

# Global warming, Bergmann's rule and body mass – are they related? The chukar partridge (*Alectoris chukar*) case

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## Abstract

Using museum specimens collected in Israel during the second half of the 20th century, no support was found for the hypothesis that body mass and tarsus length of chukar partridges *Alectoris chukar* has changed as a result of global warming. Body mass showed fluctuations during the year, reaching a maximum in late winter and spring and a minimum in summer. Bergmann's rule predicts that in warm-blooded animals, races from warm regions will be smaller than races from colder regions, and a wider explanation states that body size is positively related to latitude. Because of its topography and varied climate, Israel provides a unique opportunity to separate partly the effect of latitude from that of ambient temperature, thus testing if Bergmann's rule is related to latitude or to climatic variables. We found that body mass (and marginally also tarsus length) declined significantly with decreasing latitude in accordance with the wider explanation of Bergmann's rule, but ambient temperature explained a much smaller fraction of the variation in body mass than latitude. These results weaken the traditional explanation to Bergmann's rule that a heat conservation mechanism causes the latitudinal size variation.

**Key words:** chukar partridge, *Alectoris chukar*, body mass, Bergmann's rule, Allen's rule, global warming, Israel

## INTRODUCTION

Recent global environmental changes are providing scientists with an excellent system to study short-term ecological and biogeographical changes. These changes may enable us to examine whether patterns predicted by zoogeographical rules, such as Bergmann's (1847) and Allen's (1877) rules, change with such environmental changes.

Global mean surface temperatures have increased by 0.6 °C since the late 19th century (IPCC, 1995). In Israel, average minimum summer temperatures increased by an average of 0.26 °C per decade during the second half of the 20th century (Ben Gal *et al.*, 1999). Global warming may affect the physiology, distributions, phenology and adaptations of plants and animals (for review, see Hughes, 2000). For example, Berthold (1991) reported that many bird species in Europe had altered their migratory habits and attributed the above phenomena to global warming; Jenkins & Watson (2000) reported that the arrival date of some migratory

birds in Britain became significantly earlier between 1974 and 1999, and Crick *et al.* (1997) and McCleery & Perrins (1998) noted that laying dates of many British birds became increasingly earlier throughout 1971–97. Poleward range expansions have been reported for Arctic and alpine plants, flying insects and terrestrial vertebrates (Hughes, 2000), including British and western U.S.A. birds (Johnson, 1994; Thomas & Lennon, 1999). Morphological changes hypothesized as related to global warming have also been reported: for example, Jarvinen (1994) reported that in Finnish Lapland, the egg volume of the pied flycatcher *Ficedula hypoleuca* significantly increased between 1975 and 1993, and Yom-Tov (2001) has shown that the body size of several species of passerines declined during the second half of the 20th century, and attributed this to global warming. Although none of these studies represents a controlled experiment, these trends are explained cautiously as correlating with recent climatic change (Hughes, 2000).

Temporal and geographic intraspecific variation in adult bird body size may be related to several factors, including climate, inter- and intraspecific competition and predation. Bergmann's rule (1847) is probably the

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best known rule in zoogeography. It states that 'In warm blooded animals, races from warm regions are smaller than races from cold regions' (Mayr, 1970). Bergmann's rule has been interpreted as an adaptation to ambient temperature: the relatively larger body surface areas of the smaller races serve as efficient heat dissipaters in warm climates, while small body surface area may help in heat conservation in cold climates. Allen's rule is an extension of Bergmann's rule and states that 'in warm-blooded animals protruding body parts like bill, tail and ears are shorter in cooler than in warmer climates' (Mayr, 1970). The traditional explanation of Bergmann's rule has been supported by descriptive, theoretical and experimental studies (e.g. Yom-Tov, 1993; Ashton, Tracey & de Queiroz, 2000). Numerous studies during the past few decades have reported general correlations between body mass in fossil animals and independently established palaeoclimatic changes from various parts of the world in accordance with this rule (see Dayan *et al.*, 1991 for a review). These studies provide further support for the importance of ambient temperature in determining body mass of homoeothermic animals.

However, several authors have questioned the validity and generality of the rule, or at least the suggestion that the observed latitudinal trend in body size is a response to ambient temperatures (Scholander, 1955; Zink & Remsen, 1986; Blackburn, Gaston & Loder, 1999). This criticism is partly based on the fact that many climatic variables co-vary with latitude, and the actual factor affecting body size variation is difficult to ascertain (James, 1970). In addition, many of the studies that suggest that birds conform with Bergmann's rule used wing length as a measure of body size. Yet this factor varies among migratory and non-migratory populations, and in a review, Zink & Remsen (1986) have shown that not a single study has controlled statistically for this effect. Also, the use of body mass as an index of body size is often confounded by annual variation in body mass associated with reproductive condition and food availability (Zink & Remsen, 1986).

Predation may also affect body size, as heavier individuals may be less agile than lighter ones, and thus exposed to heavier predation rates. For example, mean body mass of the great tit *Parus major* in England increased following the disappearance of one of their predators, the sparrowhawk *Accipiter nisus*, and decreased again following its return to the woods (Gosler & Greenwood, 1995). This trend was taken by Gosler & Greenwood (1995) as evidence that predation risk is a major cost determining the optimal fat levels carried by small birds.

Because of its topography and varied climate, Israel provides a unique opportunity to separate partly the effect of latitude from that of ambient temperature, thus testing if Bergmann's rule is related to latitude or to climatic variables. Israel is constructed of three parallel geomorphological units stretched from north

to south: the Mediterranean coastal plain in the west, the central mountains (which are dissected by valleys) and the Rift Valley in the east. Along the central mountain range altitudes vary from 50 to 1212 m a.s.l., while in the Rift Valley they vary from -400 m a.s.l. near the Dead Sea, the lowest place on earth, to about 150 m a.s.l. Thus, topography confounds the effect of latitude on ambient temperature. Although temperatures in Israel (especially along the Mediterranean coastal plain) generally increase from north to south, this is not always the case. For example, temperatures in the northern regions of the Rift Valley (near the Sea of Galilee, latitude 32°40' N, elevation -214 m) are similar to those in the central Arava Valley 300 km south of it along the same valley (latitude 29°40' N, elevation 300 m). Similarly, mean annual temperature on Mount Meron in the Upper Galilee (latitude 33° N, elevation 1212 m) are similar to those of the Mount Ramon in the central Negev (30°30' N, elevation 1033 m).

The chukar partridge *Alectoris chukar* is a common resident throughout Israel. Two sub-species of chukar, *A. c. cypriotes* and *A. c. sinaica*, have traditionally been recognized in the region (Cramp & Simmons, 1980; Shirihai, 1996), although the patterns of variability of diagnostic morphological traits across their putative contact zone have not been carefully studied so far. The transition between the two has been proposed in the Northern Negev of Israel. Yet a recent study on allozyme diversity in chukar in Israel suggests that populations comprise a single sub-species, *A. c. cypriotes* (Kark *et al.*, 1999). In agreement with these findings, earlier morphological studies (Nissani, 1974) suggest that Israeli populations should all be included as *A. c. cypriotes*, and that clearly distinct *A. c. sinaica* occur only in the southern Sinai desert and that the extant isolated population in the Sinai Mountains is a post-glacial relict from the Upper Pleistocene glacials (Tchernov, 1988).

Chukar populations in Israel increased appreciably during the 1960s and 1970s as a result of legal protection and a decrease in hunting pressure (Shirihai, 1996), but during the past decade their numbers have fallen sharply throughout most of the country. The reasons for this decline are not clear, but are assumed to be partly the result of increased predation on eggs, chicks and possibly adult birds by red foxes *Vulpes vulpes* and golden jackals *Canis aureus*. The populations of these two species have increased since the 1980s because of increased availability of food in garbage dumps near human settlements.

The aims of this study were: (1) to examine whether global warming has affected body size in the Israeli chukar; (2) to examine whether size variation is related to latitude or to ambient temperature. For this analysis we used body mass and tarsus length controlled for monthly changes as measures of body size of the resident chukar, thus avoiding the confounding effects of migration and controlling for monthly changes in body parameters.

## METHODS

Museum specimens of adult birds were used for this study. The Zoological Museum of Tel Aviv University possesses *c.* 200 specimens of chukar partridges that were collected continuously throughout the second half of the 20th century. Birds were collected for the museum at various times of the year, mostly by shooting. Upon collection, these specimens were weighed to an accuracy of 1 g, and their tarsus was measured to an accuracy of 1 mm. The Zoological Museum of the Hebrew University in Jerusalem possesses about 250 specimens, most of which were collected between 1971 and 1973. These specimens were weighed to an accuracy of 1 g, and their tarsus measured as above. In addition to the museum specimens, data on body mass of 340 specimens collected by SK throughout Israel during 1995–96 were used. The effect of 7 variables (sex; latitude at the collection site, Israel grid, where  $31^\circ\text{N} = 320$ ,  $32^\circ\text{N} = 542$ ; mean January (coldest month) and August (warmest month) temperatures ( $^\circ\text{C}$ ) and potential mean annual evaporation (cm; an indicator of the total annual heat stress; Rosenzweig, 1968) in the localities of collection, and month of collection on body mass (g) and tarsus length (mm) were examined by using multiple regressions, where sex was treated as a dummy variable and the monthly variation in body mass was presented by the sinusoidal component  $\text{Sin}(2*\pi*I/12)$  where  $I = 1\dots 12$ , and 1 = January, 2 = February, etc, which was found to fit well the monthly effect. Climatological data were extracted from isotherm maps (Sofer, 1995).

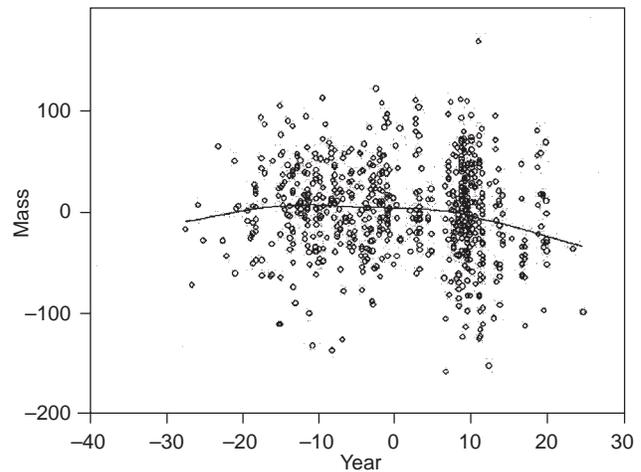
The Lowess method was used to estimate non-parametrically the dependence of residual body mass on year of collection (Cleveland, 1979; Becker, Chambers & Wilks, 1988). This method uses local linear regression in the neighbourhood of each point separately to yield the predicted value for the dependent variable. The participating points at each location have higher weights the closer they are to the point at which the relationship is estimated. Further automatic down-weighting of outliers assures the robustness of this procedure.

## RESULTS

### The effect of year of collection

After controlling for all other variables, year of collection explained only 0.6% of the variation. The calculated decrease in body mass during the 44 years of this study is 18 g, or 3.2% of body mass of a partridge living at latitude  $33^\circ 20' \text{N}$  in Mount Hermon at the extreme north of Israel. Although still significant ( $F_{1,699} = 4.159$ ,  $P = 0.0418$ ), we doubt if this result is biologically meaningful. Hence, this factor was removed from further analysis.

The dependence of body mass (adjusted for differences in sex and monthly variation), on the year (adjusted for the same variables) is also estimated non-parametrically by the Lowess method, and displayed by



**Fig. 1.** The dependence of body mass (residuals after controlling for sex and monthly variation), on the year (adjusted for the same variables). The dependency is estimated non-parametrically by the Lowess method, and displayed by the smooth curve.

the smooth curve (Fig. 1). This curve shows that over the period investigated there is an increase in body mass that stabilises and only then decreases, but no monotonous decline in body mass is evident as years progress as predicted from the linear increase in ambient temperatures during this period.

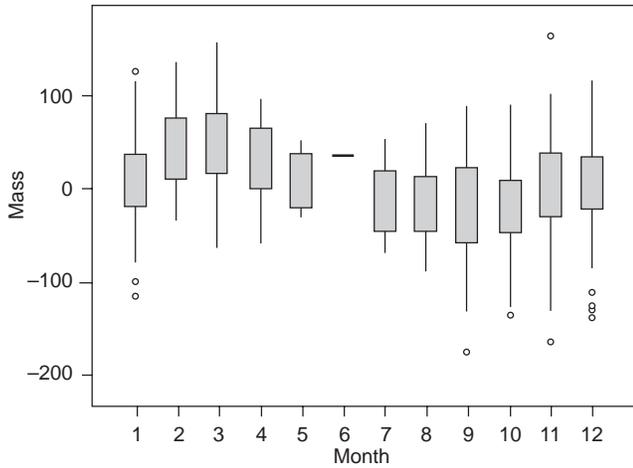
### The effect of latitude and climatological variables

Latitude was significantly and negatively related to mean January temperatures ( $r^2 = 0.027$ ,  $F_{1,753} = 21.140$ ,  $P < 0.0001$ ) and annual evaporation ( $r^2 = 0.192$ ,  $F_{1,754} = 179.454$ ,  $P < 0.0001$ ) at the localities of collection, but no significant relationship was found between latitude and mean August temperatures ( $r^2 = 0.002$ ,  $F_{1,753} = 1.285$ ,  $P = 0.2574$ ). These results suggest that in Israel only a small part of the variation in ambient temperatures and annual evaporation is explained by latitude, thus enabling one to separate (at least partly) the effect of these climatic variables from latitude.

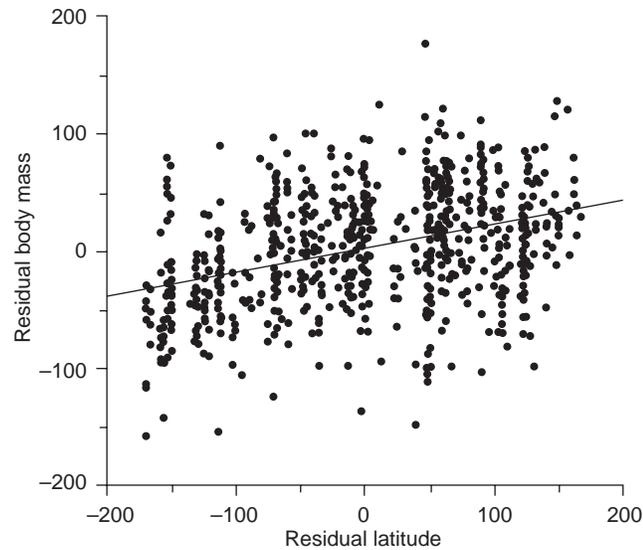
Body mass of the chukar partridge is significantly related with all seven variables examined ( $F_{7,691} = 145.82$ ,  $P < 0.0001$ ; Table 1). These variables explain 59.6% of the variation in body mass. Males are significantly heavier than females (by an average of 20%). Body mass fluctuated monthly, increasing towards maximum in spring and decreasing towards summer, and fluctuates by as much as 20% during the year ( $r^2 = 0.069$ ; Fig. 2). After controlling for the other variables, latitude is significantly and linearly related to residual body mass ( $r^2 = 0.138$ ; Fig. 3). The decrease in residual body mass is about 0.2 g/km latitudinal difference. Thus, the calculated decrease in body mass along the north–south axis of Israel (about 400 km) is 80 g, or 15% of body mass of a partridge living at latitude  $33^\circ 20' \text{N}$  in Mount Hermon at the extreme north of Israel.

**Table 1.** Regression coefficients of body mass (g) of chukar partridges against year, latitude of the locality of collection (Israel grid, where 31° N = 320, 32° N = 542), sex, month of collection, mean January and mean August temperatures (°C), and potential annual evaporation (cm). Monthly variation is expressed as  $\text{Sin}(2*\pi*I/12)$ . For details see Methods

	Coefficient	SE	Standard coefficient	t-value	P-value
Intercept	493.814	39.084	493.814	12.635	< 0.0001
Year	-0.413	0.169	-0.071	-2.441	0.0149
Latitude	0.204	0.021	0.267	9.514	< 0.0001
Sex	92.822	3.418	0.657	27.158	< 0.0001
Monthly variation	26.106	3.043	0.241	8.578	< 0.0001
Average January temperature	5.969	1.584	0.118	3.768	0.0002
Average August temperature	-10.373	1.848	-0.200	5.612	< 0.0001
Evaporation	0.536	0.199	0.097	2.695	0.0072



**Fig. 2.** The relationship between monthly variation, expressed as  $\text{Sin}(2*\pi*I/12)$ , and body mass (residuals after controlling for sex and month of collection).



**Fig. 3.** The relationship between body mass (g; residuals after controlling for sex and month of collection) and latitude (Israel grid where 31° N = 320, 32° N = 542; residuals after controlling for sex and month of collection) and, and potential annual evaporation (cm).

To test which of the climatological variables (evaporation, mean January and mean August temperatures) explains a greater proportion of the variation, multiple regressions were run for each of these variables (together with sex, monthly variation and latitude as variables) against body mass. These equations explained 50.7%, 51.8% and 52.8% of the variation in body mass for mean January temperature, mean August temperature and mean annual evaporation, respectively. Hence, mean annual evaporation explained more of the variation than the other two climatological variables, and was selected for further analysis as an indicator for temperature. At the next stage, the residual body mass (after controlling for sex and monthly variation) was related to residuals of the mean annual evaporation (after controlling for sex and monthly variation) and also to latitude (after controlling for sex and monthly variation). Residual latitude significantly ( $F_{1,697} = 114.108, P < 0.0001$ ) explained 14.1% of the variation in residual body mass, while mean annual evaporation significantly ( $F_{1,697} = 35.991, P < 0.0001$ ) explained only 4.9% of this variation.

Tarsus length was significantly related to sex, temperature, latitude and monthly variation, but not by year of collection or evaporation ( $F_{7,372} = 45.339, P < 0.0001$ ; Table 2). These variables explained 46% of the variation in tarsus length. Males had significantly longer tarsi than females (on average by 14%). Tarsus length fluctuated annually, increasing towards maximum in spring and decreasing towards summer and autumn, and this relationship explained 8.4% of the total variation. After controlling for the other variables, latitude was significantly and linearly related to residual tarsus length, but explains only 2.4% of the variation.

To test which of the above climatological variables explain more of the variation in tarsus length, we repeated the above analysis of body mass for tarsus length. We found that residual latitude significantly ( $F_{1,378} = 7.299, P < 0.0072$ ) explained 1.9% of the variation in residual tarsus length, while mean annual evaporation significantly ( $F_{1,378} = 6.183, P < 0.0133$ ) explained 1.6% of this variation.

**Table 2.** Regression coefficients of tarsus length (mm) of chukar partridges against year, latitude of the locality of collection, sex, month of collection (Israel grid, where 31° N = 320, 32° N = 542), sex, monthly variation, mean January and mean August temperatures (°C), and potential annual evaporation (cm). Monthly variation is expressed as  $\text{Sin}(2*\pi*I/12)$ . For details see Methods

	Coefficient	SE	Standard coefficient	t-value	P-value
Intercept	50.536	3.998	50.536	12.639	< 0.0001
Year	-0.051	0.032	-0.062	-1.558	0.1202
Latitude	0.004	0.002	0.080	1.960	0.0508
Sex	4.786	0.340	0.541	14.058	< 0.0001
Monthly variation	1.519	0.254	0.235	5.982	< 0.0001
Average January temperature	0.834	0.151	0.295	5.513	< 0.0001
Average August temperature	-0.604	0.174	-0.195	-3.461	0.0006
Evaporation	0.012	0.015	0.038	0.800	0.4245

## DISCUSSION

### The effect of global warming and predation

Yom-Tov (2001) has shown that four out of five species of Israeli passerines examined in his study decreased in body mass during the second half of the 20th century, and attributed this to global warming. We found that body mass (but not tarsus length) of chukar partridges (*Alectoris chukar*) collected in Israel during the second half of the 20th century declined during this period. We doubt if this result is biologically meaningful, mainly because it only explains a minute part of the variation, and is on the verge of significance. A possible reason why body mass of the chukar partridge has not been affected by global warming is its larger body size in relation to the examined passerine species. Large body size is associated with smaller surface area, making the chukar partridge less affected by elevated ambient temperatures.

Another important reason for not including a linear effect of year on body mass can be seen in Fig. 1, that shows the dependence of body mass (adjusted for differences in sex and monthly variation), on the year (adjusted for the same variables). The dependency is estimated non-parametrically by the Lowess method, and displayed by the smooth curve. It is clear from this curve that over the period investigated there is an increase in body mass that stabilizes and only then decreases. One possible explanation for such a trend may be a reaction to predation pressure. Among British passerines, reduced predation pressure by sparrowhawks *Accipiter nisus* in woodlands between 1960 and the 1980s was followed by body mass increase, and when sparrowhawk numbers recovered, body mass of their passerine prey species decreased again (Gosler & Greenwood, 1995). The number of chukar partridge in Israel fluctuated greatly during the second half of the 20th century. Before the establishment of the State of Israel (in 1948), these birds were extensively hunted and their populations were small. Legal protection and decreased poaching since the 1950s allowed populations to recover and reach a peak in the late 1980s. However, since this time annual counts by rangers of the Nature Reserve Authority of Israel in several regions of the

country have shown a great decrease in numbers of partridges. The reasons for this decline are not known, but the likely cause is that of increased predation on eggs, chicks and adult partridges by red foxes and golden jackals. The populations of these predators suffered from a poisoning campaign during 1963–64, but quickly recovered, and since the 1980s their numbers have increased greatly because of an ample supply of food from garbage dumps (Mendelssohn & Yom-Tov, 1999). Hence, reduced predation might have caused a body mass increase that stabilized and then decreased when the populations of the predators recovered. It is clear that no monotonous decline in body mass is evident as years progress.

### Bergmann's rule

In this study the body masses (controlled for seasonal variation) of resident populations of the chukar partridge were used, thus avoiding three major confounding effects (migration, using linear parameters such as wing length and seasonal fluctuations), which were often ignored in previous studies of Bergmann's rule (Zink & Remsen, 1986). Our results show that in Israel only a small part of the variation in ambient temperatures and annual evaporation is explained by latitude, thus enabling one to separate (at least partly) the effect of these climatic variables from latitude. We found that latitude and mean annual evaporation explain 14.1% and 4.9% respectively of the variation in body mass. Hence, for the chukar body mass is better related to latitude rather than to the climatic variables examined.

Residual latitude and mean annual evaporation also significantly explained only 1.9% and 1.6% of the variation in residual tarsus length, respectively. These results, although in accordance with Allen's rule, seem to be biologically meaningless, because they explain only a small fraction of the variation.

Nissani (1974) found no significant relationship between body mass and ambient temperature in the Israeli chukar partridge, and concluded that this species does not conform with Bergmann's rule. We found that temperature is significantly related to body mass, but this

relationship explains a smaller part of the variation in body mass. However, Blackburn *et al.* (1999) suggested that Bergmann's rule should be formulated as 'the tendency for a positive association between the body mass of a species ... and the latitude', rather than between body size and temperature. This definition has at least two advantages on Bergmann's original definition: it frames Bergmann's rule in terms of body mass rather than any other linear parameters that may decrease with latitude (such as wing length) as predicted by Allen's rule, and it relates body mass variation to variation in latitude rather than to climate. The significant relationship found in this study between latitude and body mass is in accordance with this new definition of Bergmann's rule. The reason that latitude explained a higher proportion of the variation of body mass than does ambient temperature may be because in Israel both temperature and precipitation are related to latitude (negatively and positively, respectively). Hence, latitude is an expression for more than one factor that may influence body mass, i.e. temperature and primary production. Our results weaken the traditional explanation that a heat conservation mechanism causes latitudinal size variation, and show that at best it is only a part of the explanation.

Our finding showing that a smaller proportion of the variation in tarsus length than in body mass was explained by latitude may be due to allometric reasons. Tarsus length is a linear measurement, while body mass is a cubic one and as such is much more likely to be detected. Another possible explanation for the difference is that the latitudinal decline in body mass is the result of a decline in the mass of soft tissues, such as fat and muscles, but not bones. There are no data available to support or refute this explanation.

### Monthly variation

Seasonal fluctuations in body mass is a common phenomenon among birds, including Galliformes (Cramp & Simmons, 1980). The seasonal trend in average body mass and tarsus length found in this study is probably a result of more than one factor. The main reason for the increase in body mass in winter and spring seems to be the increased availability of new grass and other food sources, while from May until late October no rains fall in Israel and food and water availability for the birds are restricted. Other reasons may include recruitment of young, smaller individuals into the population during late spring, and summer months may decrease the population means of both body mass and tarsus length, which decline from June until January. On the other hand, increased mortality of smaller (and presumably weaker) individuals during the summer and early winter months (December–January) may increase the population means of body mass and tarsus length during this period. The large fluctuation in body mass observed here (*c.* 20%) indicates the importance of accounting for this factor while analysing body mass data for the examination of Bergmann's rule.

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