



On the validity of Bergmann's rule

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Abstract

Aim We reviewed the occurrence of Bergmann's rule in birds (ninety-four species) and mammals (149 species), using only studies where statistical significance of the results was tested. We also tested whether studies using different characters as surrogates of body size have a different tendency to conform to Bergmann's rule, whether body size and nest type (in birds) have an influence on the tendency to conform to the rule, and whether sedentary birds conform to the rule more than migratory birds.

Location Worldwide.

Methods We reviewed published data on geographic and temporal variation in body size, using only studies where the statistical significance of the results was tested. We asked how many species conform to the rule out of all species studied in each order and family.

Results Over 72% of the birds and 65% of the mammal species follow Bergmann's rule. An overall tendency to follow the rule occurs also within orders and families. Studies using body mass in mammals show the greatest tendency to adhere to Bergmann's rule (linear measurements and dental measurements show a weaker tendency); while in birds, studies using body mass and other surrogates (linear measurements and egg size) show a similar tendency. Birds of different body mass categories exhibit a similar tendency to follow Bergmann's rule, while in mammals the lower body size categories (4–50 and 50–500 g) show a significantly lower tendency to conform to the rule. Sedentary birds tend to conform to Bergmann's rule more than migratory species. Nest type does not affect the tendency to conform to Bergmann's rule.

Main conclusions Bergmann's rule is a valid ecological generalization for birds and mammals.

Keywords

Bergmann's rule, body size, geographic variation, size clines, latitude, temperature, Aves, Mammalia.

INTRODUCTION

Bergmann's rule states in its original version that warm-blooded vertebrate species from cooler climates tend to be larger than congeners from warmer climates (Bergmann, 1847). This rule was later reformulated by Rensch (1938) to refer to populations within species: 'within a Rassenkreis (i.e. species, see Mayr, 1942) of warm-blooded animals the races living in colder climates are generally larger than the races living in warmer regions' (Rensch, 1938; see also Mayr, 1942, 1956, 1963). Although formulated for homeotherms, a wealth of research describes such patterns (or lack thereof) in poikilotherm vertebrates and in various invertebrate taxa (e.g. Lindsey, 1966; Cushman *et al.*, 1993;

Atkinson, 1994; Arnett & Gotelli, 1999; Porter & Hawkins, 2001; Ashton, 2002).

Despite a wealth of studies aiming to unravel the mechanisms controlling geographic variation in body size, surprisingly little was done to try to assess the empirical validity of these patterns of variation (Zink & Remsen, 1986; Ashton *et al.*, 2000). As biological 'rules' are, by definition, empirical generalizations (Mayr, 1963), we reviewed the literature on geographic variation in body size of both birds and mammals, and asked whether the pattern predicted by Bergmann (1847) is indeed prevalent in nature.

Bergmann's (1847) explanation for his rule was that a greater increase in size involves a more rapid increase of the volume of an animal than of its surface area. As heat production of a homeotherm is related to its volume, while heat loss to its surface, larger animals will tend to produce more heat and to lose relatively less, an advantage in cooler

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climates. James's (1970, 1991) Neo-Bergmannian model recommends use of wet-bulb temperatures as the appropriate climatic variable because it incorporates the evaporative power of the air.

It is, therefore, not surprising that much of the debate regarding Bergmann's rule and its mechanistic explanation was generated by animal physiologists who offered alternative and conflicting hypotheses (Scholander, 1955, 1956; Irving, 1957; McNab, 1971; Geist, 1987). Special emphasis has been placed on McNab's (1971) rejection of the rule on theoretical grounds, claiming that larger organisms lose absolutely more energy to the environment than do smaller organisms. This analysis disregarded the fact that while large birds and mammals do require more energy, they acquire more energy from their surroundings than do smaller ones (see exponents in Brown *et al.*, 1993; Maurer, 1998). Bergmann's (1847) rule implies that because of relatively large energy loss, smaller homeotherms have a problem obtaining enough food to meet their energetic demands (Thompson, 1942). It does not imply that these demands are absolutely higher in small organisms than those of larger ones.

Over the years, other ecological and evolutionary hypotheses were advanced to supplement or replace the thermo-regulatory mechanism proposed by Bergmann (1847) and James (1970). It was claimed that size clines can result from latitudinal differences in primary productivity (Rosenzweig, 1968; Geist, 1987), or from differences in environmental predictability, leading to improved survival of large animals in higher latitudes (Calder, 1974, 1984; Boyce, 1978, 1979; Lindstedt & Boyce, 1985; Millar & Hickling, 1990; McNab, 1999; see also Dunbrack & Ramsay, 1993). These mechanisms are not easy to tease apart, as many of the climatic variables are intercorrelated (Wigginton & Dobson, 1999). It can also be argued that the adaptive influence exerted on animal body size by these various mechanisms might be additive, and that no single such explanation can adequately describe all cases of Bergmannian size clines (Mayr, 1963; Lawton, 1996; Yom-Tov *et al.*, 2002).

Irrespective of the driving mechanism(s), Bergmann's rule as formulated by Rensch (1938) and Mayr (1956, 1963) is an empirical generalization whose significance hinges upon its prevalence among homeotherms. Clearly, other selective forces may well affect the evolution of body sizes in various populations and result in regional or global deviations from Bergmann's rule (Dayan *et al.*, 1991). However, Mayr (1956, 1963) suggested that if over 50% of species studied conform to an ecogeographic rule, its validity should not be questioned. Although Blackburn *et al.* (1999) suggest that this is rather generous in respect of a "rule", they agree that a rule probably implies that a pattern should be seen more often than not.

Rensch (1936) concluded that the majority of North American and European mammals conformed to Bergmann's rule, but Scholander (1955) questioned the biological significance of Rensch's findings, and his choice of characters. McNab's (1971) study of geographic variation in North American mammals failed to support the rule, but his method was recently criticized by Ashton *et al.* (2000), who

noted that it limited sample size and geographic range over which a correlation between size and latitude was sought. Their study of the prevalence of Bergmann's rule in mammals of the world supports the rule (Ashton *et al.*, 2000). For birds, on the other hand, the only review so far was conducted by Zink & Remsen (1986), who argued that a minority of species conform to Bergmann's rule, unless species that showed weak support were also considered.

Do mammals follow Bergmann's rule, while birds fail to do so? Zink & Remsen's (1986) review included many studies that lacked statistical analysis and that examined very small samples, so it may not be the critical evaluation that this issue merits. Patterns of geographic variation in sixty-one additional bird species were studied and published in the past 16 years since Zink & Remsen's (1986) publication, which was limited to North American birds species; so a new look at the occurrence of Bergmann's rule in birds is warranted.

In this study, we review the evidence for Bergmann's rule among avian species using only studies that include statistical testing of the data. We test for the prevalence of 'Bergmannian' size clines in species within the class as well as within orders and families of birds studied. We also ask whether there is a different tendency for birds within different size categories to conform to Bergmann's rule, as has been suggested for mammals (Mayr, 1956; Searcy, 1980; Calder, 1984; Steudel *et al.*, 1994; Ashton *et al.*, 2000).

Although Bergmann's rule was originally formulated for body mass of homeotherms, it has been tested using several different morphological characters as surrogates for body size. Different body size characters tend to be highly correlated with one another within mouse-to-elephant plots, but intraspecific comparisons reveal that the relationship may be weak (Dayan & Simberloff, 1994). Surrogates for body size may be affected by other selective forces than those responsible for Bergmann's rule. Wing length, for example, may be influenced by migratory habits (Hamilton, 1961; Zink & Remsen, 1986) and Allen's rule (in bats; Burnett, 1983). Wing length may also increase after a bird has reached its final body size (Merom *et al.*, 1999). Teeth, another common surrogate, may be influenced by competition (Dayan *et al.*, 1989a,b, 1992). Thus, characters other than mass may not accurately reflect body size (Rising & Somers, 1989; Dunning, 1993). Body mass, on the other hand, may be influenced by seasonal and daily fluctuations and by reproductive condition (Ralls & Harvey, 1985; Dunning, 1993). We, therefore, ask whether use of different surrogates for body size results in a significantly different tendency to conform to the rule.

We test three hypotheses regarding Bergmann's rule in birds. One is that sedentary species will be more likely to follow Bergmann's rule than migratory ones. Our rationale is that migratory birds do not encounter the severe climates of their breeding ranges during winter, so the selective pressures acting upon them may, therefore, be lower than those acting on sedentary birds (Hamilton, 1961; Zink & Remsen, 1986).

Another hypothesis follows Kendeigh's (1969) physiological study, which demonstrated that non-passerine birds are more strongly affected by a drop in temperatures than are passerines. This phenomenon may imply that the selective pressures acting upon non-passerines are stronger, and thus make them more inclined to vary in their body sizes in accord with Bergmann's rule.

We also test the hypothesis that there is a relationship between nest type and the tendency of bird species to comply with Bergmann's rule. Our rationale is that the same selective forces affecting birds must also affect avian eggs. As eggs in open nests may be more exposed to climatic conditions than those in closed nests, the former might be expected to show greater conformity to Bergmann's rule at the intraspecific level.

For both birds and mammals we ask: (a) whether over 50% of the species studied (within class, order, and family) show geographic size clines conforming to Bergmann's rule; (b) whether species of different size categories have differing tendencies to conform to it; (c) whether use of different morphological characters results in a differential tendency to comply with Bergmann's rule.

METHODS

We reviewed the literature concerning geographic and temporal variation in body size of birds and mammals. We used only data that were statistically tested (by the authors) for geographic variation. This conservative procedure ensures that perceived patterns used in the analysis are real and not mere artefacts of insufficient sampling (although Ashton *et al.*, 2000, found similar patterns whether all, or only statistically significant data were used). The inclusion of statistically insignificant data may confound efforts to determine whether a species conforms to Bergmann's rule or shows no geographic variation in body size. We, therefore, drew the line at the 95% confidence level, although this method of analysis has low power to reject the null hypothesis. Each species was assigned '1' (=accords with the predictions of Bergmann's rule), or '0' (=any other body size trend, or no trend at all). As many studies did not give correlation coefficients, sample sizes or even *P*-values (in the latter case simply stating their results are significant at the 0.05 level), we did not present these data in Tables 1 and 6. For the same reason we did not perform a meta-analysis test, as such an analysis will greatly limit the number of studies; hence, seriously limit the review's scope. Studies of birds and mammals using relatively large (> 1000) or small (< 100) sample sizes did not differ significantly from the general trend.

We did not attempt to separate studies into those dealing with different geographic variables such as latitude, temperature, wet bulb temperature and actual evapotranspiration (AE). The climatic data in studies of geographic variation are far from uniform (cf., e.g. Stebbings, 1973; Snell & Cunnison, 1983; Murphy, 1985; Langvatn & Albon, 1986; Yom-Tov & Nix, 1986; Erlinge, 1987; Bost *et al.*, 1992; Di-Meglio *et al.*, 1996; Olcott & Barry, 2000).

The use of different climatic variables in different studies leads to different results, the significance of which is not always clear (Wigginton & Dobson, 1999). 'Temperature' is not a single character. Body size might be influenced by the coldest temperature, the hottest one, the variance, or range of temperatures, by heat load (James, 1970) or by other temperature-related phenomena. 'Bergmannian' size clines may stem from any one, or a combination of variables, as well as from other latitude related ones. Wigginton & Dobson (1999) and Ashton *et al.* (2000) found no significant differences between latitude and temperature, in their influence on the tendency of mammals to follow Bergmann's rule. Finally, an ecological phenomenon might be the additive product of different factors (Mayr, 1956, 1963; Lawton, 1996), and so we only sought the occurrence of gross 'Bergmannian' trends.

When different abiotic variables yielded different results, priority was given to the body size changes (or lack thereof) with latitude (which may be correlated with a large number of other variables such as temperature, day length, AE, number of snow days, etc.; Yom-Tov *et al.*, 2002), over different temperature variables, then altitude, and finally AE.

We followed Gill (1995) for taxonomic designations of bird families and orders, and Monroe & Sibley (1993) for bird species. We followed Wilson & Reeder (1993) for taxonomic designations of mammals. *Neotoma magister* Baird was considered a distinct species [from *N. Floridana* (Ord), following Hayes & Richmond, 1993; see also Wilson & Reeder, 1993]. Likewise, we recognize the two species of *Arvicantis* treated by Fadda & Corti (1998).

Island mammals often differ dramatically in their body size from their mainland conspecifics, and large differences in size occur between mammals on different islands (Foster, 1964; Heaney, 1978; Lomolino, 1985; Dayan & Simberloff, 1998; Marquet & Taper, 1998). Therefore, we did not include studies in which a major source of variation is because of differences in body size between mammals inhabiting different islands [Baker *et al.*, 1978; Tideman, 1986; Kaneko, 1988; Fooden & Albrecht, 1993; Worthy *et al.*, 1996; Abe, 1996, for *Mogera wogura* (Temminck); Yom-Tov *et al.*, 1999]. We did not follow the same procedure for birds, because size changes in birds are usually found only in very small and isolated islands (McNab, 1994).

McNab's (1971) methods of dividing his data for each species into latitudinal bands serve to limit both the sample sizes, and the latitudinal range over which a correlation between size and latitude was sought. His analysis, therefore, has low power to detect a Bergmannian size cline, even if such a cline exists. In fact, many of the species [such as *Scalopus aquaticus* (Linnaeus), *Eptesicus fuscus* (Beauvois), *Panthera onca* (Linnaeus), *Puma concolor* (Linnaeus), *Lepus americanus* Erxleben, *Odocoileus virginianus* (Zimmermann) and *Sylvilagus florianus* (Allen); see Table 6] in which McNab (1971) failed to detect a cline, were found to exhibit a geographic size cline by other researchers. Therefore, we did not include McNab's (1971) data in the analysis.

When geographic variation of a species was examined in more than one study, the study encompassing the greatest

Table 1 Avian database

Order, family and species	Mass (g)	Findings	Source	Size parameter	Nest	Migratory habits
Anseriformes						
Anatidae						
<i>Anas platyrhynchos</i>	1082	1	DuBowy (2000)	L	1	s
<i>Branta canadensis</i>	2880	0	Leafloor & Rusch (1997)	L	1	m
Caprimulgiformes						
Podargidae						
<i>Podargus strigoides</i>	350	1	Ford (1986)	L	1	s
Charadriiformes						
Chionididae						
<i>Chionis minor</i>	579	1	Bried & Jouventin (1997)	L	3	s
Alcidae						
<i>Fratercula arctica</i>	381	1	Moen (1991)	L	3	m
<i>Pinguinus impennis</i>	5000	1	Burness & Monteverchi (1992)	L	1	?
Charadriidae						
<i>Vanellus vanellus</i>	218	1	Chylarecki <i>et al.</i> (1997)	EV	1	m
Scolopacidae						
<i>Calidris alba</i>	57	1	Castro <i>et al.</i> (1992)	M, L	1	m
<i>Calidris alpina</i>	52	0	Shepherd <i>et al.</i> (2001)	L	1	m
<i>Calidris maritima</i>	82	1	Summers <i>et al.</i> (1998)	M, L	1	s
Columbiformes						
Columbidae						
<i>Columba livia</i>	355	1	Johnston (1994)	L	1	s
Coraciiformes						
Alcedinidae						
<i>Ceryle rudis</i>	83	1	Kasperek (1996)	L	3	s
<i>Dacelo novaeguineae</i>	305	1	Ford (1986)	L	2	s
Falconiformes						
Accipitridae						
<i>Accipiter cooperii</i>	439	0	Whaley & White (1994)	L	1	m
<i>Accipiter fasciatus</i>	510	1	Ford (1986) and Olsen & Marples (1993)	EV	1	s
<i>Accipiter gentilis</i>	1025	0	Whaley & White (1994)	L	1	s
<i>Accipiter nisus</i>	238	1	Wyllie & Newton (1995)	L	1	s
<i>Aquila audax</i>	3500	1	Olsen & Marples (1993)	EV	1	s
<i>Buteo polyosoma</i>	950	1	Farquhar (1998)	L	1	s
<i>Buteo jamaicensis</i>	1126	0	Fitzpatrick & Dunk (1999)	L	1	s
<i>Elanus axillaris</i>	250	1	Olsen & Marples (1993)	EV	1	s
Cathartidae						
<i>Cathartes aura</i>	1467	1	Kirk & Mossman (1998)	L	1 (no nest)	m
Falconidae						
<i>Falco berigora</i>	550	1	Olsen & Marples (1993)	EV	1	s
<i>Falco columbarius</i>	191	0	Temple (1972)	L	1	m
<i>Falco longipennis</i>	253	1	Olsen & Marples (1993)	EV	1	s
<i>Falco peregrinus</i>	782	1	Olsen & Marples (1993)	EV	2	s
<i>Falco sparverius</i>	116	1	Layne & Smith (1992)	M	2, 3	m
<i>Falco subniger</i>	786	1	Olsen & Marples (1993)	EV	1	m
Pandionidae						
<i>Pandion haliaetus</i>	1486	1	Olsen & Marples (1993)	EV	1	s
Galliformes						
Numididae						
<i>Guttera pucherani</i>	1150	0	Crow (1979)	L	1	s
<i>Numida meleagris</i>	1300	1	Crow (1979)	L	1	s
Phasianidae						
<i>Alectoris chukar</i>	500	1	Nisany (1974) and Yom-Tov <i>et al.</i> (2002)	M, L	1	s
Gruiformes						
Gruidae						
<i>Grus canadensis</i>	4600	0	Johnson & Stewart (1973)	L	1	m

Table I continued

Order, family and species	Mass (g)	Findings	Source	Size parameter	Nest	Migratory habits
Passeriformes						
Alaudidae						
<i>Eremophila alpestris</i>	31	0	Niles (1973)	M, L	1	s
<i>Galerida cristata</i>	43	0	Yom-Tov (2001)	M, L	1	s
Cinclidae						
<i>Cinclus cinclus</i>	58	0	Esteban <i>et al.</i> (2000)	L	4	s
Cisticolidae						
<i>Prinia gracilis</i>	7	1	Yom-Tov (2001)	M, L	4	s
Corvidae						
<i>Cyanocitta cristata</i>	87	1	James (1970)	L	1	s
<i>Pyrrhocorax pyrrhocorax</i>	324	1*	Laiolo & Rolando (2001)	L	3	s
<i>Pyrrhocorax graculus</i>	224	1*	Laiolo & Rolando (2001)	L	3	s
Emberizidae						
<i>Atlapetes rufinucha</i>	26	0	Remsen (1993)	L	1	s
<i>Coereba flaveola</i>	9	1	Diamond (1973)	M, L	4	s
<i>Diglossa carbonaria</i>	11	1	Graves (1991)	L	1	s
<i>Melospiza melodia</i>	24	1	Smith (1998)	M	1	s
<i>Passerculus sandwichensis</i>	23	1	Rising (1988)	L	1	m
<i>Zonotrichia capensis</i>	21	1	Handford (1983) and Lougheed & Handford (1993)	L	1	s
Estrildidae						
<i>Taeniopygia guttata</i>	12	1	Clayton <i>et al.</i> (1991)	M, L	2, 3, 4	s
Fringillidae						
<i>Carduelis chloris</i>	22	1	Merilä (1997)	L	1	s
<i>Carduelis flammea</i>	13	0	Troy (1985)	L	1	m
<i>Hesperiphona vespertina</i>	59	1	Prescott (1994)	L	1	m
<i>Pinicola enucleator</i>	56	0	Adkisson (1977)	L	1	s
Hirundinidae						
<i>Hirundo rustica</i>	16	1	Möller (1995)	L	3	m
<i>Progne subis</i>	49	0	Behle (1968)	L	2, 3	m
Icteridae						
<i>Agelaius phoeniceus</i>	53	1*	Power (1969) and Mosimann & James (1979)	L	1	s
<i>Amblicercus holosericeus</i>	64	1	Kratter (1993)	L	1	s
<i>Sturnella magna</i>	89	0	James (1970)	L	4	s
<i>Xanthocephalus xanthocephalus</i>	64	1	Twedt <i>et al.</i> (1994)	M, L	1	m
Meliphagidae						
<i>Lichenostomus virescens</i>	25	1	Wooler <i>et al.</i> (1985)	M	1	s
Muscicapidae						
<i>Ficedula hypoleuca</i>	12	0	Järvinen (1994)	EV	2	m
Paridae						
<i>Parus caeruleus</i>	13	1	Martin (1991)	L	2	s
<i>Parus carolinensis</i>	10	1	James (1970)	L	2	s
Parulidae						
<i>Dendroica coronata</i>	13	1	Hubbard (1970)	L	1	m
<i>Dendroica discolor</i>	8	0	Buerkle (2000)	L	1	m
<i>Dendroica graciae</i>	8	1	Webster (1961)	L	1	m
<i>Dendroica petechia</i>	10	0	Wiedenfeld (1991)	L	1	m (north and central America, s Caribbean)
<i>Mniotilla varia</i>	11	1	Diamond (1973)	L	1	m
<i>Seiurus noveboracensis</i>	18	1	Molina <i>et al.</i> (2000)	L	1	m
Passeridae						
<i>Passer domesticus</i>	28	1	Johnston & Selander (1973), Baker (1980), Murphy (1985), McGillivray & Johnston (1987) and Yom-Tov (2001)	M, L	1, 2, 3, 4	s
<i>Passer melanurus</i>	25	1	Sloto (1996)	M, L	4	s

Table 1 continued

Order, family and species	Mass (g)	Findings	Source	Size parameter	Nest	Migratory habits
Pyconotidae						
<i>Pycnonotus barbatus</i>	36	1	Crow <i>et al.</i> (1981)	M	1	s
<i>Pycnonotus xanthopygos</i>	37	1	Yom-Tov (2001)	M, L	1	s
Sittidae						
<i>Sitta carolinensis</i>	21	1	James (1970)	L	2	s
Sturnidae						
<i>Acrocephalus tristis</i>	110	1	Baker & Moeed (1979)	L	2	s
<i>Sturnus unicolor</i>	91	1	Peris (1992)	L	2, 3	s
<i>Sturnus vulgaris</i>	82	0	Blem (1981)	M, L	2, 3	s
Sylviidae						
<i>Phylloscopus trochilus</i>	9	1	Bensch <i>et al.</i> (1999)	M, L	4	m
<i>Sylvia atricapilla</i>	16	0	Tellería & Carbonell (1999)	M, L	1	s
<i>Sylvia melanocephala</i>	11	1	Yom-Tov (2001)	M, L	1	s
Turdidae						
<i>Turdus migratorius</i>	77	1	James (1970) and Aldrich & James (1991)	L	1	m
Tyrannidae						
<i>Empidonax hammondi</i>	10	0	Johnson (1966)	M, L	1	m
<i>Suiriri suiriri</i>	15	0	Hayes (2001)	L	1	s
<i>Tyrannus tyrannus</i>	44	0	Van-Wynsberghe <i>et al.</i> (1992)	L	1	m
Vireonidae						
<i>Cyclarhis gujanensis</i>	29	1	Tubaro & Segura (1995)	L	1	s
<i>Vireo olivaceus</i>	17	0	Barlow & Power (1970)	L	1	m
<i>Vireo philadelphicus</i>	12	0	Barlow & Power (1970)	L	1	m
Pelecaniformes						
Phalacrocoracidae						
<i>Phalacrocorax atriceps</i>	2000	1	Bost <i>et al.</i> (1992) and Rasmussen (1994)	M, L	1	s
Piciformes						
Picidae						
<i>Picoides borealis</i>	44	1	Mengel & Jackson (1977)	L	2	s
<i>Picoides pubescens</i>	27	1	James (1970)	L	2	s
<i>Picoides villosus</i>	67	1	James (1970)	L	2	s
Procellariiformes						
Hydrobatidae						
<i>Oceanodroma leucorhoa</i>	36	1	Ainley (1980)	L	1	m
Spheniciformes						
Sphenicidae						
<i>Pygoscelis papua</i>	5950	1	Bost <i>et al.</i> (1992)	L	1	s
Strigiformes						
Strigidae						
<i>Bubo virginianus</i>	1380	1	McGillivray (1989) and Houston <i>et al.</i> (1998)	L	1, 2, 3	s
<i>Ninox connivens</i>	462	1	Ford (1986)	L	2	s
Tytonidae						
<i>Tyto novaehollandiae</i>	609	1	Ford (1986)	L	2, 3	s

Body mass is in grams, findings signify whether species comply ('1') or do not comply ('0') with the predictions of Bergmann's rule. Size can be linear measurements ('L'), body mass ('M'), egg volume ('EV'), or a combination of characters. A bird is designated migratory ('m') or sedentary ('s') in the area in which the research took place. Nest type can be open (1), tree cavity (2), burrow or constructed from mud (3), or a closed structure made of vegetation (4).

*The geographic variable used for this species was temperature rather than latitude.

latitudinal range was used, and studies of recent populations were preferred over studies of fossil or sub-fossil ones. The fallow deer, *Dama mesopotamica* (Brooke), for which two sub-fossil data bases (Davis, 1981; Bar-Oz *et al.*, 1999) yielded contradictory results was omitted from the analysis.

Studies with interspecific comparisons (Dunbar, 1990; Blackburn & Gaston, 1996; Panteleev *et al.*, 1998; and *Canis lupus* Linnaeus/C. *rufus* Audubon and Bachman, in

Rosenzweig, 1968) were not used. Nor did we combine measurements from different sources so as not to insert uncontrolled sources of variation into the data, owing to different measuring techniques and different geographic variables used. Studies of the genus *Homo* (Hall & Hall, 1995) were likewise omitted. Body mass, breeding habits and nest type data were obtained from the literature (see Appendix 1). As body mass was used by Bergmann (1847) as

the surrogate for size, we preferred mass over length measurements (which were preferred over dental measurements) where these different characters yielded different results in the same study (see, e.g. Yom-Tov, 2001). However, all characters were used (with their contradicting implications, if such existed) when seeking differences in the inclinations of surrogates for size to conform to Bergmann's rule.

Our data base includes ninety-four species of birds and 149 species of mammals.

We tested whether over 50% of the species studied conformed to Bergmann's rule (see Mayr, 1963). Decreases in body size with increasing latitude (or decreasing temperatures) and lack of a geographic trend in body size were both considered evidence against the rule's validity. This null hypothesis is a conservative one, as most species with a very restricted geographic range are unlikely to show any geographic variation in body size (Ashton *et al.*, 2000), as are species that were studied in only a small part of their geographical range. For this reason, however, geographic variation in body size of these species is unlikely to have been studied. This lack of analysis should not be of any concern, because even assuming that selective forces influencing size are in operation, species with a very limited range are not exposed to varying selective forces and, therefore, bear no relevance to the questions reviewed herein. On the other hand, species with a large geographic range that show no size cline across their range clearly negate the predictions of Bergmann's rule, and should, therefore, be included in the analysis.

We divided the species in the data base into body size categories in order to test whether Bergmannian size clines are more likely to occur in large species (which usually have great geographic distributions; Brown, 1995) or in small ones (for whom insulation might be of lesser, Steudel *et al.*, 1994, or greater significance, Paterson, 1990, or which are likelier to encounter periods of starvation that threaten survival, Searcy, 1980). The fossil rodent *Paraethomys* (Renaud *et al.*, 1999), whose body mass is unknown, was not included in the analysis. Body mass categories were chosen so that the lowest size category is below the modal size, and the second one containing the mode (which has been considered as optimal body mass; see Brown *et al.*, 1993; Marquet & Taper, 1998). This resulted in categories showing a fivefold increase in birds (modal body mass of about 33 g; Maurer, 1998), the categories being: 7–20 (7 g being the lowest mass for a bird in our data base), 21–100, 101–500, 501–2500, and over 2500 g. For mammals the modal mass is 'about 100 g' (actually covering a range from 50 to about 250 g; Brown *et al.*, 1993). This resulted in a tenfold increase in mass, so we partitioned the other mass categories accordingly: 4–50 (4 g being the lowest mass for a mammal in our data base), 51–500, 501–5000, 5001–50,000, > 50,001 g. These differences in modal sizes between birds and mammals, therefore, caused body size categories to differ between these two taxa.

Differences were sought between the tendency to comply with the predictions of Bergmann's (1847) rule and the characters used as measures of body size. Measurements were divided into dental measurements (for mammals),

linear measurements (all other unidimensional measurements), egg volume (for birds), and body mass. Species whose body size was estimated by more than one character were included in all relevant categories.

We also tested the relationship between nest type and the tendency to follow the predictions of Bergmann's rule, dividing birds into burrow nesters, cavity nesters, and those with open or no nests and with dome-shaped nests constructed of vegetation. Burrow nesters, and to some extent cavity nesters, were expected to be the least exposed, and therefore birds using these nests the least inclined to follow Bergmann's rule, a similar prediction to Mayr's (1956) concerning burrowing mammals.

We divided birds according to the migratory habits of the various species. We used populations instead of species for *Dendroica petechia* (Wiedenfeld, 1991), where the body size clines were different for migratory and non-migratory populations (with only sedentary populations conforming to the rule).

Tests for goodness of fit (G statistic, applying William's correction; Sokal & Rohlf, 1995) were conducted to test the validity of Bergmann's rule. The expected frequencies were calculated as 50% (Mayr, 1963).

Comparisons between the different variables analysed (body size, migratory habits, nest type, morphological character studied) were likewise based on the G statistic (tests of independence). When a significant result occurred in an $R * C$ test (Sokal & Rohlf, 1995, p. 739), further analysis followed a method for partitioning the degrees of freedom outlined by Siegel & Castellan (1988), using the χ^2 statistic.

RESULTS

Birds

Of the ninety-four bird species for which statistical analyses were carried out (Table 1), sixty-eight (72.34%) follow Bergmann's rule. Bergmann's rule is, thus, supported for birds based on this sample (corrected $G = 19.39$, $P < 0.001$).

In twelve of fourteen orders, more species followed the rule than did not. However, in only three of the orders (Passeriformes, Charadriiformes, and Falconiformes) were there sample sizes of over five. In thirty-two of forty-two families, 50% or more of the species adhered to Bergmann's rule. Only one of the families for which the rule is unsupported (Fringillidae) has more than three species sampled. Bergmann's rule is, thus, supported also at the ordinal and family levels (order: corrected $G = 7.79$, $P < 0.01$; family: corrected $G = 12.05$, $P < 0.001$).

Non-passerines show a higher percentage of species conforming to Bergmann's rule (81%, thirty-four of forty-two species) than do passerines (65%, thirty-four of fifty-two species), but the difference is not significant (corrected $G = 2.82$, $P > 0.05$).

We found no relationship between nest type and the tendency to adhere to Bergmann's rule (Table 2) (corrected

Table 2 The relationship between nest type and the adherence to Bergmann's rule in birds

Nest type	Bergmannian gradient	No Bergmannian gradient	Percentage adherence
Open or no nest	44	21	67.69
Tree cavity	16	3	84.21
Burrow	12	2	85.71
Dome	6	2	75.00

Table 3 Body mass categories and adherence to Bergmann's rule in birds

Mass (g)	Bergmannian gradient	No Bergmannian gradient	Percentage adherence
7–20	13	9	59.09
21–100	25	10	71.43
101–500	14	2	87.50
501–2500	13	3	81.25
> 2500	3	2	60.00

Table 4 The relationship between morphological character studied and adherence to Bergmann's rule in birds

Character studied	Bergmannian gradient	No Bergmannian gradient	Percentage adherence
Length	53	25	67.95
Mass	17	5	77.27
Egg volume	9	1	90

Table 5 The tendency of migrant and sedentary birds to comply with Bergmann's rule

Life history	Bergmannian gradient	No Bergmannian gradient	Percentage adherence
Migrant	17	14	54.84
Sedentary	51	12	80.95

$G = 3.36$, $P > 0.25$), and no relationship between body mass category and the tendency to follow Bergmann's rule (Table 3) (corrected $G = 4.69$, $P > 0.25$). We also found no significant relationship between the character chosen to represent body size and the tendency to follow Bergmann's rule (Table 4) (corrected $G = 2.76$, $P > 0.25$).

Sedentary birds tend to follow Bergmann's rule more than do migratory birds (Table 5) (corrected $G = 6.66$, $P < 0.01$).

Mammals

Of the 149 mammal species for which statistical analyses were carried out (Table 6), ninety-seven (65.10%) follow

Bergmann's rule. Bergmann's rule is, thus, supported for mammals based on this sample (corrected $G = 13.81$, $P < 0.001$).

Twelve of fourteen mammalian orders comprised more species that followed Bergmann's rule than species that did not. However, only in three orders (Chiroptera, Carnivora, and Rodentia) were over ten species studied. The Peremelomorpha ($n = 1$ species) and Rodentia were the only orders that failed to comply with Bergmann's rule. In twenty-six of thirty-two families, 50% or more species followed the rule. In only in two families (Heteromyidae and Mustelidae), in which fewer than 50% of species conformed to the rule, were over four species studied. The rule is, thus, supported both at the ordinal and family levels (order: corrected $G = 7.79$, $P < 0.01$; family: corrected $G = 13.37$, $P < 0.001$).

The tendency to follow Bergmann's rule changes with body mass (Table 7) (corrected $G = 19.69$, $P < 0.001$). Partitioning the degrees of freedom revealed no differences among the three highest size categories (two highest categories: $\chi^2 = 0.001$, $P > 0.9$; between the two highest combined and the 501–5000 g category: $\chi^2 = 2.07$, $P > 0.10$), and between the two lowest size categories ($\chi^2 = 0.01$, $P > 0.95$). However, a significant difference in the tendency to follow Bergmann's rule was detected between the two lowest size categories (up to 500 g) and the three highest ones (501 g and above: $\chi^2 = 15.51$, $P < 0.001$). The tendency of small (4–500 g) mammals to conform to Bergmann's rule does not differ significantly from 50% (corrected $G = 0.01$, $P > 0.95$).

Studies using body mass tend to conform to Bergmann's rule more than those using other characters (Table 8, corrected $G = 6.33$, $P < 0.05$).

DISCUSSION

Bergmann's rule appears to be a valid generalization for both birds and mammals. In both classes, the majority of species, orders, and families comply with the rule. The percentage of birds conforming to the rule is similar to the lower value (75%) put forward by Mayr (1970), rather than to the results published by Zink & Remsen (1986) (42–54%). For mammals the percentage of species conforming to the rule is similar to the lower value suggested by Mayr (1970) (65%), and slightly lower than those derived from the analyses of Ashton *et al.* (2000) (70.9% for all data, 75% for statistically significant correlations). Among mammals, studies of clines of body mass show the results most consistent with the rule, suggesting that this is indeed the character upon which natural selection operates, whatever the precise mechanism(s) involved (Bergmann, 1847; Rosenzweig, 1968; Kendigh, 1969; James, 1970; Boyce, 1978; Kolb, 1978; Searcy, 1980; Blackburn *et al.*, 1999).

When carrying out an analysis of this type, one must bear in mind potential biases inherent in the set of studies analysed. One such potential bias may be in the choice of species studied, namely, a tendency to study species for which there is some prior indication for a Bergmannian size cline. Another

Table 6 Mammalian database

Order, family and species	Mass (g)	Findings	Source	Size parameter
Artiodactyla				
Bovidae				
<i>Bos primigenius</i>	800,000	1	Davis (1981)	D, L
<i>Capra aegagros</i>	60,000	1	Davis (1981)	D, L
<i>Gazella gazella</i>	21,500	1	Davis (1981)	D, L
Cervidae				
<i>Alces alces</i>	512,000	1	Sand <i>et al.</i> (1995)	M
<i>Cervus elaphus</i>	207,000	1	Langvatn & Albon (1986) and Post <i>et al.</i> (1997)	M
<i>Odocoileus virginianus</i>	116,000	1	Rees (1969), Koch (1986) and Purdue (1989)	D, L
Suidae				
<i>Sus scrofa</i>	81,000	1	Davis (1981) and Weaver & Ingram (1969)	D, M, L
Carnivora				
Canidae				
<i>Canis aureus</i>	8800	0	Dayan <i>et al.</i> (1992)	L
<i>Canis latrans</i>	10,500	0	Rosenzweig (1968) and Thurber & Peterson (1991)	M, L
<i>Canis lupus</i>	34,000	1	Davis (1981) and Mendelsohn & Yom-Tov (1999)	D, L
<i>Canis mesomelas</i>	8500	1	Klein (1986)	D
<i>Lycaon pictus</i>	27,500	1	Klein (1986)	D
<i>Pseudoalopex culpaeus</i>	15,850	1	Fuentes & Jaksic (1979) and Jimenez <i>et al.</i> (1995)	L
<i>Pseudoalopex griseus</i>	8300	1	Fuentes & Jaksic (1979) and Jimenez <i>et al.</i> (1995)	L
<i>Urocyon cinereoargenteus</i>	3800	1	Rosenzweig (1968)	L
<i>Vulpes cana</i>	1100	1	Geffen <i>et al.</i> (1992)	M, L
<i>Vulpes chama</i>	4070	1	Klein (1986)	D
<i>Vulpes rueppelli</i>	1900	1	Dayan <i>et al.</i> (1992)	L
<i>Vulpes velox</i>	2400	0	Rosenzweig (1968)	L
<i>Vulpes vulpes</i>	3400	1	Rosenzweig (1968), Davis (1977, 1981), Cavallini (1995), Dayan <i>et al.</i> (1989b, 1992), Frafjord & Stevy (1998), Kolb (1978) and Macdonald <i>et al.</i> (1999)	D, M, L
Felidae				
<i>Acinonyx jubatus</i>	46,500	1	Klein (1986)	D
<i>Caracal caracal</i>	16,000	1	Klein (1986)	D
<i>Felis silvestris (libyca)</i>	6000	1	Klein (1986)	D
<i>Leptailurus serval</i>	16,000	1	Klein (1986)	D
<i>Lynx rufus</i>	10,500	1	Wigginton & Dobson (1999)	L
<i>Panthera leo</i>	162,000	1	Klein (1986)	D
<i>Panthera onca</i>	83,000	1	Iriarte <i>et al.</i> (1990)	L
<i>Panthera pardus</i>	54,000	0	Klein (1986)	D
<i>Puma concolor</i>	55,000	1	Kurtén (1973), Iriarte <i>et al.</i> (1990) and Gay & Best (1996)	D, M, L
Herpestidae				
<i>Atilax paludinosus</i>	2500	1	Klein (1986)	D
<i>Herpestes ichneumon</i>	2570	1	Klein (1986)	D
<i>Herpestes pulverulens</i>	600	1	Klein (1986)	D
Hyaenidae				
<i>Crocuta crocuta</i>	59,000	1	Klein (1986) and Klein & Scott (1989)	D
<i>Hyaena brunnea</i>	48,000	1	Klein (1986)	D
Mustelidae				
<i>Aonyx capensis</i>	16,600	1	Klein (1986)	D
<i>Ictonyx striatus</i>	1700	0	Klein (1986)	D
<i>Martes americana</i>	930	1	Hagmeier (1961) and Rosenzweig (1968)	L
<i>Martes foina</i>	1100	0	Dayan <i>et al.</i> (1989a) and Reig (1992)	D, L
<i>Martes marten</i>	1300	0	Reig (1992)	L
<i>Martes pennanti</i>	3400	0	Rosenzweig (1968)	L
<i>Meles meles</i>	11,500	1	Dayan <i>et al.</i> (1989a)	D
<i>Melivora capensis</i>	7800	0	Klein (1986)	D
<i>Mephitis mephitis</i>	2090	1	Koch (1986)	D

Table 6 continued

Order, family and species	Mass (g)	Findings	Source	Size parameter
<i>Mustela erminea</i>	90	1	Rosenzweig (1968), Ralls & Harvey (1985), Erlinge (1987) and Eger (1990)	M, L
<i>Mustela frenata</i>	150	0	Rosenzweig (1968) and Ralls & Harvey (1985)	L
<i>Mustela nivalis</i>	48	0	Rosenzweig (1968) and Ralls & Harvey (1985)	L
<i>Taxidea taxus</i>	7250	1	Rosenzweig (1968)	L
Procyonidae				
<i>Procyon lotor</i>	6300	1	Kennedy & Lindsay (1984), Ritke (1990) and Mugaas & Seidensticker (1993)	M, L
Ursidae				
<i>Ursus arctos</i>	245,000	0	Kojola & Laitala (2001)	M
<i>Ursus maritimus</i>	340,000	1	Kurtén (1964)	L
Cetacea				
Delphinidae				
<i>Stenella coeruleoalba</i>	82,000	1	Di-Meglio <i>et al.</i> (1996)	M, L
Chiroptera				
Megadermatidae				
<i>Macroderma gigas</i>	150	1	Hand & York (1990)	D, L
Phyllostomidae				
<i>Anoura cultrata</i>	18	0	Nagorsen & Tamsit (1981)	D, L
<i>Carollia brevicauda</i>	15	0	McLellan (1984) and Owen <i>et al.</i> (1984)	L
<i>Carollia castanea</i>	15	1	McLellan (1984)	L
<i>Carollia perspicillata</i>	20	1	McLellan (1984) and Owen <i>et al.</i> (1984)	L
<i>Carollia subrufa</i>	16	1	McLellan (1984) and Owen <i>et al.</i> (1984)	L
Pteropodidae				
<i>Cynopterus sphinx</i>	37	1	Storz <i>et al.</i> (2001)	M, L
Vespertilionidae				
<i>Eptesicus fuscus</i>	17	1	Burnett (1983)	L
<i>Miniopterus schreibersii</i>	11	1	Cardinal & Christidis (2000)	D, L
<i>Myotis californicus</i>	4	0	Bogan (1975)	L
<i>Myotis daubentonii</i>	7	1	Bogdanowicz (1990)	L
<i>Myotis fortidens</i>	7	1	Findley & Jones (1967)	L
<i>Myotis lucifugus</i>	9	1	Findley & Jones (1967) and Fujita (1986)	M, L
<i>Pipistrellus hesperinus</i>	4	1	Findley & Trau (1970)	L
<i>Pipistrellus pipistrellus</i>	4	1	Stebbing (1973)	L
<i>Scotorepens balstoni</i>	13	0	Kitchener & Caputi (1985)	D, L
<i>Scotorepens greyii</i>	10	1	Kitchener & Caputi (1985)	D, L
<i>Scotorepens orion</i>	11	1	Kitchener & Caputi (1985)	D, L
<i>Scotorepens sanborni</i>	7	0	Kitchener & Caputi (1985)	D, L
Didelphimorphia				
Didelphidae				
<i>Didelphis virginiana</i>	2700	1	Koch (1986)	D
Diprotodontia				
Macropodidae				
<i>Macropus fuliginosus</i>	54,000	1	Yom-Tov & Nix (1986)	L
<i>Macropus giganteus</i>	34,000	1	Yom-Tov & Nix (1986)	L
<i>Macropus rufus</i>	41,000	1	Yom-Tov & Nix (1986)	L
Petauridae				
<i>Petaurus breviceps</i>	120	1	Quin <i>et al.</i> (1996)	L
<i>Petaurus norfolkensis</i>	230	1	Quin <i>et al.</i> (1996)	L
Phalangeridae				
<i>Trichosurus vulpecula</i>	2650	1	Yom-Tov & Nix (1986) and Yom-Tov <i>et al.</i> (1986)	M, L
Hyracoidea				
Procaviidae				
<i>Procavia capensis</i>	2500	1	Yom-Tov (1993a)	L

Table 6 continued

Order, family and species	Mass (g)	Findings	Source	Size parameter
Insectivora				
Soricidae				
<i>Blarina brevicauda</i>	18	0	Braun & Kennedy (1983)	L
<i>Blarina carolinensis</i>	9	1	Braun & Kennedy (1983)	L
<i>Sorex cinereus</i>	4	0	Huggins & Kennedy (1989)	L
<i>Sorex fumeus</i>	8	1	Huggins & Kennedy (1989)	L
Talpidae				
<i>Mogera minor</i>	60	0	Abe (1996)	L
<i>Scalopus aquaticus</i>	69	1	Koch (1986)	D
<i>Talpa romana</i>	85	1	Loy <i>et al.</i> (1996)	L
Lagomorpha				
Leporidae				
<i>Lepus americanus</i>	1500	1	Nagorsen (1985)	L
<i>Lepus capensis</i>	2150	1	Mendelsohn & Yom-Tov (1999)	L
<i>Oryctolagus cuniculus</i>	1110	1	Gibb & Williams (1990) and Sharples <i>et al.</i> (1996)	L
<i>Sylvilagus floridanus</i>	1080	1	Olcott & Barry (2000)	D, L
Monotremata				
Tachyglossidae				
<i>Tachyglossus aculeatus</i>	4500	1	Yom-Tov & Nix (1986)	M, L
Peramelemorphia				
Peramelidae				
<i>Isoodon obesulus</i>	1050	0	Cooper (1998)	M, L
Primates				
Cercopithecidae				
<i>Macaca fuscata</i>	13,600	1	Paterson (1996)	M
<i>Macaca mulata</i>	4700	1	Clarke & O'Neil (1999)	M, L
<i>Macaca nemestrina</i>	6150	1	Albrecht (1980)	L
<i>Presbytis entellus</i>	17,000	1	Gelvin and Albercht (1996)	L
Lorisidae				
<i>Nycticebus coucang</i>	700	1	Ravosa (1998)	L
<i>Nycticebus pygmaeus</i>	480	0	Ravosa (1998)	L
Proboscidea				
Mammuthidae				
<i>Mammut americanum</i>	5,000,000	1	King & Saunders (1984)	D
Rodentia				
Geomysidae				
<i>Thomomys talpoides</i>	139	1	Hadly (1997) and Hadly <i>et al.</i> (1998)	L
Heteromyidae				
<i>Chaetodipus goldmani</i>	23	0	Straney & Patton (1980)	L
<i>Chaetodipus penicillatus</i>	15	0	Hoffmeister & Lee (1967)	L
<i>Dipodomys californicus</i>	73	0	Baumgardner & Kennedy (1993)	D, L
<i>Dipodomys compactus</i>	49	0	Baumgardner & Kennedy (1993)	D, L
<i>Dipodomys deserti</i>	105	0	Baumgardner & Kennedy (1993)	D, L
<i>Dipodomys gravipes</i>	80	0	Best (1983)	L
<i>Dipodomys merriami</i>	38	0	Baumgardner & Kennedy (1993)	D, L
<i>Dipodomys microps</i>	56	0	Baumgardner & Kennedy (1993)	D, L
<i>Dipodomys nelsoni</i>	89	0	Baumgardner & Kennedy (1993)	D, L
<i>Dipodomys nitratoides</i>	42	0	Baumgardner & Kennedy (1993)	D, L
<i>Dipodomys ordii</i>	58	1	Kennedy & Schnell (1978) and Baumgardner & Kennedy (1993)	L
<i>Dipodomys panamintinus</i>	75	0	Baumgardner & Kennedy (1993)	D, L
<i>Dipodomys phillipsii</i>	41	0	Baumgardner & Kennedy (1993)	D, L
<i>Dipodomys simulans</i>	58	0	Baumgardner & Kennedy (1993) and Sullivan & Best (1997)	D, L
<i>Dipodomys spectabilis</i>	125	0	Baumgardner & Kennedy (1993)	D, L
<i>Dipodomys venustus</i>	83	0	Baumgardner & Kennedy (1993)	D, L
<i>Heteromys gaumeri</i>	57	0	Engstrom <i>et al.</i> (1987)	L

Table 6 continued

Order, family and species	Mass (g)	Findings	Source	Size parameter
<i>Perognathus fasciatus</i>	11	1	Williams & Genoways (1979)	D, L
Muridae				
<i>Acomys cahirinus</i>	41	1	Nevo (1989)	M
<i>Acomys russatus</i>	53	1	Nevo (1989)	M
<i>Apodemus flavicollis</i>	26	1	Tchernov (1979)	D
<i>Apodemus mystacinus</i>	35	1	Tchernov (1979)	D
<i>Apodemus sylvaticus</i>	20	0	Tchernov (1979) and Alcantara (1991)	D, M, L
<i>Arvicantis niloticus</i>	81	1	Fadda & Corti (1998)	L
<i>Arvicantis testicularis</i>	115	0	Fadda & Corti (1998)	L
<i>Lophuromys flavopunctatus</i>	55	0	Afework & Corti (1994)	L
<i>Meriones tristrami</i>	70	0	Chetboun & Tchernov (1983)	L
<i>Microtus agrestis</i>	24	1	Hansson & Jaarola (1989)	M
<i>Microtus longicaudus</i>	37	0	Findley & Jones (1962)	L
<i>Microtus mexicanus</i>	35	0	Findley & Jones (1962)	L
<i>Microtus montanus</i>	33	0	Findley & Jones (1962)	L
<i>Microtus oeconomus</i>	30	1	Ims (1997)	M
<i>Microtus pennsylvanicus</i>	33	0	Snell & Cunnison (1983)	L
<i>Nannospalax ehrenbergi</i>	174	1	Nevo <i>et al.</i> (1986)	M
<i>Neotoma albigena</i>	164	1	Smith <i>et al.</i> (1998)	M
<i>Neotoma cinerea</i>	300	1	Brown & Lee (1969) and Smith <i>et al.</i> (1995)	L
<i>Neotoma floridana</i>	248	1	Hayes & Richmond (1993)	L
<i>Neotoma magister</i>	350	1	Hayes & Richmond (1993)	L
<i>Ondatra zibethicus</i>	1000	1	Boyce (1978)	M, L
<i>Paraethomys sp.</i>	No data	1	Renaud <i>et al.</i> (1999)	D
<i>Peromyscus leucopus</i>	21	1	Owen (1989)	L
<i>Peromyscus maniculatus</i>	19	0	Wasserman & Nash (1979)	L
<i>Rhabdomys pumilio</i>	37	0	Yom-Tov (1993b)	L
<i>Saccostomus campestris</i>	49	0	Ellison <i>et al.</i> (1993)	L
<i>Sigmodon hispidus</i>	104	1	Cameron & McClure (1988)	M, L
<i>Synaptomys cooperi</i>	29	0	Wilson & Choate (1997)	D, L
Sciuridae				
<i>Sciurus carolinensis</i>	536	1	Barnett (1977) and Koch (1986)	D, L
<i>Spermophilus columbianus</i>	584	0	Zammuto & Millar (1985)	M
<i>Tamiasciurus douglasii</i>	227	0	Lindsay (1986)	D, L
<i>Tamiasciurus hudsonicus</i>	207	1	Lindsay (1987)	D, L

Body mass is in grams, findings signify whether species comply ('1') or do not comply ('0') with the predictions of Bergmann's rule. Size can be linear measurements ('L'), body mass ('M'), dental measurements ('D'), or a combination of characters.

Table 7 Body mass categories and adherence to Bergmann's rule in mammals

Mass (g)	Bergmannian gradient	No Bergmannian gradient	Percentage adherence
4–50	22	23	48.89
51–500	17	17	50.00
501–5000	22	7	75.86
5001–50,000	21	3	86.96
> 50,001	14	2	87.50

may be a publication bias; it has been suggested previously that ecologists may tend to publish 'positive' results; that is, results that support a prior hypothesis, and neglect 'negative' results (Simberloff & Boecklen, 1981; Möller & Jennions, 2001). Certainly, the publication of no geographical trend is

Table 8 The relationship between morphological character studied and adherence to Bergmann's rule in mammals

Character studied	Bergmannian gradient	No Bergmannian gradient	Percentage adherence
Length	66	49	57.39
Dental	38	22	63.33
Body mass	23	5	82.14

an unattractive prospect. Moreover, journal editors and reviewers may facilitate the publication of 'positive' results. These possible sources of bias, unfortunately, cannot be readily factored out. Nevertheless, and despite using a conservative approach (species showing no variation in size counting as evidence against the rule), based on published data, Bergmann's rule is indeed a valid generalization.

While bird size has no significant affect on the tendency to conform to Bergmann's rule, among mammals we found a significantly lower tendency to conform to Bergmann's rule within the 4–50 and 51–500 g body mass categories. In fact, for this size group and for the largest mammalian order, Rodentia, Bergmann's rule cannot be considered valid at this point. Various hypotheses could account for this pattern, or lack thereof. For one, many species in this size category burrow and thus effectively are found in a favourable microclimate for most of the time. It should be noted, that in the similar-sized but non-fossorial Chiroptera, fourteen out of nineteen species conform to the rule. On the other hand, four of the five fully fossorial species in our data base [*Scalopus aquaticus*, *Talpa romana* Thomas, *Thomomys talpoides* (Richardson), *Nannospalax ehrenbergi* (Nehring), but not *Mogera minor* Kuroda] tend to follow Bergmann's rule. Many of the species in this size category are heteromyid rodents; of the seventeen heteromyid species studied, only two conform to Bergmann's rule. However, Dayan & Simberloff (1994) demonstrated the occurrence of character displacement in trophic apparatus among heteromyid rodents, which may also indirectly affect body size, and obscure Bergmannian gradients (see also Dayan *et al.*, 1991). Moreover, many heteromyid species go into torpor or even hibernate during some of the winter months, thus avoiding extremely cold ambient temperatures. This could account, in part, for the apparent lack of conformity. In addition, body sizes of heteromyid rodents may be more closely related to productivity in deserts of south-western North America than to the characters for which it was tested (J.H. Brown, pers. comm.). That being the case, perhaps Bergmann's rule within James's (1970) reformulation (using both temperature and humidity) or Rosenzweig's (1968) suggestion of actual AE, is more relevant to this group of desert species.

Ashton *et al.* (2000) carried out an analysis in which they used exclusively species that were sampled over a wide geographic range. This analysis revealed no relationship between the tendency to conform to Bergmann's rule and body mass. However, small mammals are often restricted in their range (Brown, 1995), and therefore cannot comply with this criterion set by Ashton *et al.* (2000). It is logical to expect that mammal species with large geographic ranges will be more likely to show geographic size clines than those with a more restricted range. For example, the only species of *Dipodomys* that conforms to Bergmann's rule (*D. ordii* Woodhouse) has by far the largest geographic range of the genus (Wilson & Ruff, 1999). However, clinal variation can also occur on fairly limited geographical scales (James, 1982; Nevo, 1989; Mendelsohn & Yom-Tov, 1999). Moreover, ignoring the other species in the genus because they have more restricted geographic ranges might obscure some of the observed patterns, such as the dependence of Bergmann's rule on mammalian body size.

Be that as it may, the lower body mass range is the modal range for mammals, whether bats and marine mammals are included, as in our analysis (Gardezi & da Silva, 1999; 25 g), or not (Brown *et al.*, 1993). If Bergmann's rule is invalid in this size range, the implication may be that the rule is less

common than our results so far imply. If we assume that the percentage compliance with the rule in the sample is representative for each order, and take only orders for which we have a minimum of four or five species in the data base (these orders represent 92.8% and 91% of mammalian species, respectively; Wilson & Reeder, 1993), we find that 59.57% and 58.80% (respectively) of mammals comply with Bergmann's rule.

In birds, a significantly greater number of sedentary species conform to Bergmann's rule than do migratory species. This supports our prior hypothesis that species that are subject to natural selection during all seasons will tend to be more affected by climatic factors than species that evade the cold of winter by being elsewhere. Interestingly, some studies [e.g. Castro *et al.*, 1992, who studied geographic variation in *Calidris alba* (Pallas)], found that geographic variation in size, in accordance with Bergmann's rule, occurred in the overwintering range. It might be logical to expect that birds encountering a broad range of climatic condition in the overwintering range will show patterns in accord with Bergmann's rule in winter, while not showing such a pattern in their breeding ranges.

The significantly lower tendency of migratory species to conform to Bergmann's rule brings into question the climatic variables used in various studies. The fact that relatively few migratory species comply with Bergmann's rule suggests that extreme winter temperatures exert high selective pressures on bird body size (Root, 1988), and thus have the greater influence on the evolution of body size in birds, and are hence the climatic variable suitable for their study. It is a tenable hypothesis that in warm desert conditions extreme summer temperatures may be those that govern the evolution of body size in homeotherms (Yom-Tov, 1993a; Smith & Charnov, 2001).

The tendency for egg size to comply with Bergmann's rule did not differ from that of adult bird mass, nor could we detect a significant difference in the tendency to follow Bergmann's rule between birds with different nest types. It could be argued that the overall intraspecific relationship between bird size and egg size is likely to override other affects, or that birds incubate their clutches in constant enough temperatures that we should not expect ambient temperatures to be a significant selective force. Be that as it may, our results should not come as a surprise. Most bird species reproduce during spring, when ambient temperatures are mild (Gill, 1995). Therefore, if extreme ambient temperatures are the selective mechanism influencing body size (Brown & Brown, 1998; see also Root, 1988), and thus drive Bergmannian size clines, eggs are usually not exposed to this driving mechanism. The lower tendency of migratory species to conform to Bergmann's rule is in line with this result.

In sum, our results suggest that Bergmann's rule is a valid ecological generalization for birds and mammals at the class, order, and family levels. However, insectivores and, in particular, rodents appear to deviate from this generalization. Interestingly, another order of small mammals, the Chiroptera, shows virtually an identical percentage of species

conforming to Bergmann's rule as do birds. The currently published studies do not enable the finer resolution of driving climatic factors (wet- vs. dry-bulb temperatures and various climatic correlates), and this should remain as an agenda for future research. Sedentary birds conform to the rule more than do migratory ones, suggesting that extreme overwintering conditions are the major driving microevolutionary force, where this pattern occurs.

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BIOSKETCHES

Shai Meiri is a PhD student studying the evolution of body size of island carnivores. He is interested in the evolution of body size in mammals, at both the micro-evolutionary and macroevolutionary scales. Other fields of interest are the relationship between biogeography and evolution, late Pleistocene mammalian extinctions, and major innovations in vertebrate evolution.

Tamar Dayan is an Associate Professor of Zoology, with a research interest in the evolution of mammals within ecological communities. Her research involves both recent mammals (museum specimens and ecological communities in the field) and fossil and subfossil ones. Previous morphological studies include character displacement and sexual size dimorphism.

APPENDIX I

- List of sources for body masses, migratory habits and nest types. Some of the data were collected from the papers describing geographic variation of the various species.
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