lighter than those at the core (Fig. 2a).

Badger growth continues throughout the first year of life (Newman *et al.*, 2001). During this period energy is diverted towards growth in addition to maintenance. Much of the foraging in badgers involves digging. Northern populations face solid frozen ground during the winter, and southern

populations encounter hard dry soil during summer. When digging conditions are far from optimal, badgers may have to invest considerably more energy in foraging. Consequently, more energy may be diverted into maintenance (i.e. survival) and less into growth in edge populations, resulting in smaller size.

Core areas are expected to support higher population densities. Thus, body size and mass may decrease at the core as a consequence of increased competition for resources. Indeed, a reduction in body size with increasing density has been recorded in deer (Fowler, 1987; Clutton-Brock & Albon, 1989; Conradt *et al.*, 1999), and even in badgers (Woodroffe & Macdonald, 1995; Rogers *et al.*, 1997; Macdonald *et al.*, 2002). The negative effect of population density may only become apparent when it reaches high badger densities such as in southern Britain (e.g. Rogers *et al.*, 1997). In these high-density populations, culling led to a significant increase in body size (Tuyttens *et al.*, 2000). On the other hand, in Scotland, where densities are lower (Griffiths & Thomas, 1993), a positive correlation between improved food availability and badger body mass has been observed (Kruuk & Parish, 1985). However, we are unable to evaluate the role of population density on body size reliably, because most of the locations used in this study lack population density estimates.

The trend for CBL did not fit the nonlinear relationship observed for body mass and body length (Tables 1 & 3). CBL decreased with PC1 and increased with PC2. The linear increase in CBL with latitude may suggest that head size is associated with the more carnivorous diet in northern latitudes. Consumption of insects, earthworms or soft fruit does not require enlarged jaw muscles or larger teeth. In contrast, the handling of larger animal prey, crushing of bones and consumption of frozen carcasses by badgers in northern populations may have selected for large heads.

Lastly, our study has indicated that body mass and body length, but not CBL, are highest at the centre of the latitudinal range. These results imply that the ACH is only partly supported. The relatively mixed results obtained by Meiri *et al.* (2009) for different carnivore species indicate that the pattern we observed in badgers is far from universal, and tends to be species specific. Body size is a trait under evolutionary pressure from different selective forces, of which food is probably one of the most prominent. In many cases, relationships between food (or other niche components) and position in the range are not linear but rather multimodal (Brown *et al.*, 1996; Sagarin & Gaines, 2002). Because different selective forces can spatially and temporally influence the abundance and dispersion of resources across the range of a species (Ims, 1997; Angilletta & Dunham, 2003), additional species-specific data must be included in any such analysis in order to improve model fit.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article:

Appendix S1 Sample size and data source for all European badger (*Meles meles*) populations used in this study.

Appendix S2 Percentage volume of vegetable matter, earthworms, insects, vertebrates, total animal matter and other material in the diet of 29 populations of the European badger (*Meles meles*).

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BIOSKETCH

Emilio Virgós' interests lie in the conservation and ecology of carnivores and in the response of different species to global change.