Do British birds conform to Bergmann's and Allen's rules? An analysis of body size variation with latitude for four species

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Short title: Bergmann's and Allen's rules applied to four British birds

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Summary

Capsule

An analysis of body mass and wing length for four bird species shows trends broadly in line with predictions from Bergmann’s and Allen’s rules but with species- and sex-specific trends in terms of body size variation with latitude in Britain.

Aims

To analyse body size characteristics for bird species with latitude in Britain to test Bergmann’s and Allen’s rules (over a range of *c.* 740 km).

Methods

Body mass and wing length for four bird species (Blackbird *Turdus merula*, House Sparrow *Passer domesticus*, Robin *Erithacus rubecula*, Song Thrush *T. philomelos*) were analysed using Principal Components Regression Analysis to investigate trends with latitude, longitude, or by sex and Julian day.

Results

Evidence was found for latitudinal gradients in body mass for male Blackbird, female House Sparrow (both increasing in size northwards), and female Robin (decreasing in size northwards) and in wing length for female Robin and male Song Thrush (decreasing and increasing northwards, respectively).

Conclusion

Trends were broadly in line with predictions from Bergmann’s and Allen’s rules except for Robin which had trends opposite to those expected. Differences in trends between sexes suggest a role for an interplay between natural and sexual selection with latitude that deserves further consideration.

Introduction

Individuals in colder climates tend to have larger body sizes than individuals of the same species in warmer climates. This well-known biogeographic principle proposed by Bergmann (1847) relates body size variation within species to the prevailing climate over large scales via latitude. The mechanism for this rule is proposed to act via metabolism and heat conservation because a larger body size optimises the surface area to mass ratio so that a larger body size will tend to be at a selective advantage at lower mean ambient temperatures (Mayr, 1963; Kendeigh, 1969; Lomolino et al., 2006). One criticism of Bergmann's rule is whether differences in size due to latitude would be too small to provide significant heat conservation for homeotherms (Scholander, 1955; Irving, 1957) compared to other factors. These might include maintaining a heat balance by having a higher metabolic rate (Kendeigh, 1969), dropping the core temperature (Reinertsen and Haftorn, 1986) or other factors such as greater fat deposits, increasing heat production (e.g., by shivering), or by behavioural adjustment, *viz*. by lowering the gradient (e.g., seeking shelter), by decreasing heat dissipation (e.g., by raising feathers (or fur in mammals)), and by decreasing the surface area by rolling up into a ball, or by huddling (Schmidt-Nielsen, 1997). However, reviews have found that Bergmann's rule holds for the majority (i.e., > 50%) of mammal and bird species tested with statistically significant body size trends for most species with latitude and temperature. Ashton et al. (2000) found that 78 of 110 mammal species showed significant correlations between size and latitude, and 48 of 64 mammal species showed significant negative correlations with temperature. Ashton (2002) found that 76 of 100 bird species were significantly larger at higher latitudes; and Meiri and Dayan (2003) 72% of 149 bird species and 65% of 149 mammal species followed Bergmann's rule).

Body size in birds represents a problem in terms of finding a consistent measure because the mass of birds can vary with age, sex, breeding condition, migratory status, and time of year (Connell et al., 1960; Niles, 1973; Bairlein et al., 1983; Gosler, 1994; Gosler et al., 1998). Therefore, less variable measures tend to be used as a proxy for body size such as wing, tail, or tarsus length. Wing length is a widely used proxy for bird body size and is often highly correlated with body mass (e.g., Gosler et al., 1998). However, wing length is not universally a good proxy for body size since its association with body size tends to be species-specific (Rising and Somers 1989, Gosler et al., 1998; Hogstad, 2011) and in relation to latitude, wing length may show opposite trends to those expected from Bergmann's rule because the lengths of the extremities of endotherms may be inversely related to temperature, another classic biogeographic pattern known as Allen's rule (Allen, 1877).

To our knowledge there has only been one direct published test of Bergmann's hypothesis applied to birds in Britain. Wyllie and Newton (1994) used wing-length as a proxy for body size and determined a latitudinal trend for Sparrowhawk, *Accipiter nisus*, finding an increase by an average of 0.86 mm and 0.75 mm in adult males and females, respectively, for each successive degree of latitude (c. 110 km).

Yom-Tov et al. (2006) undertook a test of body size changes with temperature over time for 14 species over a period of 30-35 years from two sites in Britain and found decreases in body size through time consistent with temperature-related trends that could be attributed to global warming (Gardner et al. 2009). Although such changes in body mass are consistent with Bergmann’s rule, Rising and Somers (1989) suggested body mass tends to be a better measure of body size for males rather than females due to gender-dependent variation in reproductive condition. Yom-Tov et al. (2006) also found increases in wing length in their study and ascribed these changes to Allen’s rule. Accordingly, we consider body mass and wing length separately in analyses and, whilst both may be useful measures of body size, changes in relation to latitude are expected where body mass is predicted to increase and wing length predicted to decrease in line with Bergmann’s and Allen’s rules, respectively.

The aims of this paper were to test whether Bergmann’s and Allen’s rules hold for a small sample of bird species in the UK. Accordingly, we hypothesise that a latitude-related temperature gradient in the UK would result in both increasing body size and decreasing wing length from south to north. Trends that do not conform to these predictions may arise due to latitudinal gradients that act via sexual rather than natural selection.

Materials and Methods

Body size variables and species selection

The data used here are derived from volunteer (or ‘citizen-science’) collected sampling of birds using standard ringing methods. For inclusion here, selected species had to be relatively common and widespread: they had to be sufficiently common to be reflected by an adequate sample size; and they had to be widespread in order to test for the geographic gradient implicit in Bergmann’s rule.

Sedentary rather than migratory species were selected because they are most likely to be present in winter when conditions are more likely to be limiting. Furthermore, being present all year round, sedentary species will tend to have lower natal and breeding dispersal distances so that records from ringing are more likely to reflect species resident in a particular locality compared to those that might be on passage or that undergo annual migratory movements (Paradis et al., 1998). Birds which undertake long migrations will tend to have exhausted fat reserves on arrival in spring and will have to build them up again before departing in autumn (Newton, 2008). Although the species selected here are considered to be native and sedentary we cannot rule out that either they undertake regional movements within Britain or that populations in the UK are not augmented by individuals from continental Europe (Wernham et al., 2002). However, the mean breeding and natal dispersal distances of the four selected species are typical of native species and are proportionally smaller than migratory species (Ranges of geometric means for natal dispersal distances are 0.21–0.59 km; and breeding dispersal distances 0.15-0.36 km (Paradis et al., 1998)). To control for any seasonal body mass and age-related variation, records were restricted to the period 1st June – 31st July (all 2010) and to birds aged 4 – 6 years old.

The choice of species was also influenced by studies elsewhere. For example, the House Sparrow *Passer domesticus* is a species that fits Bergmann's rule in the USA (Johnston and Selander, 1971) and Finland (Brommer et al., 2014). The Robin *Erithacus rubecula* is a sedentary native species and in contrast to House Sparrow, is commonly considered to exhibit only limited sexual dimorphism (e.g., Jovani et al., 2001). Two further species, Blackbird *Turdus merula* and Song Thrush *T. philomelos*, both members of the same family (Turdidae) were chosen. Attributes of the sample used in these analyses are given in Table 1.

Data Analysis

Data for the four species was supplied by the BTO and were derived from 710 separate sites and from 654 registered ringers (n = 1407). Data came from as far south as Lancing in Sussex (50°50'N 0°19'W) and as far north as Rowansgarth Greens (57°30'N 2°18'W) (Grampian Region, Scotland), a straight line distance of 752km, or 741km due north (calculated using http://www.movable-type.co.uk/scripts/latlong.html) (i.e., 7°20' difference). The mean minimum and maximum January temperatures for these locations ranged from -3.7 to 2.0 and 4.7 to 8.4 °C, respectively, from north to south, and by taking the mid-points the representative difference is 7.4 °C at the harshest time of year, approximately 1 °C per degree of latitude (data for the years 1971–2000 http://www.metoffice. gov.uk/climate/uk/averages/19712000/). In order to control for potential topographic variation the data were restricted to samples from lowland sites south of the Moray Firth and east of a line joining Inverness, Scotland, and Chichester, England thus excluding all significant upland areas.

Analyses in relation to latitude were done by calculating relative weights using Principal Components Regression Analysis (PCRA)(Johnson, 2000). Regressing against principal components yields regression weights which are free of any (linear) dependences present in the original data, because the principal components are orthogonal. These weights can be projected back onto the original data to provide estimates of regression weights for the data, free of any dependences amongst the independent variables. Although data were carefully selected on the basis of controlling for potentially confounding factors (e.g., seasonal and age-related change) there remained a complex set of cross correlations that had to be controlled for since, for example, not only does body mass vary by time of day (Rands et al., 2006) but also varies over the breeding period meaning there may be phenological-related delays due to latitude. Further, after taking into account sex, wing length can vary with age of bird and migratory distance (at least in Blackcap *Sylvia atricapilla* Pérez-Tris and Tellería, 2003), and stage of moult (in Great Tit *Parus major*: Dhondt, 1981). PCRA was chosen because this method addresses cross correlations between predictor variables (Schielzeth, 2010).

Separate models were constructed for wing length and body mass. Both models included latitude, longitude, Julian day and sex, and in addition, the model for body mass included wing length because its inclusion controls the mass analysis for the effects of body size to allow inferences about variation in mass with latitude independently of size.

The data selected were restricted to the period 1st June – 31st July encompassing the breeding season and for Blackbirds the end of the breeding season. Body mass is particularly sensitive to breeding – most birds show an interrupted foraging response and add mass while breeding (MacLeod et al., 2005). This is lost at the end of the breeding season; therefore Julian Day was included to take into account any seasonal effects on body mass. As moult follows after breeding, Julian Day was also included in the analysis of wing length. PCRA was done in R version 3.1 (no date) and tests of differences between males and females using Analysis of Variance (ANOVA) were done in Minitab (2010).

Results

For all species, females had a statistically significantly greater body mass compared to males, whereas wing length was longer for males compared to females (Table 2). Tables 3 and 4 present the results of the PCRA analyses. All but one of the analyses of regression weights for body mass were statistically significant with total percentage variance explained varying from 6.95% to 25.6%. However, latitude accounted for the greater part of the variance in only three models: male Blackbird (5.4%), female House Sparrow (6.8%), and female Robin (12.8%)(Table 3, Figure 1). Longitude explained the greatest amount of variance for one species, male Song Thrush; Julian day explained the greatest amount of variance for female Song Thrush; and wing length explained the greatest amount of variance for male and female Blackbird, female House Sparrow, male Robin, and male Song Thrush (Table 3). The percentage variance explained in all cases were low with no model exceeding 25.6% overall and with latitude explaining no more than 12.8% in any single model.

For wing length there were statistically significant models for female Blackbird and female Robin (with that for male Song Thrush being marginally non-significant) although for Blackbird the overall R^2 was very small at 3.5%. The total R^2 values for female Robin and male Song Thrush were 11.9% and 8.8% respectively with latitude accounting the majority of the variation in both cases (Table 4). Except for Blackbird, these relationships are shown in Figure 2 where the data are presented along with those for the opposite sex (which were not statistically significant) for comparison. Wing length for male Song Thrush increased whilst that for female Robin decreased with latitude, respectively.

Discussion

Overall there were several statistically significant relationships for body mass and wing length with latitude but overall explanatory power was low. Increases in body size with latitude may be attributed to Bergmann's rule if they act on both males and females simultaneously. In the PCRA analyses only Blackbird and Song Thrush had statistically significant results for both males and females as predicted by Bergmann's rule but the percentage variance explained by latitude was greater than 5% for just male Blackbird and less than 2% for female Blackbird and both sexes of Song Thrush (Table 3). For House Sparrow and Robin the percentage variance explained by latitude was greater than 5% for just female House Sparrow and female Robin but, in contrast to the other species, body mass for both male and female Robin decreased with latitude (Figure 1). The expected change in body mass for those three species with the highest percentage variation explained by latitude, male Blackbird, female House Sparrow, and female Robin from the most southern to the most northern stations were 6.2 g (equivalent to 6.5% of their mean mass), 1.8 g (6.5%), and -2.4 g (-13.4%), respectively (Table 3). Thus, with the exception of Robin, the results are broadly in agreement with Bergmann's rule. For female House Sparrow this result is consistent with published trends for USA and Finland but unfortunately body mass was not used in these studies to enable a specific comparison of variation with latitude to be made (Johnston and Selander 1971, Brommer et al., 2014).

Results for wing length were statistically significant for only single sexes of two species and, although statistically significant, female Blackbird had a very low percentage variance explained by latitude so can be disregarded (Table 4). Female Robin had a percentage variance explained of 9.9% and the trend was consistent with Allen's rule (Figure 2); male Song Thrush was marginally non-significant but showed an increasing trend counter to that expected from Allen's rule (Figure 2, Table 4).

Hence only female Blackbird showed any consistency between the analyses for both body mass and wing length in line with predictions from Bergmann's and Allen's rules simultaneously but the percentage variance explained was very small (1.6% and 1.3%, respectively). Female Robin also showed statistically significant results in both sets of analyses but whereas the results for wing length were consistent with Allen's rule (in that wing length was shorter with increasing latitude), they ran counter to predictions from Bergmann's rule as body mass declined with latitude (Figures 1 and 2).

The reasons why these results do not all conform to the expected patterns from Bergmann's and Allen's rules may be due to sex-related allometric scaling relationships, resulting from an interplay between sexual and natural selection with latitude (Blanckenhorn et al., 2006). Thus, any body size clines will depend upon the strength of selection of the opposing pressures. If, for example, a warmer climate in the south leads to better survival rates (e.g., of nestlings), or in greater food supply (e.g., of invertebrates), this could lead to higher populations and thus greater competition for territory resulting in higher selection pressure on mate choice. Shine (1989) suggested such a process could result in greater sexual dimorphism in warmer climates and, conversely, less sexual size differentiation when conditions are limiting. Tobias (1997), for example, suggested that temperature affects territoriality in Robin *Erithacus rubecula* and that social behaviour may be disrupted by food supply and environmental conditions (as could be the case in the north). Further evidence for sexual selection-related effects with latitude come from a study by Badyaev (1997) who proposed a hypothesis related to elevation that could easily be transferred to latitude. Badyaev examined 126 species of cardueline finches and found that interspecific variation in sexual dimorphism was more strongly associated with changes in elevation than with other potential factors such as habitat, nest dispersion and placement, and migratory status. He attributed this pattern to colder temperatures at higher elevations and the need for biparental care for successful breeding in birds under such conditions.

As previously noted, the only previous direct analysis of Bergmann's rule in Britain found that wing length increased with latitude for Sparrowhawk (Wyllie and Newton 1994) – a finding at variance with Allen's rule but consistent with Bergmann's. Sparrowhawks are also sexually dimorphic – more so in terms of body size than any of the four species considered here. Thus, explanations as to whether wing length conforms to Allen's or Bergmann's rule deserve further consideration but may also lie in the degree of sexual dimorphism with latitude.

The findings presented here represent a preliminary study with only a limited number of species being analysed. It is recommended that analyses should be extended to a greater range of species, plus differences between sexes with latitude in relation to population density, food supply and, the relative strengths of sexual versus natural selection. Also, of particular interest would be a study of Robin and why it shows trends opposite to those expected.

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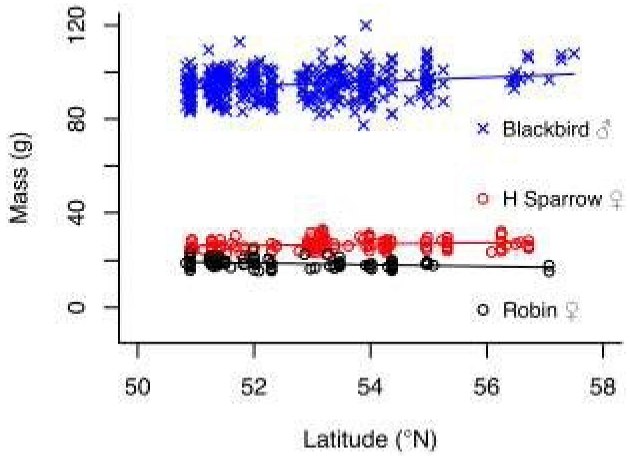
Figures

Figure 1. Body mass versus latitude for male Blackbird (upper, blue), female House Sparrow (middle, red), and female Robin (lower, black). Only the first two of these are consistent with Bergmann's rule.

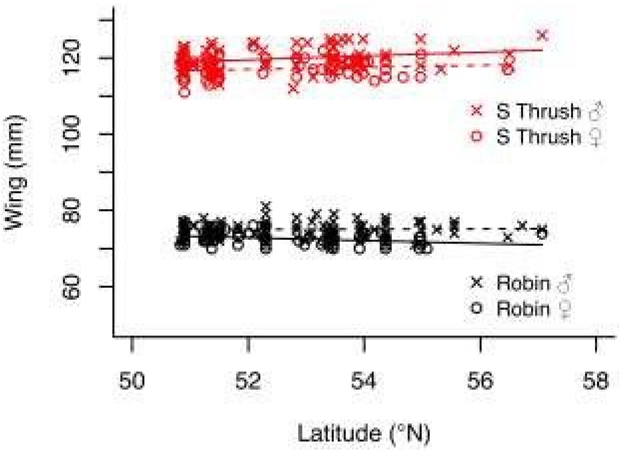
Figure 2. Wing length versus latitude for male and female Song Thrush (upper pair, red, increase with latitude) and Robin (lower pair, black, decrease with latitude), respectively. Significant relationships (male Song Thrush, female Robin) are shown by solid lines, non-significant relationships (female Song Thrush, male Robin) by dashed lines.

Figure 1



120
80
40
0
Mass (g)
Blackbird ♂
H Sparrow ♀
Robin ♀
50
52
54
56
58
Latitude (°N)

Figure 2



S Thrush ♂
S Thrush ♀
Robin ♂
Robin ♀
Wing (mm)
Latitude (°N)
60
80
100
120
50
52
54
56
58

Table 1. Summary statistics for the species chosen for this study by sex.

Common name		Blackbird		Song Thrush		House Sparrow		Robin	
	Sex	♂	♀	♂	♀	♂	♀	♂	♀
Wing length (mm)	n	383	282	85	59	160	148	116	78
	Min	121.0	118.0	112.0	111.0	72.0	68.0	70.0	70.0
	Max	141.0	138.0	126.0	123.0	82.0	79.0	81.0	77.0
	Mean	131.3	126.4	119.8	117.2	77.9	75.2	75.1	72.6
	SD	3.38	3.13	2.98	2.45	1.74	1.66	1.81	1.61
Body mass (g)	n	368	266	81	58	141	140	114	83
	Min	77.4	75.5	61.9	62.0	23.3	22.6	15.7	15.4
	Max	120.0	133.7	80.3	90.0	32.0	32.8	20.6	24.3
	Mean	94.8	95.9	69.3	75.9	26.9	26.9	18.1	18.7
	SD	5.96	7.86	3.73	6.74	1.49	2.2	1.04	1.86

Table 2. Results of ANOVA for differences between male and female body mass and wing length giving number of cases, n, the F-statistic, and level of significance, p. All tests were statistically significant.

	Statistic	Body mass	Wing length
Blackbird	n (♂:♀)	352:257	367:273
	F	4.2	183.0
	p	0.04	<0.001
Song Thrush	n (♂:♀)	78:52	82:53
	F	21.3	13.7
	p	<0.001	<0.001
House Sparrow	n (♂:♀)	141:140	160:148
	F	3.4	99.3
	p	0.04	<0.001
Robin	n (♂:♀)	110:81	112:76
	F	5.3	37.3
	p	0.006	<0.001

Table 3. PCRA regression weights of body mass against latitude, longitude, Julian day, and wing length. Statistically significant p-values indicated in bold. Variation provides estimates of body mass from the southern-most to the northern-most stations.

Species	Sex	% variance explained by				Total % R^2	p-value	Variation south to north (g)
		Latitude	Longitude	Day	Wing			
Blackbird	♂	5.4	0.3	0.8	6.9	13.5	**<<0.001**	93.0 - 99.2
	♀	1.6	0.1	2.6	2.7	7.0	**<0.001**	94.3 – 99.9
Song Thrush	♂	0.8	6.6	1.4	16.8	25.6	**<0.001**	68.2 – 72.9
	♀	0.2	0.0	12.0	11.5	23.7	**0.013**	75.8 – 76.5
House Sparrow	♂	0.4	0.2	0.4	2.1	2.9	0.34	
	♀	6.8	1.4	0.0	4.8	13.0	**<0.001**	26.2 – 28.0
Robin	♂	1.5	0.0	0.6	9.4	11.5	**0.02**	18.2 – 17.7
	♀	12.8	0.2	3.0	4.8	20.8	**0.013**	19.4 – 17.0

Footnote. Regression of body mass against latitude for each species, both sexes combined but with sex as a categorical variable, indicates that only Robin has a significant difference between the sexes in terms of body mass variation with latitude ($p<0.05$).

Table 4. PCRA regression weights of wing length against latitude, longitude, and Julian day. Statistically significant p-values indicated in bold.

Species	Sex	% variance explained			Total % R^2	p-value	Variation south to north (mm)
		Latitude	Longitude	Day			
Blackbird	♂	0.3	0.1	0.0	0.5	0.61	
	♀	1.3	0.9	1.3	3.5	**0.019**	125.8 – 127.8
Song Thrush	♂	6.8	0.3	1.7	8.8	0.058	
	♀	2.7	0.1	0.6	3.4	0.59	
House Sparrow	♂	1.2	0.2	0.5	1.9	0.39	
	♀	0.1	0.2	0.6	0.9	0.74	
Robin	♂	1.0	3.3	0.0	4.4	0.17	
	♀	9.9	2.0	0.0	11.9	**0.024**	73.4 – 70.8

Footnote. Regression of wing length against latitude for each species, both sexes combined but with sex as a categorical variable, indicates that only Robin has a significant difference between the sexes in terms of wing length variation with latitude ($p<0.05$).