



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 thermoregulatory 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 *Arvicanthis* 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 floridanus* (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 & Montevecchi (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 novaeguinae</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 1 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>Pyrrhonorax pyrrhonorax</i>	324	1*	Laiolo & Rolando (2001)	L	3	s
<i>Pyrrhonorax 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 Loughheed & 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>Lichenostmus virescens</i>	25	1	Wooler <i>et al.</i> (1985)	M	1	s
Mucicapidae						
<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>Mniotilta 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>Acridotheres 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 trochylus</i>	9	1	Bensch <i>et al.</i> (1999)	M, L	4	m
<i>Sylvia atricapilla</i>	16	0	Telleria & 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* (Wiedefeld, 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 Peremorphia ($n = 1$ 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; Ken-deigh, 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>Lycan 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 martes</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 daubentoni</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 hesperus</i>	4	1	Findley & Traut (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 virginianus</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 norfolcensis</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	Mendelssohn & 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
Peremelemorphia				
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>Presbitis 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				
Mammutidae				
<i>Mammut americanum</i>	5,000,000	1	King & Saunders (1984)	D
Rodentia				
Geomyidae				
<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> Muridae	11	1	Williams & Genoways (1979)	D, L
<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>Arvicanthis niloticus</i>	81	1	Fadda & Corti (1998)	L
<i>Arvicanthis 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 ebrenbergi</i>	174	1	Nevo <i>et al.</i> (1986)	M
<i>Neotoma albigula</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 effect 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; Mendelssohn & 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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REFERENCES

- Abe, H. (1996) Habitat factors affecting the geographic size variation of Japanese moles. *Mammal Study*, **21**, 71–87.
- Adkisson, C.S. (1977) Morphological variation in North American pine grosbeaks. *Wilson Bulletin*, **89**, 380–395.
- Afework, B. & Corti, M. (1994) Multivariate morphometrics of the Ethiopian populations of harsh-furred rat (*Lophuromys*: Mammalia, Rodentia). *Journal of Zoology*, **232**, 675–689.
- Ainley, D.G. (1980) Geographic variation in Leach's storm petrel. *Auk*, **97**, 837–853.
- Albrecht, G.H. (1980) Latitudinal, taxonomic, sexual and insular determinants of size variation in pigtail macaques, *Macaca nemestrina*. *International Journal of Primatology*, **1**, 142–152.
- Alcantara, M. (1991) Geographic variation in body size of the wood mouse *Apodemus sylvaticus* L. *Mammal Review*, **21**, 143–150.
- Aldrich, J.W. & James, F.C. (1991) Ecogeographic variation in the American robin (*Turdus migratorius*). *Auk*, **108**, 230–249.
- Arnett, A.E. & Gotelli, N.J. (1999) Geographic variation in life-history traits of the ant lion, *Myrmeleon immaculatus*: evolutionary implications of Bergmann's rule. *Evolution*, **53**, 1180–1188.
- Ashton, K.G. (2002) Do amphibians follow Bergmann's rule? *Canadian Journal of Zoology*, **80**, 708–716.
- Ashton, K.G., Tracy, M.C. & de Queiroz, A. (2000) Is Bergmann's rule valid for mammals? *American Naturalist*, **156**, 390–415.
- Atkinson, D. (1994) Temperature and organism size – a biological law for ectotherms? *Advances in Ecological Research*, **25**, 1–58.
- Baker, A.J. (1980) Morphometric differentiation in New Zealand populations of the house sparrow (*Passer domesticus*). *Evolution*, **34**, 638–653.
- Baker, A.J. & Moeed, A. (1979) Evolution in the introduced New Zealand populations of the common myna, *Acridotheres tristis* (Aves: Sturnidae). *Canadian Journal of Zoology*, **57**, 570–584.
- Baker, A.J., Peterson, R.L., Eger, J.L. & Manning, T.H. (1978) Statistical analysis of geographic variation in the skull of the arctic hare (*Lepus arcticus*). *Canadian Journal of Zoology*, **56**, 2067–2082.
- Barlow, J.C. & Power, D.M. (1970) An analysis of character variation in red-eyed and Philadelphia vireos (Aves: Vireonidae) in Canada. *Canadian Journal of Zoology*, **48**, 673–680.
- Barnett, R.J. (1977) Bergmann's rule and variation in the structures related to feeding in the gray squirrel. *Evolution*, **31**, 538–545.
- Bar-Oz, G., Dayan, T. & Kaufman, D. (1999) The epipalaeolithic sequence in Israel: a view from Neve David. *Journal of Archaeological Science*, **26**, 67–82.
- Baumgardner, G.D. & Kennedy, M.L. (1993) Morphometric variation in Kangaroo-rats (Genus *Dipodomys*) and its relationship to selected abiotic variables. *Journal of Mammalogy*, **74**, 69–85.
- Behle, W.H. (1968) A new race of the purple martin from Utah. *Condor*, **70**, 166–169.
- Bensch, S., Anderson, T. & Akesson, S. (1999) Morphological and molecular variation across a migratory divide in willow warblers, *Phylloscopus trochilus*. *Evolution*, **53**, 1925–1935.
- Bergmann, C. (1847) Ueber die verhältnisse der wärmeökonomie der thiere zu ihrer grösse. *Gottinger studien*, **3**, 595–708.
- Best, T.L. (1983) Morphologic variation in the San Quintin kangaroo rat (*Dipodomys gravipes* Huey 1925). *American Midland Naturalist*, **109**, 409–413.
- Blackburn, T.M. & Gaston, K.J. (1996) Spatial patterns in the body size of bird species in the New World. *Oikos*, **77**, 436–446.
- Blackburn, T.M., Gaston, K.J. & Loder, N. (1999) Geographic gradients in body size: a clarification of Bergmann's rule. *Diversity and Distribution*, **5**, 165–174.
- Blem, C.R. (1981) Geographic variation in mean winter body composition of starlings. *Condor*, **83**, 370–376.
- Bogan, M.A. (1975) Geographic variation in *Myotis californicus* in the southwestern United States and Mexico. *Wildlife Research Report, U.S. Fish and Wildlife Service*, **3**, 1–31.
- Bogdanowicz, W. (1990) Geographic variation and taxonomy of Daubenton's bat, *Myotis daubentoni* in Europe. *Journal of Mammalogy*, **71**, 205–218.
- Bost, C.A., Jouventin, P. & Du Sel, N.P. (1992) Morphometric variability on a microgeographical scale in two inshore seabirds. *Journal of Zoology*, **226**, 135–149.
- Boyce, M.S. (1978) Climatic variability and body size variation in the muskrats (*Ondatra zibethicus*) of North America. *Oecologia*, **36**, 1–20.
- Boyce, M.S. (1979) Seasonality and patterns of natural selection for life histories. *American Naturalist*, **114**, 569–583.
- Braun, J.K. & Kennedy, M.L. (1983) Systematics of the genus *Blarina* in Tennessee and adjacent areas. *Journal of Mammalogy*, **64**, 414–425.
- Bried, J. & Jouventin, P. (1997) Morphological and vocal variations among subspecies of the black-faced Sheathbill. *Condor*, **99**, 818–825.
- Brown, C.R. & Brown, M.B. (1998) Intense natural selection on body size and wing and tail asymmetry in cliff swallows during severe weather. *Evolution*, **52**, 1461–1475.
- Brown, J.H. (1995) *Macroecology*. The University of Chicago Press, Chicago.

- Brown, J.H. & Lee, A.K. (1969) Bergmann's rule and climatic adaptation in woodrats (*Neotoma*). *Evolution*, **23**, 329–338.
- Brown, J.H., Marquet, P.A. & Taper, M.L. (1993) Evolution of body size: consequences of an energetic definition of fitness. *American Naturalist*, **142**, 573–584.
- Buerkle, C.A. (2000) Morphological variation among migratory and non-migratory populations of Prairie Warblers. *Wilson Bulletin*, **112**, 99–107.
- Burness, G.P. & Montevecchi, W.A. (1992) Oceanographic-related variation in the body sizes of extinct great Auks. *Polar Biology*, **11**, 545–551.
- Burnett, C.D. (1983) Geographic and climatic correlates of morphological variation in *Eptesicus fuscus*. *Journal of Mammalogy*, **64**, 437–444.
- Calder, W. A., III (1974) Consequences of body size for avian energetics. *Avian energetics* (ed. R.A. Paynter Jr.), pp. 86–151. Nuttall Ornithological Club, Cambridge.
- Calder, W.A., III. (1984) *Size, function and life history*. Harvard University Press, Cambridge.
- Cameron, G.N. & McClure, P.A. (1988) Geographic variation in life history traits of the hispid cotton rat (*Sigmodon hispidus*). *Evolution of life histories of mammals: theory and pattern* (ed. M.S. Boyce), pp. 33–64. Yale University Press, New Haven.
- Cardinal, B.R. & Christidis, L. (2000) Mitochondrial DNA and morphology reveal three geographically distinct lineages of the large bentwing bat (*Miniopterus schreibersii*) in Australia. *Australian Journal of Zoology*, **48**, 1–19.
- Castro, G., Myers, J.P. & Ricklefs, R.E. (1992) Ecology and energetics of sanderlings migrating to 4 latitudes. *Ecology*, **73**, 833–844.
- Cavallini, P. (1995) Variation in the body size of the red fox. *Annales Zoologici Fennici*, **32**, 421–427.
- Chetboun, R. & Tchernov, E. (1983) Temporal and spatial morphological variation in *Meriones tristrami* (Rodentia: Gerbillidae) from Israel. *Israel Journal of Zoology*, **32**, 63–90.
- Chylarecki, P., Kuczynski, L., Vogrin, M. & Tryjanowski, P. (1997) Geographic variation in egg measurements of the lapwing *Vanellus vanellus*. *Acta Ornithologica*, **32**, 137–148.
- Clarke, M.R. & O'Neil, J.A. (1999) Morphometric comparison of Chinese-origin and Indian-derived Rhesus monkeys (*Macaca mulata*). *American Journal of Primatology*, **47**, 335–346.
- Clayton, N.S., Hodson, D. & Zann, R.A. (1991) Geographic variation in Zebra finch subspecies. *Emu*, **91**, 2–11.
- Cooper, M.L. (1998) Geographic variation in size and shape in the southern brown bandicoot, *Isodon obesulus* (Peramelidae: Marsupialia), in Western Australia. *Australian Journal of Zoology*, **46**, 145–152.
- Crow, T.M. (1979) Adaptive morphological variation in helmeted guineafowl *Numida meleagris* and crested guineafowl *Guttera pucherani*. *Ibis*, **121**, 313–320.
- Crow, T.M., Rebelo, A.G., Lawson, W.J. & Manson, A.J. (1981) Patterns of variation in body mass of the black-eyed bulbul *Pycnonotus barbatus*. *Ibis*, **123**, 336–345.
- Cushman, J.H., Lanton, J.H. & Manly, B.F.J. (1993) Latitudinal patterns in European ant assemblages: variation in species richness and body size. *Oecologia*, **95**, 30–37.
- Davis, S. (1977) Size variation of the fox, *Vulpes vulpes* in the palaeartic today and in Israel during the late Quaternary. *Journal of Zoology*, **182**, 343–351.
- Davis, S. (1981) The effects of temperature change and domestication on the body size of late Pleistocene to Holocene mammals of Israel. *Paleobiology*, **7**, 101–114.
- Dayan, T. & Simberloff, D. (1994) Morphological relationships among coexisting heteromyids: an incisive dental character. *American Naturalist*, **143**, 162–177.
- Dayan, T. & Simberloff, D. (1998) Size patterns among competitors: ecological character displacement and character release in mammals, with special reference to island populations. *Mammal Review*, **28**, 99–124.
- Dayan, T., Simberloff, D., Tchernov, E. & Yom-Tov, Y. (1989a) Inter- and intraspecific character displacement in mustelids. *Ecology*, **70**, 1526–1539.
- Dayan, T., Tchernov, E., Yom-Tov, Y. & Simberloff, D. (1989b) Ecological character displacement in Saharo-Arabian *Vulpes*: outfoxing Bergmann's rule. *Oikos*, **55**, 263–272.
- Dayan, T., Simberloff, D., Tchernov, E. & Yom-Tov, Y. (1991) Calibrating the paleothermometer: climate, communities, and the evolution of size. *Paleobiology*, **17**, 189–199.
- Dayan, T., Simberloff, D., Tchernov, E. & Yom-Tov, Y. (1992) Canine carnassials: character displacement in the wolves, jackals and foxes of Israel. *Biological Journal of the Linnean Society*, **45**, 315–331.
- Di-Meglio, N., Romero-Alvarez, R. & Collet, A. (1996) Growth comparison in striped dolphins, *Stenella coeruleoalba*, from the Atlantic and Mediterranean coasts of France. *Aquatic Mammals*, **22**, 11–19.
- Diamond, A.W. (1973) Altitudinal variation in a resident and a migrant passerine on Jamaica. *Auk*, **90**, 610–618.
- DuBowy, P.J. (2000) Morphological correlates of community structure in north American waterfowl. *Community Ecology*, **1**, 147–156.
- Dunbar, R.I.M. (1990) Environmental determinants of intraspecific variation in body weights in baboons (*Papio* spp.). *Journal of Zoology*, **220**, 157–169.
- Dunbrack, R.L. & Ramsay, M.A. (1993) The allometry of mammalian adaptations to seasonal environments: a critique of the fasting endurance hypothesis. *Oikos*, **66**, 336–342.
- Dunning, J.B. Jr., (1993) *CRC handbook of avian body masses*. CRC Press, Boca Raton, FL.
- Eger, J.L. (1990) Patterns of geographic variation in the skull of Nearctic Ermine (*Mustela erminea*). *Canadian Journal of Zoology*, **68**, 1241–1249.
- Ellison, G.T.H., Talor, P.J., Nix, H.A., Bronner, G.N. & McMahon, J.P. (1993) Climatic adaptation of body-size among pouched mice (*Saccostomus campestris*, Cricetidae) in the southern African subregion. *Global Ecology and Biogeography Letters*, **3**, 41–47.
- Engstrom, M.D., Genoways, H.H. & Tucker, P.K. (1987) Morphological variation, karyology, and systematic relationships of *Heteromys gaumeri* (Rodentia: Heteromyidae). *Studies in Neotropical mammalogy: essays in honor of Philip Hershkovits* (ed. B.D. Patterson and R.M. Timm). *Fieldiana Zoology New Series*, Vol. **39**, pp. 289–303.
- Erlinge, S. (1987) Why do European stoats *Mustela erminea* not follow Bergmann's rule? *Holarctic Ecology*, **10**, 33–39.
- Esteban, L., Campos, F. & Arino, A.H. (2000) Biometrics amongst dippers *Cinclus cinclus* in the North of Spain. *Ring and Migration*, **20**, 9–14.

- Fadda, C. & Corti, M. (1998) Geographic variation of *Arvicanthus* (Rodentia, Muridae) in the Nile Valley. *Zeitschrift für Säugetierkunde*, **63**, 104–113.
- Farquhar, C.C. (1998) *Buteo polyosoma* and *B. poecliochrous*, the 'red-backed buzzards' of South America, are conspecific. *Condor*, **100**, 27–43.
- Findley, J.S. & Jones, C. (1962) Distribution and variation of voles of the genus *Microtus* in New Mexico and adjacent areas. *Journal of Mammalogy*, **43**, 154–166.
- Findley, J.S. & Jones, C. (1967) Taxonomic relationships of bats of the species *Myotis fortidens*, *M. lucifugus* and *M. occultus*. *Journal of Mammalogy*, **48**, 429–444.
- Findley, J.S. & Traut, G.L. (1970) Geographic variation in *Pipistrellus hesperus*. *Journal of Mammalogy*, **51**, 741–765.
- Fitzpatrick, B.M. & Dunk, J.R. (1999) Ecogeographic variation in morphology of Red-Tailed hawks in western North America. *Journal of Raptor Research*, **33**, 305–312.
- Fooden, J. & Albrecht, G.H. (1993) Latitudinal and insular variation in crab-eating macaques (Primates, Cercopithecidae: *Macaca fascicularis*). *American Journal of Physical Anthropology*, **92**, 521–538.
- Ford, J. (1986) Avian hybridization and allopatry in the region of the Einsleigh uplands and Burdekin-Lynde divide, North-Eastern Queensland. *Emu*, **86**, 87–110.
- Foster, B.J. (1964) Evolution of mammals on islands. *Nature*, **202**, 234–235.
- Frafjord, K. & Stevy, I. (1998) The red fox in Norway: morphological adaptation or random variation in size? *Zeitschrift für Säugetierkunde*, **63**, 16–25.
- Fuentes, E.R. & Jaksic, F.M. (1979) Latitudinal size variation of Chilean foxes: tests of alternative hypothesis. *Ecology*, **60**, 43–47.
- Fujita, M.S. (1986) A latitudinal comparison of growth and development in the little brown bat, *Myotis lucifugus*, with implications for geographic variation in adult morphology. PhD dissertation, University of Boston.
- Gardezi, T. & da Silva, J. (1999) Diversity in relation to body size in mammals: a comparative study. *American Naturalist*, **153**, 110–123.
- Gay, S.W. & Best, T.L. (1996) Relationship between abiotic variables and geographic variation in skulls of pumas (*Puma concolor*: Mammalia, Felidae) in North and South America. *Zoological Journal of the Linnean Society*, **117**, 259–282.
- Geffen, E., Hefner, R., Macdonald, W. & Ucko, M. (1992) Morphological adaptations and seasonal weight changes in Blandford's fox *Vulpes cana*. *Journal of Arid Environments*, **23**, 287–292.
- Geist, V. (1987) Bergmann's rule is invalid. *Canadian Journal of Zoology*, **65**, 1035–1038.
- Gelvin, B.R. & Albercht, G.H. (1996) Latitudinal size variation in Hanuman langurs (*Presbytis entellus*). *American Journal of Physical Anthropology*, **22** (Suppl.), 111.
- Gibb, J.A. & Williams, J.M. (1990) European rabbit. *The handbook of New Zealand mammals* (ed. C.M. King), pp. 138–160. Oxford University Press, Oxford.
- Gill, F.B. (1995) *Ornithology*, 2nd edn. W.W. Freeman, New York.
- Graves, G.R. (1991) Bergmann's rule near the equator: latitudinal clines in body size of an Andean passerine bird. *Proceedings of the National Academy of Science USA*, **88**, 2322–2325.
- Hadly, E.A. (1997) Evolutionary and ecological response of pocket gophers (*Thomomys talpoides*) to late-Holocene climatic change. *Biological Journal of the Linnean Society*, **60**, 277–296.
- Hadly, E.A., Kohn, M.H., Leonard, J.A. & Wayne, R.K. (1998) A genetic record of population isolation in pocket gophers during Holocene climatic change. *Proceedings of the National Academy of Science USA*, **95**, 6893–6896.
- Hagmeier, E.M. (1961) Variation and relationships in North American marten. *Canadian Field Naturalist*, **75**, 122–138.
- Hall, R.L. & Hall, D.A. (1995) Geographic variation of native people along the Pacific Coast. *Human Biology*, **67**, 407–426.
- Hamilton, T.H. (1961) The adaptive significance of intraspecific trends of variation in wing length and body size among bird species. *Evolution*, **15**, 180–195.
- Hand, S. & York, A. (1990) Morphological variation in the dentition and skull of the Australian ghost bat *Macroderma gigas* (Microchiroptera: Megadermatidae). *Australian Journal of Zoology*, **38**, 263–286.
- Handford, P. (1983) Continental patterns of morphological variation in a South American sparrow. *Evolution*, **37**, 920–930.
- Hansson, L. & Jaarola, M. (1989) Body size related to cyclicality in microtines: dominance behavior or digestive efficiency? *Oikos*, **55**, 356–364.
- Hayes, F.E. (2001) Geographic variation, hybridization and leapfrog pattern of evolution in the suiriri flycatcher (*Suiriri suiriri*) complex. *Auk*, **118**, 457–471.
- Hayes, J.P. & Richmond, M.E. (1993) Clinal variation and morphology of woodrats (*Neotoma*) of the eastern United States. *Journal of Mammalogy*, **74**, 204–216.
- Heaney, L.R. (1978) Island area and body size of insular mammals: evidence from the tri-colored squirrel (*Callosciurus prevosti*) of Southeast Asia. *Evolution*, **32**, 29–44.
- Hoffmeister, D.F. & Lee, M.R. (1967) Revision of the pocket mice, *Perognathus penicillatus*. *Journal of Mammalogy*, **48**, 361–380.
- Houston, S.C., Smith, D.G. and Rohner, C. (1998) Great horned owl (*Bubo virginianus*). *The birds of North America* #372 (ed. A. Poole and F. Gill). The Academy of Natural Sciences, Philadelphia, and the American Ornithologists Union, Washington DC.
- Hubbard, J.P. (1970) Geographic variation in the *Dendroica coronata* complex. *Wilson Bulletin*, **82**, 355–369.
- Huggins, J.A. & Kennedy, M.L. (1989) Morphologic variation in the masked shrew (*Sorex cinereus*) and the smoky shrew (*S. fumeus*). *American Midland Naturalist*, **122**, 11–25.
- Ims, R.A. (1997) Determinants of geographic variation in growth and reproductive traits in the root vole. *Ecology*, **78**, 461–470.
- Iriarte, J.A., Franklin, W.L., Johnson, W.E. & Redford, K.H. (1990) Biogeographic variation of food habits and body size of the American puma. *Oecologia*, **85**, 185–190.
- Irving, L. (1957) The usefulness of Scholanders' views on adaptive insulation of animals. *Evolution*, **11**, 257–259.
- James, F.C. (1970) Geographic size variation in birds and its relationship to climate. *Ecology*, **51**, 365–390.

- James, F.C. (1982) The ecological morphology of birds: a review. *Annales Zoologici Fennici*, **19**, 265–275.
- James, F.C. (1991) Complementary descriptive and experimental studies of clinal variation in birds. *American Zoologist*, **31**, 694–706.
- Järvinen, A. (1994) Global warming and egg size of birds. *Ecography*, **17**, 108–110.
- Jimenez, J.E., Yanez, J.L., Tabilo, E.L. & Jaksic, F.M. (1995) Body size of Chilean foxes – a new pattern in light of new data. *Acta Theriologica*, **40**, 321–326.
- Johnson, D.H. & Stewart, R.E. (1973) Racial composition of migrant populations of sandhill cranes in the northern plain states. *Wilson Bulletin*, **85**, 148–162.
- Johnson, N.K. (1966) Morphologic stability versus adaptive variation in the Hammond's flycatcher. *Auk*, **83**, 179–200.
- Johnston, R.F. (1994) Geographic variation of size in feral pigeons. *Auk*, **111**, 398–404.
- Johnston, R.F. & Selander, R.K. (1973) Evolution in the house sparrow III. Variation in size and sexual dimorphism in Europe and North and South America. *American Naturalist*, **107**, 373–390.
- Kaneko, Y. (1988) Relationship of skull dimensions with latitude in the Japanese field vole. *Acta Theriologica*, **33**, 35–46.
- Kasperek, M. (1996) On the identity of *Ceryle rudis syriaca*. *Journal of Ornithology*, **137**, 357–358.
- Kendeigh, S.C. (1969) Tolerance of cold and Bergmann's rule. *Auk*, **86**, 13–25.
- Kennedy, M.L. & Lindsay, S.L. (1984) Morphologic variation in the raccoon, *Procyon lotor*, and its relationship to genic and environmental variation. *Journal of Mammalogy*, **65**, 195–205.
- Kennedy, M.L. & Schnell, G.D. (1978) Geographic variation and sexual dimorphism in Ord's Kangaroo rat, *Dipodomys ordii*. *Journal of Mammalogy*, **59**, 45–59.
- King, J.E. & Saunders, J.J. (1984) Environmental insularity and the extinction of the American mastodont. *Quaternary extinctions, a prehistoric revolution* (ed. P.S. Martin and R.G. Klein), pp. 315–339. The University of Arizona Press, Tucson.
- Kirk, D.A. & Mossman, M.J. (1998) Turkey vulture (*Cathartes aura*). *The birds of North America* #339. (ed. A. Poole and F. Gill). The Academy of Natural Sciences, Philadelphia, and the American Ornithologists Union, Washington DC.
- Kitchener, D.J. & Caputi, N. (1985) Systematic revision of Australian *Scoteanax* and *Scoterepens* (Chiroptera: Vespertilionidae), with remarks on relationships to other Nycticeini. *Records of the Western Australian Museum*, **12**, 85–146.
- Klein, R.G. (1986) Carnivore size and quaternary climatic change in Southern Africa. *Quaternary Research*, **26**, 153–170.
- Klein, R.G. & Scott, K. (1989) Glacial/interglacial size variation in fossil spotted Hyena (*Crocota crocuta*) from Britain. *Quaternary Research*, **32**, 88–95.
- Koch, P.L. (1986) Clinal geographic variation in mammals: implications for the study of chronoclines. *Paleobiology*, **12**, 269–281.
- Kojola, I. & Laitala, H.M. (2001) Body size variation of brown bear in Finland. *Annales Zoologici Fennici*, **38**, 173–178.
- Kolb, H.H. (1978) Variation in the size of foxes in Scotland. *Biological Journal of the Linnean Society*, **10**, 291–304.
- Kratter, A.W. (1993) Geographic variation in the yellow-billed Caciue *Amblycercus holosericeus*. A partial bamboo specialist. *Condor*, **95**, 641–651.
- Kurtén, B. (1964) The evolution of the polar bear *Ursus maritimus* Phipps. *Acta Zoologica Fennica*, **108**, 3–30.
- Kurtén, B. (1973) Geographic variation in size in the Puma (*Felis concolor*). *Commentationes Biologicae*, **63**, 1–8.
- Laiolo, P. & Rolando, A. (2001) Ecogeographic correlates of morphometric variation in the red-billed chough *Pyrrhocorax pyrrhocorax* and the alpine chough *Pyrrhocorax graculus*. *Ibis*, **143**, 602–616.
- Langvatn, R. & Albon, S.D. (1986) Geographic clines in body weight of Norwegian red deer: a novel explanation to Bergmann's rule? *Holarctic Ecology*, **9**, 285–293.
- Lawton, J.H. (1996) Patterns in ecology. *Oikos*, **75**, 145–147.
- Layne, J.N. & Smith, P.R. (1992) Size comparison of resident and wintering American Kestrels in south-central Florida. *Journal of Field Ornithology*, **63**, 256–263.
- Leafloor, J.O. & Rusch, D.H. (1997) Clinal size variation in Canada geese affects morphometric discrimination techniques. *Journal of Wildlife Management*, **61**, 183–190.
- Lindsay, S.L. (1986) Geographic size variation in *Tamiasciurus douglasii*: significance in relation to conifer cone morphology. *Journal of Mammalogy*, **67**, 317–325.
- Lindsay, S.L. (1987) Geographic size and non-size variation in Rocky mountain *Tamiasciurus hudsonicus*: significance in relation to Allen's rule and vicariant biogeography. *Journal of Mammalogy*, **68**, 39–48.
- Lindsey, C.C. (1966) Body sizes of Poikilotherm vertebrates at different latitudes. *Evolution*, **20**, 456–465.
- Lindestedt, S.L. & Boyce, M.S. (1985) Seasonality, fasting endurance, and body size in mammals. *American Naturalist*, **125**, 873–878.
- Lomolino, M.V. (1985) Body size of mammals on islands: the island rule reexamined. *American Naturalist*, **125**, 310–316.
- Lougheed, S.C. & Handford, P. (1993) Covariation of morphological and allozyme frequency characters in populations of the Rufous-collard sparrow (*Zonotrichia capensis*). *Auk*, **110**, 179–188.
- Loy, A., Di-Martino, S. & Capolago, D. (1996) Patterns of geographic variation of *Talpa romana* Thomas (Insectivora, Talpidae). Preliminary results derived from a geometric morphometrics approach. *Mammalia*, **60**, 77–89.
- Macdonald, D.W., Courtenay, O., Forbes, S. & Mathews, F. (1999) The red fox (*Vulpes vulpes*) in Saudi Arabia: loose-knit groupings in the absence of territoriality. *Journal of Zoology*, **249**, 383–391.
- Marquet, P.A. & Taper, M.L. (1998) On size and area: patterns of mammalian body size extremes across landmasses. *Evolutionary Ecology*, **12**, 127–139.
- Martin, J.L. (1991) Patterns and significance of geographic variation in the blue tit (*Parus caeruleus*). *Auk*, **108**, 820–832.
- Maurer, B.A. (1998) The evolution of body size in birds II. The role of reproductive power. *Evolutionary Ecology*, **12**, 935–944.
- Mayr, E. (1942) *Systematics and the origin of species*. Columbia University Press, New York.

- Mayr, E. (1956) Geographical character gradients and climatic adaptation. *Evolution*, **10**, 105–108.
- Mayr, E. (1963) *Animal species and evolution*. Harvard University Press, Cambridge.
- Mayr, E. (1970) *Populations, species and evolution*. Belknap Press, Cambridge.
- McGillivray, B.W. (1989) Geographic variation in size and reverse size dimorphism of the great horned owl in North America. *Condor*, **91**, 777–786.
- McGillivray, B.W. & Johnston, R.F. (1987) Differences in sexual size dimorphism and body proportions between adult and subadult house sparrows in North America. *Auk*, **104**, 681–687.
- McLellan, L.J. (1984) A morphometric analysis of *Carollia* (Chiroptera, Glossophaginae). *American Museum Novitates*, **2791**, 1–35.
- McNab, B.K. (1971) On the ecological significance of Bergmann's rule. *Ecology*, **52**, 845–854.
- McNab, B.K. (1994) Resource use and the survival of land and freshwater vertebrates on islands. *American Naturalist*, **144**, 643–660.
- McNab, B.K. (1999) On the comparative ecological and evolutionary significance of total and mass-specific rates of metabolism. *Physiological and Biochemical Zoology*, **72**, 642–644.
- Mendelssohn, H. & Yom-Tov, Y. (1999) *Mammalia of Israel*. The Israel Academy of Sciences and Humanities, Jerusalem.
- Mengel, R.M. & Jackson, J.A. (1977) Geographic variation of the red-cockaded woodpecker. *Condor*, **79**, 349–355.
- Merilä, J. (1997) Quantitative trait and allozyme divergence in the Greenfinch (*Carduelis chloris*, Aves: Fringillidae). *Biological Journal of the Linnean Society*, **61**, 243–266.
- Merom, K., McCleery, R. & Yom-Tov, Y. (1999) Age-related changes in wing length and body mass in the Reed Warbler *Acrocephalus scirpaceus* and clamorous Reed Warbler *A. stentoreus*. *Bird Study*, **46**, 249–255.
- Millar, J.S. & Hickling, G.J. (1990) Fasting endurance and the evolution of mammalian body size. *Functional Ecology*, **4**, 5–12.
- Moen, S.M. (1991) Morphologic and genetic variation among breeding colonies of the Atlantic puffin (*Fratercula arctica*). *Auk*, **108**, 755–763.
- Molina, P., Ouellet, H. & McNeil, R. (2000) Geographic variation and taxonomy of the Northern Waterthrush. *Wilson Bulletin*, **112**, 337–346.
- Möller, A.P. (1995) Sexual selection in the barn swallow (*Hirundo rustica*). V. Geographic variation in ornament size. *Journal of Evolutionary Biology*, **8**, 3–19.
- Möller, A.P. & Jennions, M.D. (2001) Testing and adjusting for publication bias. *Trends in Ecology and Evolution*, **16**, 580–586.
- Monroe, B.L. Jr. & Sibley, C.G. (1993) *A world checklist of birds*. Yale University Press, New Haven.
- Mosimann, J.E. & James, F.C. (1979) New statistical methods for allometry with application to Florida Red-winged Blackbirds. *Evolution*, **33**, 444–459.
- Mugaas, J.N. & Seidensticker, J. (1993) Geographic variation of lean body mass and a model of its effect on the capacity of the raccoon to fatten and fast. *Bulletin of the Florida Museum of Natural History Biological Sciences*, **36**, 85–107.
- Murphy, E.L. (1985) Bergmann's rule, seasonality and geographic variation in body size of house sparrows. *Evolution*, **39**, 1327–1334.
- Nagorsen, D.W. (1985) A morphometric study of geographic variation in the snowshoe hare (*Lepus americanus*). *Canadian Journal of Zoology*, **63**, 567–579.
- Nagorsen, D.W. & Tamsit, J.R. (1981) Systematics of *Anoura cultrata*, *A. Brevirostrum* and *A. Werckleae*. *Journal of Mammalogy*, **62**, 82–100.
- Nevo, A. (1989) Natural selection of body size differentiation in spiny mice, *Acomys*. *Zeitschrift für Säugetierkunde*, **54**, 81–99.
- Nevo, E., Beiles, A., Heth, G. & Simson, S. (1986) Adaptive differentiation of body size in speciating mole rats. *Oecologia*, **69**, 327–333.
- Niles, D.M. (1973) Adaptive variation in body size and skeletal proportions of horned larks of the Southwestern United States. *Evolution*, **27**, 405–426.
- Nisany, R. (1974) Geographic variability in the Chukar partridge *Alectoris chukar* (Gray) and Bergmann's rule. MSc Thesis, Hebrew University (in Hebrew).
- Olcott, S.P. & Barry, R.E. (2000) Environmental correlates of geographic variation in body size of eastern cottontail (*Sylvilagus floridanus*). *Journal of Mammalogy*, **81**, 986–998.
- Olsen, P. & Marples, T.G. (1993) Geographic variation in egg size, clutch size and date of laying of Australian raptors (Falconiformes and Strigiformes). *Emu*, **93**, 167–179.
- Owen, J.G. (1989) Population and geographic variation of *Peromyscus leucopus* in relation to climatic factors. *Journal of Mammalogy*, **70**, 98–109.
- Owen, J.G., Schmidly, D.J. & Davis, W.B. (1984) A morphometric analysis of three species of *Carollia* (Chiroptera, Glossophaginae) from Middle America. *Mammalia*, **48**, 85–93.
- Pantelev, P.A., Le Berre, M., Terekhina, A.N. & Ramouz, R. (1998) Application of Bergmann's rule to hibernating animals: an example of the genus *Marmota*. *Russian Journal of Ecology*, **29**, 224–228.
- Paterson, J.D. (1990) Comment – Bergmann's rule is invalid: a reply to V. Geist. *Canadian Journal of Zoology*, **68**, 1610–1612.
- Paterson, J.D. (1996) Coming to America: acclimation in macaque body structures and Bergmann's rule. *International Journal of Primatology*, **17**, 585–611.
- Peris, S.J. (1992) A note on the geographical variation of the spotless starling *Sturnus unicolor* Temm. *Ardea*, **80**, 311–314.
- Porter, E.E. & Hawkins, B.A. (2001) Latitudinal gradients in colony size for social insects: termites and ants show different patterns. *American Naturalist*, **157**, 97–106.
- Post, E., Stenseth, N.C., Langvatn, R. & Fromentin, J.-M. (1997) Global climatic change and phenotypic variation among red deer cohorts. *Proceedings of the Royal Society of London. B. Biological Sciences*, **264**, 1317–1324.
- Power, D.M. (1969) Evolutionary implications of wing and size variation in the red-winged blackbird in relation to geographic and climatic factors: a multiple regression analysis. *Systematic Zoology*, **18**, 363–373.
- Prescott, D.R.C. (1994) Intraspecific and geographical trends in body size of a differential migrant, the evening grosbeak. *Auk*, **111**, 693–702.

- Purdue, J.R. (1989) Changes during the Holocene in the size of white tailed deer (*Odocoileus virginianus*) from central Illinois. *Quaternary Research*, **32**, 307–316.
- Quin, D.G., Smith, A.P. & Norton, T.W. (1996) Ecogeographic variation in size and sexual dimorphism in sugar gliders and squirrel gliders (Marsupialia: Petauridae). *Australian Journal of Zoology*, **44**, 19–45.
- Ralls, K. & Harvey, P.H. (1985) Geographic variation in size and sexual dimorphism of North American weasels. *Biological Journal of the Linnean Society*, **25**, 119–167.
- Rasmussen, P.C. (1994) Geographic variation in morphology and allozymes of South-American Imperial Shags. *Auk*, **111**, 143–161.
- Ravosa, M. (1998) Cranial allometry and geographic variation in Slow-Loris (*Nycticebus*). *American Journal of Primatology*, **45**, 225–243.
- Rees, J.W. (1969) Morphologic variation in the mandible of the white tailed deer (*Odocoileus virginianus*): a study by principle component and canonical Analysis. *Journal of Morphology*, **128**, 113–130.
- Reig, S. (1992) Geographic variation in pine marten (*Martes martes*) and beech marten (*M. foina*) in Europe. *Journal of Mammalogy*, **73**, 744–769.
- Remsen, J.V. (1993) Zoogeography and Geographic variation of *Atlapetes rufinucha* (Aves, Emberizinae), including a distinct new subspecies, in southern Peru and Bolivia. *Proceedings of the Biological Society of Washington*, **106**, 429–435.
- Renaud, S., Benammi, M. & Jaeger, J.J. (1999) Morphological evolution of the murine rodent *Paraethomys* in response to climatic variations (Mio-Pleistocene of North Africa). *Paleobiology*, **25**, 369–382.
- Rensch, B. (1936) Studien über klimatische parallelität der markmalsausrprägung bei Vögeln und säugern. *Archiv Fuer Naturgeschichte (N.F.)*, **5**, 317–363.
- Rensch, B. (1938) Some problems of geographical variation and species formation. *Proceedings of the Linnean Society of London*, **150**, 275–285.
- Rising, J.D. (1988) Geographic variation in sex ratios and body size in wintering flocks of savannah sparrows (*Passerculus sandwichensis*). *Wilson Bulletin*, **100**, 183–203.
- Rising, J.D. & Somers, K.M. (1989) The measurement of overall body size in birds. *Auk*, **106**, 666–674.
- Ritke, M.E. (1990) Quantitative assessment of variation in litter size of the raccoon *Procyon lotor*. *American Midland Naturalist*, **123**, 390–398.
- Root, T. (1988) Energy constraints on avian distribution and abundances. *Ecology*, **69**, 330–339.
- Rosenzweig, M.L. (1968) The strategy of body size in mammalian carnivores. *American Midland Naturalist*, **80**, 299–315.
- Sand, H., Cederlund, G. & Danell, K. (1995) Geographic and latitudinal variation in growth patterns and adult body size of Swedish moose (*Alces alces*). *Oecologia*, **102**, 433–442.
- Scholander, P.F. (1955) Evolution of climatic adaptation in homeotherms. *Evolution*, **9**, 15–26.
- Scholander, P.F. (1956) Climatic rules. *Evolution*, **10**, 39–40.
- Searcy, W.A. (1980) Optimum body sizes at different ambient temperatures: an energetics explanation of Bergmann's rule. *Journal of Theoretical Biology*, **83**, 579–593.
- Sharples, C.M., Fa, J.E. & Bell, J.D. (1996) Geographic variation in size in the European rabbit *Oryctolagus cuniculus* (Lagomorpha: Leporidae) in Western Europe and North America. *Zoological Journal of the Linnean Society*, **117**, 141–158.
- Shepherd, P.C.F., Lank, D.B., Smith, B.D., Warnock, N., Kaiser, G.W. & Williams, T.D. (2001) Sex ratios of Dunlin wintering at two latitudes on the Pacific coast. *Condor*, **103**, 352–360.
- Siegel, S. & Castellan, J.N., Jr. (1988) *Nonparametric statistics*, 2nd edn. McGraw-Hill, Boston.
- Simberloff, D. & Boecklen, W. (1981) Santa Rosalia reconsidered: size ratios and competition. *Evolution*, **35**, 1206–1228.
- Sloto, W.R. (1996) Ecogeographic variations in body size and shape of cape sparrows (*Passer melanurus*) in South Africa. *Journal of Zoology*, **238**, 279–286.
- Smith, F.A., Betancourt, J.L. & Brown, J.H. (1995) Evolution of body size in the Woodrat over the past 25000 years of climate change. *Science*, **270**, 2012–2014.
- Smith, F.A., Browning, H. & Shepherd, U.L. (1998) The influence of climate change on the body mass of woodrats *Neotoma* in an arid region of New Mexico, USA. *Ecography*, **21**, 140–148.
- Smith, F.A. & Charnov, E.L. (2001) Fitness tradeoffs select for semelparous reproduction in an extreme environment. *Evolutionary Ecology Research*, **3**, 595–602.
- Smith, J.I. (1998) Allometric influence on phenotypic variation in the song sparrow (*Melospiza melodia*). *Zoological Journal of the Linnean Society*, **122**, 427–454.
- Snell, R.R. & Cunnison, K.M. (1983) Relation of geographic variation in the skull of *Microtus pennsylvanicus* to climate. *Canadian Journal of Zoology*, **61**, 1232–1241.
- Sokal, R.R. & Rohlf, F.J. (1995) *Biometry*, 3rd edn. W.H. Freeman, New York.
- Stebbins, R.E. (1973) Size clines in the bat *Pipistrellus pipistrellus* related to climatic factors. *Periodicum Biologorum*, **75**, 189–194.
- Studel, K., Porter, W.P. & Sher, D. (1994) The biophysics of Bergmann's rule – a comparison of the effects of pelage and body-size variation on metabolic rate. *Canadian Journal of Zoology*, **72**, 70–77.
- Storz, J.F., Balasingh, J., Bhat, H.R., Nathan, P.T., Doss, D.P.S., Prakash, A.A. & Kunz, T.H. (2001) Clinal variation in body size and sexual dimorphism in an Indian fruit bat, *Cynopterus sphinx* (Chiroptera: pteropodidae). *Biological Journal of the Linnean Society*, **72**, 17–31.
- Straney, D.O. & Patton, J.L. (1980) Phylogenetic and environmental determinants of geographic variation of the pocket mouse *Perognathus goldmani* Osgud. *Evolution*, **34**, 888–903.
- Sullivan, R.M. & Best, T.L. (1997) Effects of environment on phenotypic variation and sexual dimorphism in *Dipodomys simulans* (Rodentia: Heteromyidae). *Journal of Mammalogy*, **78**, 798–810.
- Summers, R.W., Piersma, T., Strann, K.B. & Wiersma, P. (1998) How do purple sandpipers *Calidris maritima* survive the winter north of the arctic circle? *Ardea*, **86**, 51–58.
- Tchernov, E. (1979) Polymorphism, size trends and Pleistocene paleoclimatic response of the subgenus *Sylvaemus* (Mammalia: Rodentia) in Israel. *Israel Journal of Zoology*, **28**, 131–159.
- Telleria, J.L. & Carbonell, R. (1999). Morphometric variation of five Iberian Blackcap *Sylvia atricapilla* populations. *Journal of Avian Biology*, **30**, 63–71.

- Temple, S.A. (1972) Systematics and evolution of the North American merlins. *Auk*, **89**, 325–338.
- Thompson, D.W. (1942) *On growth and form*. Cambridge University Press, Cambridge.
- Thurber, J.M. & Peterson, R.O. (1991) Changes in body size associated with range expansion in the coyote (*Canis latrans*). *Journal of Mammalogy*, **72**, 750–755.
- Tideman, C.R. (1986) Morphological variation in Australian and island populations of Gould's wattled bat, *Chalinolobus gouldii* (Gray) (Chiroptera: Vespertilionidae). *Australian Journal of Zoology*, **34**, 503–514.
- Troy, D.M. (1985) A phenetic analysis of the redpolls *Carduelis flammea flammea* and *C. hornemanni exilipes*. *Auk*, **102**, 82–96.
- Tubaro, P.L. & Segura, E.T. (1995) Geographic Ecological and subspecific variation in the song of the Rufous-browed Peppershrike (*Cyclarhis gujanensis*). *Condor*, **97**, 792–803.
- Twedt, D.J., Bleier, W.J. & Linz, G.M. (1994) Geographic variation in yellow-headed blackbirds from the northern great-plains. *Condor*, **96**, 1030–1036.
- Van-Wynsberghe, N.R., Rising, J.D. & Mackenzie, D.I. (1992) Geographic variation in size of the eastern kingbird. *Wilson Bulletin*, **104**, 612–629.
- Wasserman, D. & Nash, D.J. (1979) Variation in body size, hair length, and hair density in the deer mouse *Peromyscus maniculatus* along an altitudinal gradient. *Holarctic Ecology*, **2**, 115–118.
- Weaver, M.E. & Ingram, D.L. (1969) Morphological changes in swine associated with environmental temperature. *Ecology*, **50**, 710–713.
- Webster, J.D. (1961) A revision of Grace's warbler. *Auk*, **78**, 554–566.
- Whaley, W.H. & White, C.M. (1994) Trends in geographic variation of Cooper's hawk and Northern goshawk in Northern America: a multivariate analysis. *Proceedings of the Western Foundation of Vertebrate Zoology*, **5**, 161–209.
- Wiedenfled, D.A. (1991) Geographic morphology of male yellow warbler. *Condor*, **93**, 712–723.
- Wigginton, J.D. & Dobson, F.S. (1999) Environmental influences on geographic variation in body size of western bobcats. *Canadian Journal of Zoology*, **77**, 802–813.
- Williams, D.F. & Genoways, H.H. (1979) A systematic review of the olive-backed pocket mouse, *Perognathus fasciatus* (Rodentia, Heteromyidae). *Annals of the Carnegie Museum*, **48**, 73–102.
- Wilson, D.E. & Reeder, D.M. (1993) *Mammal species of the world*, 2nd edn. Smithsonian Institution Press, Washington DC.
- Wilson, D.E. & Ruff, S. (1999) *The Smithsonian book of North American mammals*. Smithsonian Institution Press, Washington DC.
- Wilson, G.M. & Choate, J.R. (1997) Taxonomic status and biogeography of the southern bog lemming, *Synaptomys cooperi*, on the central great plains. *Journal of Mammalogy*, **78**, 444–458.
- Wooler, R.D., Sannders, D.A., Bradley, J.S. & De-Rebeira, C.P. (1985) Geographic variation in size of an Australian honeyeater (Aves: Meliphagidae): an example of Bergmann's rule. *Biological Journal of the Linnean Society*, **25**, 355–363.
- Worthy, T.H., Daniel, M.J. & Hill, J.E. (1996) An analysis of skeletal size variation in *Mystacina robusta* Dwyer, 1962 (Chiroptera: Mystacinidae). *New Zealand Journal of Zoology*, **23**, 99–110.
- Wyllie, I. & Newton, I. (1995) Latitudinal variation in body size of Sparrowhawks *Accipiter nisus* within Britain. *Ibis*, **136**, 434–440.
- Yom-Tov, Y. (1993a) Does the rock Hyrax, *Procapra capensis* conform with Bergmann's rule? *Zoological Journal of the Linnean Society*, **108**, 171–177.
- Yom-Tov, Y. (1993b) Size variation in *Rhabdomys pumilio*: a case of character release? *Zeitschrift für Saugetierkunde*, **58**, 48–53.
- Yom-Tov, Y. (2001) Global warming and body mass decline in Israeli passerine birds. *Proceedings of the Royal Society of London. B. Biological Sciences*, **268**, 947–952.
- Yom-Tov, Y. & Nix, H. (1986) Climatological correlates for body size of five species of Australian mammals. *Biological Journal of the Linnean Society*, **29**, 245–262.
- Yom-Tov, Y., Green, W.O. & Coleman, J.D. (1986) Morphological trends in the common brushtail possum, *Trichosurus vulpecula* in New Zealand. *Journal of Zoology*, **208**, 583–593.
- Yom-Tov, Y., Yom-Tov, S. & Moller, H. (1999) Competition, coexistence and adaptation amongst rodent invaders to Pacific and New Zealand islands. *Journal of Biogeography*, **26**, 947–958.
- Yom-Tov, Y., Benjamini, Y. & Kark, S. (2002) Global warming, Bergmann's rule and body mass – are they related? The chukar partridge (*Alectoris chukar*) case. *Journal of Zoology*, **257**, 449–455.
- Zammuto, R.M. & Millar, J.S. (1985) Environmental predictability, variability and *Spermophilus columbianus* life history over an elevational gradient. *Ecology*, **66**, 1784–1794.
- Zink, R.M. & Remsen, J. V., Jr. (1986) Evolutionary processes and patterns of geographic variation in birds. Current ornithology (ed. R.F. Johnston), Vol. 4, pp. 1–69. Plenum Press, New York.

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.
- Baicich, P.J. & Harrison, C.J.O. (1997) *A guide to the nests, eggs, and nestlings of North American birds*. Academic Press, San Diego.
- Best, T.L. (1988) *Dipodomys nelsoni*. *Mammalian Species*, **326**, 1–4.
- Best, T.L. & Lackey, J.A. (1985) *Dipodomys gravipes*. *Mammalian Species*, **236**, 1–4.
- Blakers, M., Davies, S.J.J.F. & Reilly, P.N. (1984) *The atlas of Australian birds*. Melbourne University Press, Carlton.
- Bond, J. (1947) *Field guide to birds of the West Indies*. Macmillan, New York.
- Brown, J.H. & Nicoletto, P.F. (1991) Spatial scaling of species composition: body masses of North American land mammals. *American Naturalist*, **138**, 1478–1512.
- Cramp, S. (1977) *Handbook of the birds of Europe, the Middle East and North Africa: the birds of the Western Palearctic*. Oxford University Press, Oxford.
- De La Rosa, C.L. & Nocke, C.C. (2000) *A guide to the carnivores of Central America*. University of Texas Press, Austin.
- Del Hoyo, J., Elliott, A. & Sargatal, J. (1992) *Handbook of the birds of the world*. Lynx Edicions, Barcelona.
- Dickinson, M.B. (1999) *National geographic field guide to the birds of North America*. National Geographic, Washington DC.
- Dunning, J.B., Jr. (1993) *CRC handbook of avian body masses*. CRC Press, Boca Raton, FL.
- Ehrlich, P.R., Dobkin, D.S. & Wheye, D. (1988) *The Birder's handbook. A field guide to the natural history of North American birds*. Simon & Schuster, New York.
- Ehrlich, P.R., Dobkin, D.S. & Wheye, D. (1994) *The bird-watcher's handbook: a guide to the natural history of the birds of Britain and Europe*. Oxford University Press, Oxford.
- Fjeldsa, J. & Krabbe, N. (1990) *Birds of the high Andes: a manual to the birds of the temperate zone of the Andes and Patagonia, South America*. Zoological Museum, University of Copenhagen and Apollo Books, Copenhagen.
- Ginn, P.J., McAllister W.G. & Le Milstein, P.S. (1989) *The complete book of southern African birds*. Struik Winchester, Cape Town.
- Heinzel, H., Fitter, R. & Parslow, J. (1979) *The birds of Britain and Europe*, 4th edn. William Collins Sons & Co, London.
- Hilty, S.L. & Brown, W.L. (1986) *A guide to the birds of Columbia*. Princeton University Press, Princeton.
- Kingdon, J. (1997) *The Kingdon field guide to African mammals*. Academic Press, San Diego.
- Marchant, S. & Higgins, P.J. (1990) *Handbook of Australian, New Zealand & Antarctic birds*. Oxford University Press, Melbourne.
- Mendelssohn, H. & Yom-Tov, Y. (1999) *Mammalia of Israel*. The Israel Academy of Sciences and Humanities, Jerusalem.
- Nettleship, D.N. & Birkhead, T.R. (1985) *The Atlantic Alcidae: the evolution, distribution, and biology of the auks inhabiting the Atlantic Ocean and adjacent water areas*. Academic Press, London.
- Nowak, R.M. (1999) *Walker's 'Mammals of the world'*, 6th edn. Johns Hopkins University Press, Baltimore.
- Paz, U. (1987) Birds. *Plants and animals of the land of Israel* (ed. A. Alon), Vol. 7. Ministry of Defense/The Publishing House Society for Protection of Nature, Tel Aviv.
- Pizzey, G. (1980) *A field guide to the birds of Australia*. Collins, Sydney.
- Reilly, P. (1994) *Penguins of the world*. Oxford University Press, Oxford.
- Ridgely, R.S. & Tudor, G. (1989). *The birds of South America*. University of Texas Press, Austin.
- Shalmon, B. (1993) *A field guide to the land mammals of Israel*. Keter, Jerusalem.
- Sibley, D.A. (2000) *The Sibley guide to birds*. Alfred A. Knopf, New York.
- Silva, M. & Downing, J.A. (1995) *CRC handbook of mammalian body masses*. CRC Press, New York.
- Simpson, K. & Day, N. (1999) *Birds of Australia*. Princeton University Press, Princeton.
- Strahan, R. (1995) *Mammals of Australia*. Smithsonian Institution Press, Washington DC.
- Wetmore, A., Pasquier, R.F. & Olson, S.L. (1984) *The birds of the Republic of Panama*. Smithsonian Institution Press, Washington DC.
- Wilson, D.E. & Ruff, S. (1999) *The Smithsonian book of North American mammals*. Smithsonian Institution Press, Washington DC.