



Patterns of within-species body size variation of birds: strong evidence for Bergmann's rule

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ABSTRACT

Aim The aim of this study is to test whether Bergmann's rule, a general intraspecific tendency towards larger body size in cooler areas and at higher latitudes, holds for birds throughout the world.

Location This study includes information on species of birds from throughout the world.

Methods I gathered data on body size variation from the literature and used two general meta-analytical procedures to test the validity of Bergmann's rule in birds: a modified vote-counting approach and calculation of overall effect sizes. Related species may show similar body size trends, thus I performed all analyses using nonphylogenetic and phylogenetic methods. I used tests of phylogenetic signal for each data set to decide which type of statistical analysis (nonphylogenetic or phylogenetic) was more appropriate.

Results The majority of species of birds (76 of 100 species) are larger at higher latitudes, and in cooler areas (20 of 22

species). Birds show a grand mean correlation coefficient of +0.32 for body size and latitude, and -0.81 for body size and temperature, both significant trends. Sedentary species show stronger body size trends in some, but not all, analyses. Neither males nor females consistently have stronger body size trends. Additionally, the strength of body size trends does not vary with latitude or body mass.

Conclusions Bergmann's rule holds for birds throughout the world, regardless of whether temperature or latitude (as a proxy) is used. Previous studies have suggested that Bergmann's rule is stronger for sedentary than migratory species, males than females and temperate than tropical taxa. I did not find strong support for any of these as general themes for birds, although few studies of tropical taxa have been conducted. The processes responsible for Bergmann's rule remain somewhat of a black box; however, fasting endurance is probably a more important factor than the traditional hypothesis of heat conservation.

Key words Bergmann's rule, birds, body size, geographical variation, latitude, meta-analysis, temperature.

INTRODUCTION

Bergmann's rule, a general within-species tendency for larger body size in cooler areas for birds and mammals, has long served as a prominent example of adaptive divergence among populations within a species (Mayr, 1963; Ridley, 1996; Futuyma, 1998; see Blackburn *et al.*, 1999 and Ashton, 2001b for discussion of the proper name for this pattern). The original explanation for Bergmann's rule is based on heat conservation. Specifically, larger body size is selected for in cooler areas because the lower surface area to mass ratio results in a lower relative heat loss, leading presumably to

increased survival (Mayr, 1956, 1963). Conversely, smaller body size may be favoured in warmer environments as it increases the surface area to mass ratio, thereby increasing heat dissipation (Brown & Lee, 1969; McNab, 1979). The validity of the heat conservation mechanism has been challenged, primarily on the grounds that changes in fur and feathers or other heat-conserving mechanisms have greater importance in determining rates of heat loss and gain (Scholander, 1955, 1956; Irving, 1957; McNab, 1971). Partly because of these criticisms, Bergmann's rule has been dismissed as a general pattern (e.g. Geist, 1987). However, the validity of Bergmann's rule is not tied to the heat conservation mechanism (Mayr, 1956). In other words, Bergmann's rule is valid if it is true that the majority of species show a negative intraspecific relationship between body size and temperature (or a positive relationship between body size and latitude, if

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latitude is used as a proxy for temperature). Ashton *et al.* (2000) found broad support for Bergmann's rule in mammals. Here I focus on within-species body size trends in birds.

The first general review of Bergmann's rule for birds was by Rensch (1936) who found, using latitude as a proxy for temperature, that 28 of 42 North American bird species were larger at higher latitudes. In addition, a higher percentage of sedentary (13/17) than migratory (15/25) species followed Bergmann's rule. However, Rensch's (1936) analyses have been criticized because they were based on comparisons between mean values for subspecies, whereas the ideal data for comparison are population or individual measurements (McNab, 1971). The next review of general size variation for birds was that of James (1970); all eight species of birds examined from North America showed a negative relationship between body size and wet-bulb temperature, a stronger predictor of body size than dry-bulb temperature. In addition, 10 of 12 species were larger at higher latitudes (James, 1970). Zink & Remsen (1986) provided the most recent, and extensive, review of patterns of intraspecific size variation. In a narrative review of published literature for North American birds they found that only 39 of 92 species (42%) followed Bergmann's rule with respect to latitude. Like Rensch (1936), they found that sedentary species followed Bergmann's rule more strongly than migratory species. Thus, the most extensive review of within-species body size patterns for birds did not find broad support for Bergmann's rule.

Here I present the first quantitative, meta-analytical review of within-species patterns of body size variation relative to latitude and temperature for birds throughout the world. Previous reviews have been narrative and although quite useful, formal meta-analytical techniques offer several advantages (see Gurevitch *et al.*, 2001). Latitude is often used as a proxy for temperature in tests of Bergmann's rule, thus I present analyses separately for latitude and temperature. The generality of overall trends are tested by examining patterns within each major taxonomic group. Strengths of trends are compared between migratory and sedentary species, and also between males and females because sex differences in size trends have been documented (e.g. Fleischer & Johnston, 1984).

METHODS

Data

Information concerning within-species relationships between body size and latitude, elevation and environmental temperature were gathered from the literature for species found throughout the world. Most studies of body size variation used latitude as a proxy for temperature. Any study reporting body size variation was included, regardless of whether results were presented qualitatively (positive or negative

relationship) or quantitatively (correlation coefficient). Each species was classified as migratory or sedentary based on Zink & Remsen (1986) or information presented in original citations. If more than one study was available for a species I used the study that sampled the greatest number of populations and over the greatest range of latitudes or temperatures. Studies reporting size variation relative to latitude were combined with studies of size relative to elevation because both are similar proxies for temperature. Data were gathered using literature searches for recent publications, searching references provided in other reviews and papers (e.g. Zink & Remsen, 1986), and perusing ornithological and zoological journals. I found data on size variation relative to latitude for 100 species, relative to elevation for three species, and relative to temperature for 22 species (Table 1).

Wing length was by far the most frequently used measure of body size (Table 1). Previous authors have pointed out that other indicators of body size should be used because wing length may not be a good proxy for body size as it can vary based on migratory tendencies and habitat occupied (Hamilton, 1961; Aldrich, 1984; Zink & Remsen, 1986). However, wing length is significantly related to other measures of body size for many species of birds (Rand, 1961; Manning, 1964; Power, 1969; Graves, 1991; Wyllie & Newton, 1994) but not all (Miller, 1941; Johnston & Selander, 1964). Thus, wing length is generally, but not always, a good indicator of body size. Alternative size measures have been recommended (Zink & Remsen, 1986); however, data on wing length remain the most frequently used in studies of size variation of birds. Thus, for most species, wing length is used as the measure of body size.

Publication bias

Publication bias, the selective reporting of research results, can influence the results of a meta-analysis (Rosenthal, 1979, 1991; Begg, 1994; Palmer, 1999; Gurevitch *et al.*, 2001). Publication bias occurs if certain studies, such as those based on small sample sizes, are not published and therefore are not included in a meta-analysis. Qualitative and quantitative diagnostics to assess the presence of publication bias have been proposed (Palmer, 1999, 2000). One qualitative diagnostic is a plot of effect size vs. some factor, such as sample size, that might bias publication of results. In this case, publication bias may be present if studies based on small sample size are under-represented (Palmer, 2000). A quantitative measure of publication bias is testing for a significant relationship between effect size and some factor, such as sample size (Palmer, 2000). If a significant relationship exists, then it is possible that publication bias is present.

To test for publication bias in my dataset I plotted correlation coefficients between body size and latitude (the most frequently reported measure of effect size; Table 1) vs. the

Table I Within-species relationships between body size and latitude, elevation or temperature. Body size trends for each species are reported qualitatively as increasing (+) or decreasing (-) in size with latitude/elevation or temperature, or quantitatively (correlation coefficient) depending on available data. *P*-values refer to the statistical significance of any trend (based on correlation or regression analyses). Species are arranged based on migratory tendency (migratory or sedentary), then alphabetically by order, family and species (following American Ornithologists' Union, 1983; Sibley & Monroe, 1990) within these two categories. *N* = number of populations or individuals (noted with an *) studied. Range (mean) = range and mean of latitudes (degrees) studied. *r* (lat.) = correlation between body size and latitude/elevation. *r* (temp.) = correlation between body size and temperature. *M* = male. *F* = female. † = excluded from all analyses (see text). PCA = principal components analysis. *W* = weight. *H* = humerus. *I* = isophane. *S* = skull length. *T* = annual wet-bulb temperature. *E* = elevation

Taxon	<i>N</i>	Range (mean)	<i>r</i> (lat.)	<i>P</i> (lat.)	<i>r</i> (temp.)	<i>P</i> (temp.)	Source
Migratory							
APODIFORMES							
Apodidae							
<i>Aeronautes saxatalis</i>			+				Behle, 1973
ANSERIFORMES							
Anatidae							
<i>Anser albifrons</i>			+				Elgas, 1970
<i>Anser fabalis</i>			+ (W)				Van Impe, 1987
<i>Branta canadensis</i>	6	16 (50.5)	F: -0.95(S)	< 0.01			Leafloor & Rusch, 1997
CAPRIMULGIFORMES							
Caprimulgidae							
<i>Chordeiles minor</i>	10	10 (33)	0.53	0.12			James, 1970
CHARADRIIFORMES							
Alcidae							
<i>Cephus columba</i>	4	19 (47.3)	-0.72	0.28			Storer, 1950
Laridae							
<i>Larus argentatus</i>	7	12 (64)	M: 0.94	< 0.01			Monaghan <i>et al.</i> , 1983
<i>Stercorarius longicaudus</i>			-				Manning, 1964
Scolopacidae							
<i>Tringa solitaria</i>			+				Conover, 1944
COLUMBIFORMES							
Columbidae							
<i>Columba fasciata</i>			+				Brodkorb, 1943
<i>Zenaida asiatica</i> †			M: 0.34 F: -0.27		0.57 0.66		Aldrich, 1981
FALCONIFORMES							
Accipitridae							
<i>Buteo lineatus</i>	14	15 (35.5)	M: 0.75	< 0.01			James, 1970
Falconidae							
<i>Falco sparverius</i>	9		19 (37.5)	M: 0.70 F: 0.68	< 0.05 < 0.05		James, 1970
12							
GRUIFORMES							
Rallidae							
<i>Rallus longirostris</i>			-				Banks & Tomlinson, 1974
PASSERIFORMES							
Alaudidae							
<i>Eremophila alpestris</i>	32	10	M: + F: + (PCA)	< 0.01 < 0.05			Niles, 1973
Corvidae							
<i>Cyanocitta cristata</i>	51	18 (37)	M: 0.77	< 0.01	M: -0.81(T)	< 0.01	James, 1970
	30		F: 0.44	< 0.05	F: -0.52(T)	< 0.01	
Emberizidae							
<i>Agelaius phoeniceus</i>	54	25 (47.5)	M: 0.58(I)	< 0.01	M: -(T)	< 0.05	Power, 1969, 1970
	38		F: 0.63(I)	< 0.01	F: -(T)	< 0.05	
<i>Dendroica auduboni</i>			-				Hubbard, 1970
<i>Dendroica coronata</i>			+				Hubbard, 1970
<i>Dendroica graciae</i>			+				Webster, 1961
<i>Dendroica petechia</i>	20	65 (33)	-0.47(W)	< 0.05			Wiedenfeld, 1991

Table I continued.

Taxon	N	Range (mean)	r (lat.)	P (lat.)	r (temp.)	P (temp.)	Source
<i>Dendroica townsendi</i>			—				Morrison, 1983
<i>Geothlypis trichas</i>			—				Behle, 1950
<i>Guiraca caerulea</i>	13	25 (24.3)	M: -0.74	< 0.01			Storer & Zimmerman, 1959
<i>Icterus galbula</i>	46	30 (35)	M: -0.39	< 0.01			Rising, 1970
<i>Melospiza lincolni</i>			—				Miller & McCabe, 1935
<i>Melospiza melodia</i>			+				Aldrich, 1984
<i>Oporornis philadelphus</i>	21	15 (51.5)	-0.49 (PCA)	< 0.05			Pitocchelli, 1992
<i>Passerculus sandwichensis</i>	7	24 (24.6)	M: 0.48 F: 0.48	0.28 0.28			Hubbard, 1974
<i>Passerella iliaca</i>			M: — F: —				Zink, 1986
<i>Passerina ciris</i>	7	9 (32.1)	0.49	0.26			Storer, 1951
<i>Pipilo erythrorthalmus</i>			+				Dickinson, 1952
<i>Piranga flava</i>			+				Sutton & Phillips, 1942
<i>Quiscalus quiscula</i>	22	20	M: +	< 0.001			Huntington, 1952
<i>Seiurus noveboracensis</i>			+				Eaton, 1957
<i>Sturnella magna</i>	26	12 (32)	M: 0.34	> 0.05	M: -0.43 (T)	< 0.05	James, 1970
<i>Xanthocephalus xanthocephalus</i> †			M: 0.08	F: -0.41	0.83	0.21	Twedd <i>et al.</i> , 1994
<i>Zonotrichia leucophrys</i>			+ (E)				Banks, 1964
Fringillidae							
<i>Pinicola enucleator</i>	45*	24	—	< 0.001	—		Adkisson, 1977
Hirundinidae							
<i>Hirundo pyrrhonota</i>			+				Behle, 1976
<i>Progne subis</i>			+				Behle, 1968
Muscicapidae							
<i>Catharus guttatus</i>					—		Aldrich, 1968
<i>Regulus calendula</i>			M: —				Browning, 1979
<i>Turdus migratorius</i>	14	10 (39)	M: 0.64	< 0.05	M: -0.90(T)	< 0.01	James, 1970
Paridae							
<i>Parus major</i>					—		Snow, 1954
Sturnidae							
<i>Sturnus vulgaris</i>	10	17 (38.4)	M: 0.22 F: 0.49	0.54 0.15	M: -0.42	< 0.05	Blem, 1981
Tyrannidae							
<i>Contopus sordidulus</i>			+				Browning, 1977
<i>Empidonax difficilis</i>					M: — F: —		Johnson, 1980
<i>Empidonax traillii</i>			+				Phillips, 1948; Aldrich, 1951
<i>Tyrannus tyrannus</i>	18	22 (42)	M: 0.45	0.05			Van Wijnsberghe <i>et al.</i> , 1992
	10	23 (42)	F: 0.62	0.05			
Vireonidae							
<i>Vireo gilvus</i>			—				Hamilton, 1958
<i>Vireo griseus</i>			+				Burleigh & Lowery, 1945;
<i>Vireo olivaceus</i>	7	8 (53)	0.78(I)	< 0.05			Hamilton, 1958
<i>Vireo philadelphicus</i>	7	8 (53)	0.81(I)	< 0.05	-0.06	0.90	Barlow & Power, 1970
<i>Vireo solitarius</i>			—				Barlow & Power, 1970
							Hamilton, 1958
PICIFORMES							
Picidae							
<i>Colaptes auratus</i>	8	11 (33.5)	0.85	< 0.01			James, 1970
PROCELLARIIFORMES							
Hydrobatidae							
<i>Oceanodroma leucorhoa</i>	13				-0.72	< 0.01	Ainley, 1980

Table I continued.

Taxon	N	Range (mean)	<i>r</i> (lat.)	<i>P</i> (lat.)	<i>r</i> (temp.)	<i>P</i> (temp.)	Source
Sedentary							
CICONIIFORMES							
Chionidae			+				Bried & Jouventin, 1997
<i>Chionis minor</i>							
COLUMBIFORMES							
Columbidae							
<i>Columba livia</i>	11	9	22 (40)	M: 0.53 F: 0.66 (PCA)	0.06		Johnston, 1990, 1994
CORACIIFORMES							
Dacelonidae							
<i>Dacelo gigas</i>	92*	23 (26.5)	0.40	< 0.001			Ford, 1986
FALCONIFORMES							
Accipitridae							
<i>Accipiter fasciatus</i>				M: + F: +			Ford, 1986
<i>Accipiter nisus</i>	8	6 (54)		M: 0.87 F: 0.75	< 0.001 < 0.001		Wyllie & Newton, 1994
<i>Buteo jamaicensis</i>	6	25				F: 0.35	< 0.05
GALLIFORMES							
Phasianidae							
<i>Callipepla squamata</i>				+			Rea, 1973
<i>Colinus virginianus</i>				+			Aldrich, 1946
PASSEKIFORMES							
Certhidae							
<i>Cinnycerthia peruviana</i>	91*	18 (9)		M: -0.79 F: -0.79 (PCA)	< 0.001		Brumfield & Remsen, 1996
<i>85*</i>							
Corvidae							
<i>Aphelocoma coerulescens</i>				+			Pitelka, 1945
<i>Corvus corax</i>				M: + F: +			Willett, 1941
<i>Cyanocitta stelleri</i>	13	45 (24.7)		M: 0.63	< 0.05		Brown, 1963
<i>Myiagra inquieta</i>	80*	23 (26.5)		0.47	< 0.001		Ford, 1986
<i>Perisoreus canadensis</i>	5	20 (51.6)		-0.42	0.31		Aldrich, 1943
Emberizidae							
<i>Aimophila ruficeps</i>				+			Hubbard, 1975
<i>Amblycercus holosericeus</i>	8	21 (12.5)		M: 0.67 F: 0.57 (PCA)	< 0.001		Kratter, 1993
<i>Diglossa carbonaria</i>	215*	18 (9)		M: 0.16 F: 0.25	< 0.001 < 0.001		Graves, 1991
<i>87*</i>							
<i>Pipilo fuscus</i>				M: + F: +			Davis, 1951
<i>Quiscalus major</i>				+			Stevenson, 1978
Fringillidae							
<i>Carduelis chloris</i>	12	28 (51)		0.81(H)	< 0.01		Merila, 1997
Maluridae							
<i>Malurus cyaneus</i>				M: + F: +			Tideman & Schodde, 1989
<i>Malurus lamberti†</i>				M: - F: +			Tideman & Schodde, 1989
<i>Malurus leucopterus</i>	4	20		M: + F: +	< 0.05		Tideman & Schodde, 1989
Meliphagidae							
<i>Lichenostomus flavus</i>				+			Ford, 1986
<i>Meliphaga virescens</i>	28	24 (25)		0.91(W)	< 0.001		Wooller <i>et al.</i> , 1985

Table I continued.

Taxon	N	Range (mean)	r (lat.)	P (lat.)	r (temp.)	P (temp.)	Source
Muscicapidae							
<i>Chamaea fasciata</i>			+		–		Bowers, 1960
<i>Cyornis hyacinthinus</i>			M: +(E)				Mayr, 1944
Paridae							
<i>Parus caeruleus</i>			+				Martin, 1991
<i>Parus carolinensis</i>	22	6 (33)	M: 0.65 F: 0.57	< 0.01 < 0.05	M: –0.74(T) F: –0.55(T)	< 0.01 < 0.05	James, 1970
<i>Parus cristatus</i>	19				–		Snow, 1954
Passeridae							
<i>Passer domesticus</i>	19	25 (36.5)	M: 0.55 F: 0.58	< 0.01 < 0.01	M: –0.64 F: –0.68	< 0.01 < 0.01	Murphy, 1985
<i>Passer melanurus</i>			+				Slotow & Goodfriend, 1996
<i>Quelea quelea</i>	4	27 (13.6)	M: –0.58	0.42			Ward, 1966
Ploceidae							
<i>Euplectes orix</i>			+				Craig, 1993
Pomatostomidae							
<i>Pomatostomus temporalis</i>			–				Edwards & Kot, 1995
Sittidae							
<i>Sitta carolinensis</i>	42	14 (35)	M: 0.88 F: 0.068	< 0.01 > 0.05	M: –0.89(T) F: –0.32(T)	< 0.01 > 0.05	James, 1970
<i>Sitta pusilla</i>	32						
<i>Sitta pygmaea</i>	8	15 (33.1)	M: 0.88 F: 0.86	< 0.01 < 0.01			Norris, 1958
<i>Sitta pygmaea</i>			M: – F: –				Norris, 1958
Troglodytidae							
<i>Thryothorus ludovicianus</i>	4	15 (32.4)	M: –0.64 F: –0.62	0.36 0.38			Lowery, 1940
Tyrannidae							
<i>Empidonax hammondi</i>	8	30 (50.1)	M: 0.20 F: 0.47	0.63 0.34			Johnson, 1966
Vireonidae							
<i>Cyclarhis gujanensis</i>	93*	35 (17.5)	0.54(PCA) +(E)	< 0.001			Tubaro & Segura, 1995
<i>Vireo buttoni</i>					+		Hamilton, 1958
PELECANIFORMES							
Phalacrocoracidae							
<i>Phalacrocorax atriceps</i>	55*	15 (47.5)	M: 0.42 F: 0.44 (PCA)	< 0.01 < 0.01			Rasmussen, 1994
<i>Phalacrocorax atriceps</i>	116*						
PICIFORMES							
Picidae							
<i>Picoides borealis</i>	24		+			< 0.001	Mengel & Jackson, 1977
<i>Picoides pubescens</i>	76	18 (35)	–0.889	< 0.05	–0.915(T)	< 0.01	James, 1970
<i>Picoides villosus</i>	17	6 (35)	M: 0.19	> 0.05	M: –0.62(T)	< 0.01	James, 1970
<i>Picoides villosus</i>	26		F: 0.61	< 0.01	F: –0.79(T)	< 0.01	
STRIGIFORMES							
Podargidae							
<i>Podargus strigoides</i>			M: + F: +				Ford, 1986
Strigidae							
<i>Bubo virginianus</i>	5	17 (37.7)	M: 0.58 F: 0.57	0.31 0.32			McGillivray, 1989
<i>Ninox connivens</i>			+				
<i>Otus asio</i>	17	10 (35)	M: 0.52 F: 0.84	< 0.05 < 0.01	M: –0.69(T) F: –0.87(T)	< 0.01 < 0.01	Ford, 1986 James, 1970
<i>Otus kennicottii</i>	16						
Tytonidae			+ +				Miller & Miller, 1951
<i>Tyto novaehollandiae</i>			+				Ford, 1986

number of populations sampled for 39 species (not shown). Studies based on small sample size are not under-represented. Further, there is no relationship between effect size (r) and the number of populations sampled ($r^2 = 0.0085$, $F = 0.32$, d.f. = 1, 37, $P = 0.58$). Thus, no evidence of publication bias exists for the dataset.

Phylogenetic considerations

Another factor that may influence the results of a meta-analysis using species as data points is the phylogenetic non-independence of the data. Species are related and therefore traits of closely related species may be similar. It has been argued that if species values have phylogenetic signal (i.e. related species have similar trait values) then standard statistical methods are inappropriate and phylogenetic versions of statistical analyses must be performed (Harvey & Pagel, 1991; Garland *et al.*, 1999; Garland & Ives, 2000). Tests for detecting phylogenetic signal in comparative datasets have been proposed (Maddison & Slatkin, 1991; Pagel, 1999); however, the exact statistical properties (e.g. power) of the tests remain to be determined. Nonphylogenetic and phylogenetic versions of each statistical analysis are presented because of uncertainty regarding the power of tests for phylogenetic signal in comparative data. I used tests of phylogenetic signal to indicate which type of analysis was probably most appropriate for each dataset.

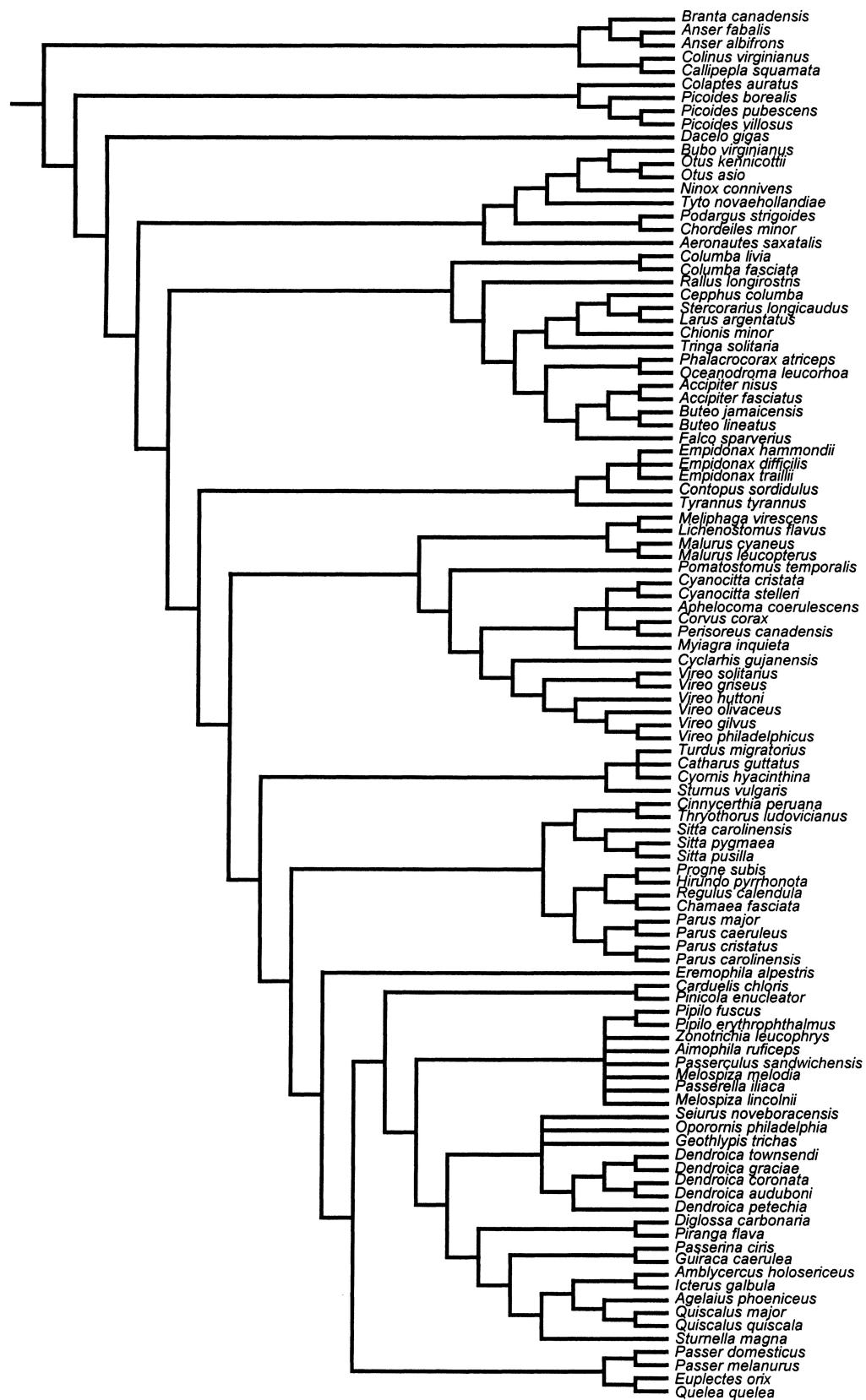
Vote-counting analyses

I tested the relationship between body size and latitude/elevation (hereafter referred to as latitude) or temperature using two general meta-analytical procedures. In the first approach, a vote-counting technique, I used all the data regardless of whether information for each species was qualitative (positive or negative association) or quantitative (correlation coefficient). In other words, any species showing a positive relationship between size and latitude or a negative association between size and temperature was counted as evidence for Bergmann's rule and any species showing the opposite trend was counted as evidence for the converse to Bergmann's rule. This approach maximized the number of species included because only qualitative statements about body size trends were available for some species (Table 1). I tested whether birds in general showed a significant relationship between size and latitude or temperature with the G statistic goodness-of-fit test with Yates's correction for continuity. The observed values were the number of species that showed a positive or negative relationship between size and latitude or temperature, and the expected values were equal proportions of species with positive and negative associations. Species with trends in opposite directions for males and females were excluded from all analyses (latitude: three species; Table 1).

For phylogenetic versions of the vote-counting analyses I generated phylogenetically correct null distributions because standard statistical null distributions may be inappropriate in comparative analyses. Assuming an evolutionary model of Brownian motion and using the known phylogenetic relationships for birds (Fig. 1), I generated 1000 simulated datasets using PDSIMUL (Garland *et al.*, 1993). For the simulations I assumed upper and lower bounds of +1.0 and -1.0 (limits for correlation coefficients), starting correlation coefficients (value at the root of the tree) of 0 and variances of 1.0. Each simulated dataset had the same number of taxa as the actual data. For each of the 1000 simulated datasets I counted the proportion of species with positive relationships of body size and latitude or temperature, and generated a histogram of the proportions positive, creating a phylogenetically correct null distribution of the vote-count data. I compared the actual vote-counts (proportions positive) to the phylogenetically correct null distributions of vote-counts and assessed significance (i.e. a trend is significant if the proportions positive are below the 2.5 percentile or above the 97.5 percentile).

To examine whether nonphylogenetic or phylogenetic methods are more appropriate for the vote-count datasets I tested for phylogenetic signal of the data using the method of Maddison & Slatkin (1991), implemented by MacClade 4.0 (Maddison & Maddison, 2001). I mapped the discrete vote-count data (i.e. positive or negative associations of size with latitude or temperature) onto the known topology (Fig. 1), trimmed as necessary, and counted the number of steps required to generate the distribution of character states. I then randomly shuffled the character states on the phylogenies 1000 times to generate null distributions of the number of evolutionary steps. I compared the tree scores (numbers of steps) of the actual data to the null distributions; scores significantly shorter than the null indicate phylogenetic signal.

Inclusion of species values that are only qualitative in nature, or which lack significance, in the vote-counting analyses may be questioned. There is no reason to expect a bias in direction of effect for nonsignificant species values, thus if most nonsignificant species values follow a particular direction it is probably because a real effect exists, but the analyses lack significance because of low statistical power for most species. Accordingly, all species values should be included because they are relevant to overall trends and do contribute significance to any overall patterns (Hunter & Schmidt, 1990; Bushman, 1994). However, at least some of the included studies had good statistical power and therefore I also included vote-counting analyses for latitude and temperature, coding each species as showing a significant positive, significant negative, or nonsignificant trend. I limited these analyses to species for which ≥ 10 populations or ≥ 100 individuals were sampled, and populations were sampled over $\geq 10^\circ$ latitude or $\geq 10^\circ\text{C}$. If a greater number of species showed a



significant positive relationship between body size and latitude than the number of species with negative relationships plus the number of species that failed to show a significant trend, then Bergmann's rule is supported.

In order to examine whether any overall trends are consistent among different phylogenetic groups I partitioned the data according to orders and families. I then counted the numbers of species showing positive and negative associations between body size and latitude or temperature within orders and families. Only higher-level groups with data from more than one species were included. Eight orders and 18 families met this criterion for studies of size and latitude, two orders and five families for temperature.

Grand mean correlation coefficient analyses

The second meta-analytical approach to test for Bergmann's rule consisted of combining the correlation coefficient values and calculating overall effect sizes (i.e. grand mean correlation coefficients) following the methods of Hedges & Olkin (1985). To calculate an overall effect size I first Z-transformed all of the correlation values, then weighted the Z-transformed effect sizes based on sample sizes using the procedures of Hedges & Olkin (1985). An overall, Z-transformed, effect size was calculated and then converted to an overall correlation value using tables in Zar (1996). This method can use only correlation coefficients based on more than three populations; data for 39 species with respect to latitude and 13 species for temperature satisfied this criterion (Table 1). If different correlation coefficients were reported for males and females of a particular species I used the correlation coefficient based on the greatest number of populations surveyed; if both sexes were sampled equally, then I used the average of the two values.

For phylogenetic versions of the grand mean correlation coefficient analyses I generated phylogenetically correct null distributions of grand mean correlation coefficients. Using PDSIMUL (Garland *et al.*, 1993), I created 1000 simulated datasets (i.e. simulated correlation coefficients) assuming a model of Brownian motion and using the known phylogeny (Fig. 1). Simulation parameters were: starting values (correlation coefficient at the root of the tree) of 0, variances of 1.0, and upper and lower bounds of +1.0 and -1.0 (limits for correlation coefficients). I calculated grand mean correlation coefficients for each of the 1000 simulated datasets in PDTIPS (Garland *et al.*, 1993). I compared the actual grand mean correlation coefficients to histograms of the 1000 simulated

grand mean correlation coefficients (phylogenetically correct null distributions); actual grand mean correlation coefficients are significant if below the 2.5 percentile or above the 97.5 percentile of the simulated correlations.

To examine whether nonphylogenetic or phylogenetic versions of the grand mean correlation coefficient analyses are more appropriate I tested for phylogenetic signal of the data following Blomberg *et al.* (2001). This method is analogous to the Maddison & Slatkin (1991) test but operates on continuous characters. I plotted the correlation coefficient data onto the known phylogeny (Fig. 1) and calculated the variance of the contrasts of the actual correlation coefficients using PDTREE (Garland *et al.*, 1999; Garland & Ives, 2000). I then generated 1000 random datasets of correlation coefficients by shuffling the actual correlation coefficients across the phylogenies using PDRANDOM (Lapointe & Garland, 2001). I used PDERROR (Diaz-Uriarte & Garland, 1996) to calculate the variances of the contrasts for the 1000 random datasets. The variances of the contrasts of the randomized datasets should generally be larger than for the actual datasets if phylogenetic signal is present. I compared the actual variances of the contrasts of correlation coefficients to the phylogenetically random distributions; variances significantly lower than the null (i.e. less than 95% of the random datasets) indicate phylogenetic signal. Simulation studies indicate that the foregoing procedure has adequate statistical power (approximately 0.8) for phylogenies with 20 or more species (T. Garland, pers. comm.).

The second analytical approach, calculating overall effect sizes using data for species for which correlation values are available, is potentially a more rigorous test for patterns (Hunter & Schmidt, 1990; Gurevitch *et al.*, 2001) and accounts for variation in sample size among studies. However, the number of species with reported correlation values is relatively small, and therefore these analyses are supplemental to the more inclusive vote-counting analyses using all the species. In addition, Bergmann's rule is stated in terms of the number of species following a particular trend; the vote-counting procedure is the only method that provides data directly testing the rule as currently stated.

Relationship between Bergmann's rule and latitude

The strength of body size trends may vary with latitude and therefore I tested whether the strength of Bergmann's rule was significantly related to latitude. Correlation coefficients for size and latitude were more commonly reported than correlation

Fig. 1 Phylogenetic relationships among species included in this study. The phylogeny is primarily based on relationships presented in Sibley & Ahlquist (1990) and Sibley & Monroe (1990) with the following additions/revisions: Icterini from Klicka *et al.* (2000); Vireo from Murray *et al.* (1994) with the placement of *V. huttoni* from Johnson *et al.* (1988); *Malurus* from Christidis & Schodde (1997); *Parus* from Kvist *et al.* (1996) and Slikas *et al.* (1996); *Dendroica* from Lovette & Bermingham (1999); genera of Parulini from Price *et al.* (1998); Emberizidae unresolved due to conflicts among studies (Zink & Blackwell, 1996; Groth, 1998; Patten & Fugate, 1998; Klicka *et al.*, 2000).

coefficients for size and temperature, so I used the former. I calculated the mean latitude of populations or individuals for each species; if sampling locations were not reported then I used the midpoint of the range of latitudes sampled. If correlation coefficients were reported separately for males and females of the same species then I used the correlation coefficient based on the greatest number of populations surveyed. If both sexes were sampled equally, then I used the average of the correlation coefficients. I performed analyses nonphylogenetically using regression and phylogenetically using independent contrasts (Felsenstein, 1985) as implemented by PDTREE (Garland *et al.*, 1999; Garland & Ives, 2000). The independent contrasts analysis used the known phylogeny (Fig. 1), pruned to include only necessary taxa. Contrasts were standardized appropriately, according to diagnostics of Garland *et al.* (1992), using equal branch lengths. To test for phylogenetic signal of the data I used the same approach as for the phylogenetic grand mean correlation coefficient analyses.

Relationship between Bergmann's rule and body mass

The strength of body size trends may also vary with body size. In fact, biophysical models of the relative influences of fur and body size on heat loss in mammals suggest that smaller species should show a stronger Bergmann's rule trend (Porter *et al.*, 1994; Steudel *et al.*, 1994). Although the relative effects of variation in properties of feathers and body size on heat loss have not been investigated for birds, a similar prediction might be made. I tested the relationship between the strength of Bergmann's rule (correlation coefficient between size and latitude) and body mass for 44 species. Body mass data are from Dunning (1993). If correlation coefficients were reported separately for males and females of the same species then I used the correlation coefficient based on the greatest number of populations surveyed. If both sexes were sampled equally, then I used the average of the correlation coefficients. I performed analyses nonphylogenetically and phylogenetically as for analyses of Bergmann's rule and latitude.

RESULTS

Vote-counting analyses

Seventy-six of 100 species of birds have positive within-species relationships of body size and latitude (Table 1), a significant trend in accord with Bergmann's rule (nonphylogenetic analysis: $G = 27.28$, $P < 0.001$; phylogenetic analysis: $P < 0.05$). Twenty of 22 species have negative associations between body size and temperature (Table 1). This trend is also significantly in accord with Bergmann's rule (nonphylogenetic analysis: $G = 14.92$, $P < 0.001$; phylogenetic analysis: $P < 0.01$).

If only well-sampled species are included (see Methods), 18 species have significant positive associations between body size and latitude, five have significant negative relationships, and four fail to show significant relationships. Thus, 18 of 27 species show trends supporting Bergmann's rule with respect to latitude. All 10 species from the well-sampled temperature dataset have negative associations of body size and temperature.

When the data are separated into orders and families to assess the phylogenetic breadth of Bergmann's rule, seven of eight orders and 17 of 19 families have more species with positive associations between body size and latitude than the opposite (Table 2). The one order (Charadriiformes) and two families (Laridae and Fringillidae) that do not follow Bergmann's rule have the same numbers of species showing positive and negative trends, and data for fewer than four species are available for each group (Table 2). Data for temperature are available for two orders and five families. Both orders and four of the five families have more species with negative relationships between body size and temperature than the opposite (Table 3). The only family that is an exception (Vireonidae) has one species showing a positive relationship and the other a negative relationship (Table 3).

Neither the latitude nor temperature vote-count datasets contain phylogenetic signal. Twenty steps are required to optimize the latitude data on the phylogeny, while the randomly shuffled datasets range from 16 to 27 steps ($P = 0.094$). Two steps are necessary to optimize the temperature vote-count data onto the phylogeny, while the randomly shuffled datasets range from one to two steps ($P = 1.0$).

Grand mean correlation coefficient analyses

The results using the meta-analytical technique of the grand mean correlation coefficient are similar to those from the vote-counting procedure. Birds have a significant overall positive correlation ($r = +0.32$) between body size and latitude (nonphylogenetic analysis: $Z = 7.82$, $P < 0.001$; phylogenetic analysis: $P < 0.05$; 39 species). The grand mean correlation coefficient between body size and temperature ($r = -0.81$) is also significantly in accord with Bergmann's rule (nonphylogenetic analysis: $Z = 19.41$, $P < 0.0001$; phylogenetic analysis: $P < 0.001$; 13 species).

As with the vote-count data, neither the latitude nor temperature grand mean correlation coefficient datasets contain phylogenetic signal. The actual variance of the contrasts of the latitude grand mean correlation dataset is 0.22, while the variances of the contrasts in the 1000 randomly generated datasets range from 0.12 to 0.29 ($P = 0.50$). For the temperature dataset, the actual variance of the contrasts of the correlation coefficients is 0.11, while contrasts for the randomly generated datasets range from 0.033 to 0.13 ($P = 0.69$).

Table 2 Number of species within major groups of birds showing a positive or negative within-species relationship between body size and latitude/elevation

Taxon	Total no. of species studied	No. of species with positive association	No. of species with negative association
Anseriformes	3	2	1
Anatidae	3	2	1
Charadriiformes	4	2	2
Alcidae	1	0	1
Laridae	2	1	1
Scolopacidae	1	1	0
Columbiformes	2	2	0
Columbidae	2	2	0
Falconiformes	4	4	0
Accipitridae	3	3	0
Falconidae	1	1	0
Galliformes	2	2	0
Phasianidae	2	2	0
Passeriformes	69	50	19
Alaudidae	1	1	0
Certhidae	1	0	1
Corvidae	6	5	1
Emberizidae	26	17	9
Fringillidae	2	1	1
Hirundinidae	2	2	0
Maluridae	2	2	0
Meliphagidae	2	2	0
Muscicapidae	4	3	1
Paridae	2	2	0
Passeridae	3	2	1
Ploceidae	1	1	0
Pomatostomidae	1	0	1
Sittidae	3	2	1
Sturnidae	1	1	0
Troglodytidae	1	0	1
Tyrannidae	4	4	0
Vireonidae	7	5	2
Piciformes	4	3	1
Picidae	4	3	1
Strigiformes	6	6	0
Podargidae	1	1	0
Strigidae	4	4	0
Tytonidae	1	1	0

Migratory vs. sedentary species

Thirty-four of 51 migratory species have positive relationships between body size and latitude (nonphylogenetic analysis: $G = 5.11$, $P < 0.05$; phylogenetic analysis: $P > 0.05$) whereas 42 of 49 sedentary species are larger at higher latitudes (non-phylogenetic analysis: $G = 25.99$, $P < 0.001$; phylogenetic analysis: $P < 0.01$; Table 1). A 2×2 test revealed that the proportion of species showing positive relationships between

body size and latitude is significantly greater for sedentary species ($\chi^2 = 4.06$; $P < 0.05$). Eleven of 11 migratory species (nonphylogenetic analysis: $G = 11.18$, $P < 0.001$; phylogenetic analysis: $P < 0.05$) and nine of 11 sedentary species (non-phylogenetic analysis: $G = 3.46$, $0.05 < P < 0.10$; phylogenetic analysis: $P = 0.06$) are larger in cooler environments (Table 1). A 2×2 test showed that migratory species have a significantly greater proportion of species with negative relationships between body size and temperature ($\chi^2 = 12.03$; $P < 0.001$).

Table 3 Number of species within major groups of birds showing a positive or negative within-species relationship between body size and temperature

Taxon	Total no. of species studied	No. of species with positive association	No. of species with negative association
Passeriformes	16	1	15
Corvidae	1	0	1
Emberizidae	2	0	2
Fringillidae	1	0	1
Muscicapidae	3	0	3
Paridae	3	0	3
Passeridae	1	0	1
Sittidae	1	0	1
Sturnidae	1	0	1
Tyrannidae	1	0	1
Vireonidae	2	1	1
Piciformes	3	0	3
Picidae	3	0	3

Migratory species have a stronger overall correlation between body size and latitude ($r = +0.34$; nonphylogenetic: $Z = 6.05$, $P < 0.001$; phylogenetic: $P < 0.05$; 21 species) than sedentary species ($r = +0.28$; nonphylogenetic: $Z = 4.69$, $P < 0.001$; phylogenetic: $P = 0.08$; 18 species), albeit not significantly so ($Z = 0.78$, $0.2 < P < 0.5$). Sedentary species have a slightly stronger grand mean correlation between body size and temperature ($r = -0.85$; nonphylogenetic: $Z = 17.37$, $P < 0.0001$; phylogenetic: $P < 0.001$; seven species) than migratory species ($r = -0.72$; nonphylogenetic: $Z = 9.24$, $P < 0.0001$; phylogenetic: $P < 0.01$; six species), but the correlation coefficients are not significantly different ($Z = 1.08$, $0.2 < P < 0.5$).

Neither the vote-count (latitude) datasets for migratory nor sedentary species contain phylogenetic signal. Fourteen steps are required to optimize the data for migratory species on the phylogeny, while the randomly shuffled datasets range from 8 to 17 steps ($P = 0.75$). Optimizing the data for sedentary species on the phylogeny requires six steps, while the randomly shuffled datasets range from four to seven steps ($P = 0.28$). Similarly, neither the correlation coefficient (latitude) datasets for migratory nor sedentary species contain phylogenetic signal. For migratory species, the actual variance of the contrasts is 0.23, while the variances for the random datasets range from 0.087 to 0.34 ($P = 0.39$). The variance of the contrasts for sedentary species is 0.26, while those for the random datasets range from 0.067 to 0.29 ($P = 0.77$). Data for temperature are not sufficient for testing for phylogenetic signal.

Males vs. females

To evaluate whether body sizes of males or females have a tendency to show stronger relationships with latitude or

temperature, I counted the number of species with stronger correlations for males or females (regardless of statistical significance), or equal correlations (to two significant figures) for the two sexes. Males have a stronger relationship between size and latitude for nine species, females have a stronger relationship for 10 species, and the relationships are equal between the sexes for two species (Table 1). With respect to temperature, males have a stronger association for three species and females have a stronger association for three species (Table 1).

Relationship between Bergmann's rule and latitude

The strength of Bergmann's rule does not vary with mean latitude (nonphylogenetic analysis: $r^2 = 0.022$, $F = 0.97$, d.f. = 1, 43, $P = 0.33$; phylogenetic analysis: $r^2 = 0.0079$, $F = 0.34$, d.f. = 43, $P > 0.05$; 45 species; Fig. 2). The correlation coefficients used in this analysis do not show phylogenetic signal ($P = 0.24$); the variance of the contrasts of the actual correlation coefficients is 0.19, whereas the variances of the contrasts of the randomly generated datasets range from 0.12 to 0.27.

Relationship between Bergmann's rule and body mass

The strength of Bergmann's rule does not vary with body mass (nonphylogenetic analysis: $r^2 = 0.0036$, $F = 0.15$, d.f. = 42, $P > 0.05$; phylogenetic analysis: $r^2 = 0.00057$, $F = 0.024$, d.f. = 42, $P > 0.05$; Fig. 3). The correlation coefficients show no evidence of phylogenetic signal ($P = 0.23$); the actual variance of the contrasts is 0.19, while the variances of the contrasts of the randomly generated datasets range from 0.12 to 0.27.

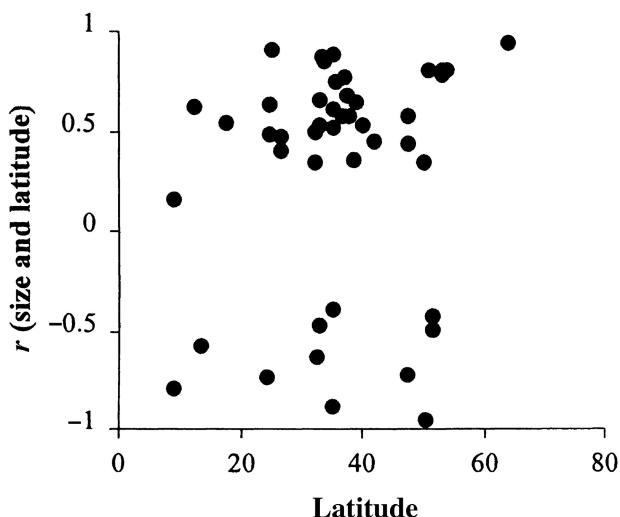


Fig. 2 Relationship between the strength of within-species body size trends (correlation coefficient between body size and latitude) and mean latitude for species of birds ($r^2 = 0.022$, $P > 0.05$; 45 species). The nonphylogenetic analysis is presented because the data do not show a phylogenetic signal (see text).

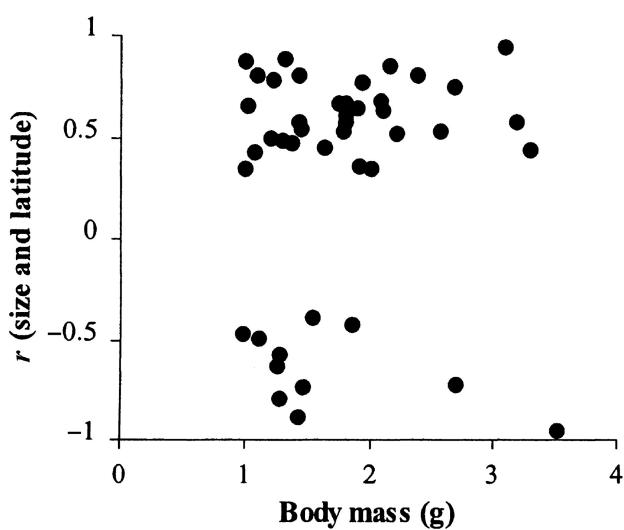


Fig. 3 Relationship between the strength of within-species body size trends (correlation coefficient between body size and latitude) and body mass (log-transformed) for species of birds ($r^2 = 0.0036$, $P > 0.05$; 44 species). The nonphylogenetic analysis is presented because the data do not show a phylogenetic signal (see text).

DISCUSSION

Birds in general have a strong intraspecific tendency towards larger body sizes at higher latitudes and in cooler environments. Seventy-six of 100 species have positive relationships between body size and latitude, while 20 of 22 species have

negative relationships of body size and temperature (Table 1). These trends are consistent when only data for well-sampled species (i.e. those with high statistical power) are included, with 18 of 27 species showing significant positive associations of body size with latitude and 10 of 10 species significant negative relationships of body size and temperature. Similarly, the more robust meta-analyses, calculations of grand mean correlation coefficients, show strong support for Bergmann's rule. Birds have a significant positive overall relationship between body size and latitude ($r = +0.32$) and a significant negative relationship of size and temperature ($r = -0.81$). Therefore, Bergmann's rule is a significant trend for birds.

The result of the overall vote-count analysis of size vs. latitude differs markedly from that of Zink & Remsen (1986), even though the datasets overlap. The difference in results is at least partly due to how the data were classified for analysis. For the overall analysis I divided the data into two categories: species with positive trends and those with negative trends. Zink & Remsen (1986) partitioned species' body size trends into four categories with respect to Bergmann's rule: unambiguously in accord, weakly in accord, not in accord, and contradictory. Only species classified as showing a trend unambiguously in accord with Bergmann's rule were counted as evidence for Bergmann's rule. Species in the other three categories were counted as evidence against. This partitioning may be reasonable if each study has high power, but if studies lack statistical power this method will bias the results toward not detecting any trend (see Ashton *et al.*, 2000). When only studies with high power are used, permitting dividing the data in a manner similar to that used by Zink & Remsen (1986), the results are concordant with my overall vote-count analysis (see above).

Throughout I present nonphylogenetic and phylogenetic versions of statistical analyses. However, I find no evidence of phylogenetic signal in any dataset. The lack of phylogenetic signal in body size trends of birds has two implications. First, the nonphylogenetic analyses are more appropriate for each dataset, although it deserves noting that the nonphylogenetic and phylogenetic results are generally concordant. Secondly, Bergmann's rule appears to be a general trend across phylogenetic groups of birds represented in these analyses. Further evidence for the phylogenetic breadth of Bergmann's rule is provided by the higher level vote-counting analyses (Tables 2 and 3). Bergmann's rule holds for species in the majority of families and orders of birds (Tables 2 and 3) and no groups are identified as strong exceptions.

Previous reviews found that migratory and sedentary species differed in the proportions of species following Bergmann's rule, with a lower proportion of migratory species in accord (Rensch, 1936; Zink & Remsen, 1986). Presumably migration decreases the influence of the environment, particularly cold temperatures or periods of seasonal stress, on body size. My results do not completely agree with previous

studies. The vote-count analysis of latitude data shows a greater proportion of sedentary (86%) than migratory species (67%) following Bergmann's rule; however, data for size and temperature have the opposite trend with a greater proportion of migratory (100%) than sedentary species (82%) following Bergmann's rule. Comparisons of the grand mean correlation coefficients of size and latitude or temperature for migratory and sedentary species provide stronger tests for differences. The grand mean correlation coefficients are not significantly different for the latitude or temperature datasets. Thus, I did not find consistent evidence for a difference in the strength of Bergmann's rule between migratory and sedentary species.

The strength of Bergmann's rule may differ between sexes of the same species (Fleischer & Johnston, 1984) and I therefore examined whether correlation coefficients are generally greater for males or females of the same species. I found no evidence for a general trend because the number of species with stronger trends for males is roughly equal to the number of species with stronger trends for females (latitude: 9 : 10; temperature: 3 : 3; males and females, respectively). Thus, no general relationship exists between sex and the strength of Bergmann's rule.

The strength of body size trends has been suggested to vary with latitude (McNab, 1971; but see Ashton *et al.*, 2000). However, no general relationship exists between the strength of Bergmann's rule and latitude for birds (Fig. 2). Examination of the data concerning Bergmann's rule vs. latitude indicates that the majority of studies are from temperate regions with few studies < 20° latitude (Fig. 2). Only five studies have focused on species in tropical regions (Table 1). Three of those species have significant positive relationships between body size and latitude (Graves, 1991; Kratter, 1993; Tubaro & Segura, 1995), one has a significant negative relationship of size and latitude (Brumfield & Remsen, 1996) and one has a nonsignificant negative trend of size with latitude (Ward, 1966). More sampling of species from tropical areas is necessary to evaluate further the geographical breadth of Bergmann's rule. If Bergmann's rule is a response to temperature then tropical species are expected generally not to follow Bergmann's rule with respect to latitude, but they may still show a Bergmann's rule pattern with elevation.

I have shown that the pattern of Bergmann's rule, a general positive relationship between body size and latitude or a negative association of size with temperature, holds in general for birds, across phylogenetic groups, irrespective of migratory tendency, sex and latitude. Discussion of the pattern would not be complete without mention of potential explanations. Several possible causes of Bergmann's rule have been proposed for birds and other organisms (see Hamilton, 1961; James, 1970; Blackburn *et al.*, 1999; Ashton *et al.*, 2000). Here I mention two: heat conservation and fasting endurance.

The heat conservation explanation was originally proposed by Bergmann (1847) and posits that because larger animals

have a decreased surface area to mass ratio, larger body size is favoured in cooler environments for endotherms because it decreases heat loss. Although body size does influence heat loss (Birkebak *et al.*, 1966), other characters, such as the insulative properties of feathers or fur, are probably more important to heat loss or gain (Scholander, 1955, 1956; McNab, 1971; Geist, 1987). Further, although larger body size causes a relative decrease in heat loss, it results in an absolute increase in heat loss and energy expenditure (Kendeigh, 1969; McNab, 1971; Calder, 1974). Theoretical arguments aside, does any evidence exist to support or refute the heat conservation mechanism? Two lines of empirical evidence suggest the heat conservation mechanism cannot fully explain Bergmann's rule. First, the heat conservation explanation assumes internal heat production; however, groups of organisms that do not produce internal heat (i.e. amphibians, chelonians) also follow Bergmann's rule (Ashton, 2001a, 2002). Heat conservation cannot explain the general tendency for larger body size in cooler environments for these organisms. Yet, it is possible that heat conservation explains body size trends only in mammals and birds and that an alternative explanation accounts for the pattern among ectotherms. The second line of empirical evidence against the heat conservation hypothesis comes from tests of the predictions of a biophysical model of the relative influence of changes in body size and insulation for mammals. Smaller mammals were predicted to follow Bergmann's rule more strongly because changes in body size have a greater influence on heat loss, relative to larger mammals (Porter *et al.*, 1994; Steudel *et al.*, 1994). A similar prediction might be made for birds. Neither mammals (Ashton *et al.*, 2000) nor birds (Fig. 3) show any relationship between the strength of Bergmann's rule and body size. Thus, if the biophysical model is correct, heat conservation cannot explain Bergmann's rule for mammals or birds.

The fasting endurance hypothesis proposes that larger size is favoured in more seasonal environments because larger animals can store more fat and can use those fat stores for greater survival during seasonal stress (Boyce, 1979; Lindstet & Boyce, 1985). The mass of body fat scales as total body mass to the 1.19 power for mammals (Lindstet & Boyce, 1985) and to greater than the 1.0 power for birds (Calder, 1974), indicating that larger endotherms have relatively and absolutely greater fat stores. Metabolism scales as body mass to the 3/4 power (Kleiber, 1961); thus larger animals have a lower weight-specific metabolic rate. Survival time, or fasting endurance, is equal to the amount of stored energy (mass of body fat) divided by metabolic rate. This relationship scales to the 0.44 power for mammals (Lindstet & Boyce, 1985) and between 0.40 and 0.60 for birds (Calder, 1974). Therefore, the scaling of fat stores and metabolism with body size confers an absolutely (but not relatively) longer survival time, i.e. greater fasting endurance, during seasonal resource shortages for larger animals. These scaling relationships are based

on interspecific data, but it has been suggested that the benefits of larger body size for fasting endurance should be even greater within-species (Lindstet & Boyce, 1985). Millar & Hickling (1990) found that fasting endurance scaled to the 0.40 power of mass within-species of mammals. Therefore, it appears that a similar relationship between fasting endurance and body size is observed within and between species.

Dunbrack & Ramsay (1993) argued that the fasting endurance explanation ignores alternative means of survival that may favour smaller body size during seasonal stress. For instance, smaller animals may better reduce metabolic rates by torpor or hibernation, take advantage of external food stores or exploit microclimates than larger animals (Dunbrack & Ramsay, 1993). However, the data necessary to support any of these suggestions are lacking. Additionally, Dunbrack & Ramsay (1993: 340) make the incorrect assumption that 'biogeographic patterns in body size, such as that described by Bergmann's rule, presumably refer to indicators of body size that exclude fat, such as lean mass or measurements of skeletal dimensions.' Bergmann's rule concerns total body size, which includes fat stores, and examples exist of animals that show greater variation in fat stores than lean body mass among populations (e.g. Blem, 1973; Mugaas & Seidensticker, 1993; Sand *et al.*, 1995). Further indirect support of fasting endurance as an explanation for Bergmann's rule in birds and mammals is provided by studies that have found body size to be better explained by seasonality than alternative general factors, including latitude, temperature, wet-bulb temperature and actual evapotranspiration rates (e.g. Boyce, 1978; Murphy, 1985; Wigginton & Dobson, 1999). Fasting endurance appears to be a more likely explanation for Bergmann's rule in endotherms and has the additional advantage of potentially being able to explain Bergmann's rule-like patterns in ectotherms as well (Cushman *et al.*, 1993; Ashton, 2001c).

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BIOSKETCH

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