

## Recent changes in body weight and wing length among some British passerine birds

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We tested the prediction that global warming has caused recent decreases in body weight (Bergmann's rule) and increases in wing length (Allen's rule) in 14 species of passerine birds at two localities in England: Wicken Fen (1968–2003) and Treswell Wood (1973–2003).

Predicted long-term linear decreases in residual body weight occurred in four species: dunnocks (Wicken Fen), and great tits, blue tits and bullfinches (Treswell Wood). Non-linear decreases also occurred in reed warblers and blackcaps at Wicken Fen, which also had a surprising linear increase in residual body weight in blackbirds.

Residual wing lengths increased linearly, as predicted, in six of seven species at Wicken Fen. Whereas there were non-linear long-term increases in wrens, dunnocks and blackbirds in Treswell Wood. Unexpected linear decreases also occurred in residual wing lengths in willow warblers (Wicken Fen), and blue tits, great tits and chaffinches (Treswell Wood).

The most parsimonious explanation for such long-term changes in body weight is global warming, as predicted by Bergmann's rule. Greater site and species-specific effects on wing length (e.g. non-linear changes plus shorter wings in the woodland habitat) suggest a less straightforward conclusion concerning Allen's rule, probably because wing length involved variation in both bone and feather growth.

Changes in residual body weights and wing lengths often differed between species and were sometimes non-linear, perhaps reflecting short-term modifications in selection pressures. Human-induced influences are discussed, such as avian predator population densities and land-use change. Short-term variation in temperature had little effect, but rainfall did explain the unusual increase in blackbird body weight, possibly as a result of improving food (earthworm) availability.

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

correlation between morphological variation and ambient temperature, and tends to be valid for changes of body weight with latitude (Mayr 1970). During the past few decades, numerous studies have reported general correlations between body weight (in extant and fossil animals) and ambient temperature and independently established paleoclimatic changes in various parts of the

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world, in accordance with this rule (reviewed by Dayan et al. 1991). These studies provided further support for the importance of ambient temperature in determining body weight of homeothermic animals.

Bergmann's rule has been interpreted as an adaptation to ambient temperature: the relatively larger body surface area of the smaller races serves as an efficient heat dissipater in warm climates, while relatively small body surface area may help in heat conservation in cold climates. The traditional explanation of Bergmann's rule has been supported by descriptive, theoretical and experimental studies (reviewed by Yom-Tov 1993). Weight change in homeothermic animals can occur rapidly, as reported for animals introduced into new environments. For example, within 100 years of its introduction into North America and New Zealand, the body weight of the house sparrow *Passer domesticus* correlated positively with seasonality and annual temperature range in both regions (Selander and Johnston 1967, Johnston and Selander 1971, Baker 1980, Lowther and Cink 1992). Similarly, within 50 years of its introduction into New Zealand, the skull size of the brushtail possum, *Trichosurus vulpecula*, correlated with ambient temperature (Yom-Tov et al. 1986), just as it does in Australia from where it was introduced.

Global mean surface temperatures increased by 0.6°C from the late 19th century to 1994 (IPCC 1995). Global warming may affect the physiology, distribution, phenology and adaptation of plants and animals (reviewed by Hughes 2000, Parmesan and Yohe 2003, Root et al. 2003). For example, since 1966 the growing season of plants has advanced by about eight days in northern latitudes (Myneni et al. 1997), arrival dates of some migratory birds in Britain became significantly earlier between 1974–1999 (Jenkins and Watson 2000), and laying dates of many British birds became earlier between 1971–1997 (Crick et al. 1997, McCleery and Perrins 1998). Similarly, Berthold (1991) reported that many bird species in Europe had altered their migratory habits, and he attributed this phenomena to global warming. Poleward range expansions have been reported for Arctic and alpine plants, flying insects and terrestrial vertebrates (Hughes 2000), including British and western USA birds (Johnson 1994, Thomas and Lennon 1999). Morphological changes due to global warming have also been reported. For example, Gosler (2002) has shown that the rate of afternoon fat reserve accumulation in the great tit (*Parus major*) has declined during the last 20 years in correspondence with elevated temperatures. Recently, it has been claimed that global warming has affected body size in several species of passerine birds (Yom-Tov 2001) and in a rodent (Smith et al. 1998). Although none of these studies represents a controlled experiment, these

trends are explained most parsimoniously by a correlation with recent climate change (Hughes 2000).

Other factors, such as predation, may also affect body size. Heavier individuals may be less agile than lighter ones, and thus exposed to heavier predation rates. For example, mean body weight of the great tit 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 et al. 1995). Recent changes in wing length have also been reported for passerines, such as the decrease in wing length observed in the red-backed shrike (*Lanius collurio*) in southern Germany during the 1990s, which has been attributed to an increase in environmental variance (Jakober and Stauber 2000).

Allen's rule states, "in warm blooded animals the relative size of the exposed portions of the body decreases with decrease in mean ambient temperature" (Welty 1962). According to Huxley (1942, p. 213), this applies to wing length in almost 80% of birds in five families of non-migratory North American birds. In this study, a difference of one percent in wing length corresponds to a difference of 2°N latitude in redpolls, (*Carduelis flammea*), of 1° in puffins, (*Fratercula arctica*), and a little over 1° in wrens (*Troglodytes troglodytes*). However, since feathers do not dissipate heat, the positive relationship between ambient temperature and wing length is difficult to interpret, unless the length of feathers is correlated with wing bone length. Johnston (1969) found that in the house sparrow across Europe there is a persistent positive relationship between summer temperatures and wing bone lengths, as predicted by Allen's rule. In this case, wing bone lengths (humerus and ulna) correlated with wing length (correlation coefficients vary between 0.278 and 0.561). However, although wing bones and feathers vary in length in the same direction, they show different quantitative relationships with temperature, indicating that bones and feathers may be subject to contrasting selective pressures (Johnston 1969). Another possibility is that bones (and the muscles they carry) react differently to feathers in response to the same selection pressures. This is likely given the alternative adaptations involved here: (a) when the body becomes heavier in response to decreasing ambient temperatures, wing area should increase in order to compensate for heavier wing loading; and (b) Allen's rule predicts that wing bones should decrease in length in colder regions. Hence, adaptations for efficient flying and body heat conservation act in opposite directions, and this might explain why bones and feathers show similar but different relationships to changes in temperature (Johnston 1969).

In this study, we used wing length and body weight data from several species of passerines, accumulated over more than 30 years during regular ringing activities in England, in order to examine how body sizes in birds

have changed during the last 30 years or more. We predicted that body weight would decrease, as expected from Bergmann's rule, and wing length would increase, as expected from Allen's rule.

## Methods

### Allometric data collection

For this study we used data from 14 species of passerine birds ringed at two localities in Britain: Wicken Fen, Cambridgeshire (11 species) between 1968–2003 (for the dunnoek, willow warbler and wren there were insufficient data until 1969), and Treswell Wood, Nottinghamshire (11 species) between 1973–2003. All the species are either residents or summer breeders in England. Wicken Fen (52°18'N 00°17'E) is an isolated remnant of fen habitats, comprising 320 ha of woodland, scrub, reed (*Phragmites australis*) and sedge (*Cladium nariscus*) beds and open water (Friday and Harley 2000). Treswell Wood (53°18'N 0°51'W) is composed of 47 ha of mature broad-leaved trees, mainly ash (*Fraxinus excelsior*) with some oak (*Quercus robur*), and predominantly hazel (*Corylus avellana*) understorey (du Feu and McMeeking 1991).

The species selected were those where sample sizes provided at least 540 and 330 individual records per species for each of the two localities for the entire period of study, respectively (i.e. an average of 15 individuals species<sup>-1</sup> year<sup>-1</sup>). In order to avoid confounding effects, such as age and birds wintering in Britain, we used only adult birds caught and ringed between May–October. To avoid pseudoreplication and confounding effect of post-capture weight changes, we included in our analysis only the first record as an adult between May and October from each individual caught more than once. After capture, each bird was weighed by Pesola spring balance to an accuracy of 0.1 g (but 1 g for the blackbird and the song thrush at Treswell Wood) and wing length was measured by calipers or end-stop ruler to an accuracy of 1 mm. Although the method of measuring wing length used by some British ringers changed during the 1980s (A. Gosler, pers. comm.), in this study it remained the same throughout for both localities and one of us (CJRT) also ringed continuously at Wicken Fen throughout the study period as did others (John McMeeking during the entire period and Chris du Feu since 1978) in Treswell Wood.

Body weight and wing length can be related to climate conditions in the year in which they were measured. Hence, we also checked whether changes in body size measurements were related to ambient temperature and rainfall. Mean monthly tempe-

rature data for central England were kindly provided by Dr. Mike Hulme, and mean monthly temperature and rainfall data for Swaffham Prior, 6 km from Wicken Fen, were taken from Clarke (1967–2003).

### Statistical analyses

Body weights of birds are known to be dependent upon species and sex, but also of day (lower body weights in the morning; Lehtikainen 1981), month (lighter during summer; van Balen 1967, Lehtikainen 1981) and variation in ambient temperature (lighter on warm days; Gosler 2002). Wing length is also related to species, sex and changes during the year due to wear and abrasion and moult (van Balen 1967). Hence, in the main analyses we used residuals after testing (and controlling) for the effects of species, sex, month and time of day. Similarly, wing length was analyzed using residuals after testing (controlling) for species, sex and month.

When testing for the long-term year effects of global warming we used residual values for daily temperature in order to test separately for the short-term effects of weather. We also tested for both linear (year) and second order polynomial terms (year<sup>2</sup> effects), but present only those covariates or regressions that provided the best fit. Two-tailed significance and a critical P-value of 0.05 are used throughout.

## Results

### Controlling out extraneous factors

Between 1968–2002 mean annual temperature in central England increased significantly by 1.07°C (temperature = 0.031 × year – 52.220;  $r^2 = 0.301$ ,  $n = 34$ ,  $P < 0.001$ ). At Swaffham Prior, mean ambient temperature increased by 0.86°C between 1968–2003 (temperature = 0.025 × year – 39.214;  $r^2 = 0.120$ ,  $n = 34$ ,  $P = 0.042$ ). Daily residual values from these overall linear effects of year are therefore used below to represent any short-term variation in time of day not attributed to global warming.

Table 1 shows the results of a nested ANCOVA used to control out obvious factors affecting body size in birds, which are not of primary interest here. As expected, for body weight at both Wicken Fen and Treswell Wood (Table 1a) there was a significant effect of species, as well as significant effects of sex, month of capture/measurement, and time of day, and/or significant interactions of these variables with species. Similarly, wing length (Table 1b) at both sites showed the expected significant effects of species,

Table 1. Results of ANCOVA models used to produce residual values from analyses of: (a) body weight; and (b) wing length in different species of birds measured at Wicken Fen and Treswell Wood in different months of the year. Note that the variable sex contains a third intermediate value for 'unknown' in order to ensure that all individuals were included. The effect of year (and the non-linear term year<sup>2</sup>) and residual variation in daily temperature (controlling for the effect of year) are included as covariates in both models. Time of day is included only as a covariate for body weight. All additional interactions terms were NS and so were not included here. Significant P-values are underlined.

	Wicken Fen			Treswell Wood		
	F ratio	df	P	F ratio	Df	P
(a) Weight						
Species	869.09	6,4.20	<0.001	1135.19	12,82.58	<0.001
Sex	1.08	2,3.08	0.442	2.50	2,25.85	0.102
Month	4.20	5,37.74	0.018	2.08	5,72.06	0.078
Time	41.56	1,8251	<0.001	39.88	1,7760	<0.001
Year	1.81	1,8251	0.178	2.67	1,7760	0.103
Year <sup>2</sup>	0.08	1,8251	0.776	0.06	1,7760	0.807
Temperature	1.28	1,8251	0.258	1.35	1,7760	0.246
Species × sex	76.51	3,8251	<0.001	23.00	24,7760	<0.001
Species × month	10.14	30,8251	<0.001	6.49	57,7760	<0.001
Species × time	20.76	7,8251	<0.001	1.19	12,7760	0.282
Species × year	8.69	6,8251	<0.001	2.00	12,7760	0.021
Species × year <sup>2</sup>	3.31	6,8251	0.003	1.13	12,7760	0.332
Species × temp	0.28	6,8251	>0.948	0.80	12,7760	0.653
(b) Wing						
Species	182.30	6,3.20	<0.001	927.28	12,33.26	<0.001
Sex	5.84	2,3.03	0.091	31.10	2,25.01	<0.001
Month	1.80	5,43.10	0.134	1.20	5,79.48	0.317
Year	93.19	1,8233	<0.001	1.00	1,7841	0.317
Year <sup>2</sup>	50.17	1,8233	<0.001	16.46	1,7841	<0.001
Temperature	1.60	1,8233	0.206	0.08	1,7841	0.784
Species × sex	228.71	3,8233	<0.001	41.26	24,7841	<0.001
Species × month	6.21	30,8233	<0.001	4.57	57,7841	<0.001
Species × year	3.59	6,8233	0.001	3.80	12,7841	<0.001
Species × year <sup>2</sup>	4.65	6,8233	<0.001	0.82	12,7841	0.496
Species × temp	2.13	6,8233	0.047	1.61	12,7841	0.849

sex, and month of capture/measurement, and/or significant interactions between species and sex or month. The following analyses were therefore carried out using the standardized residuals from these ANCOVA models.

### Residual body weight changes

Residual body weights for both sites did not differ between species, which is perhaps unsurprising as this factor was controlled out in the analyses above. There were also no effects of residual variation in daily temperature, and no interaction with species. Although, there were also no overall effects of year or year<sup>2</sup>, there were significant interaction terms between species and year in both Wicken Fen and Treswell Wood, and between species and year<sup>2</sup> in Wicken Fen.

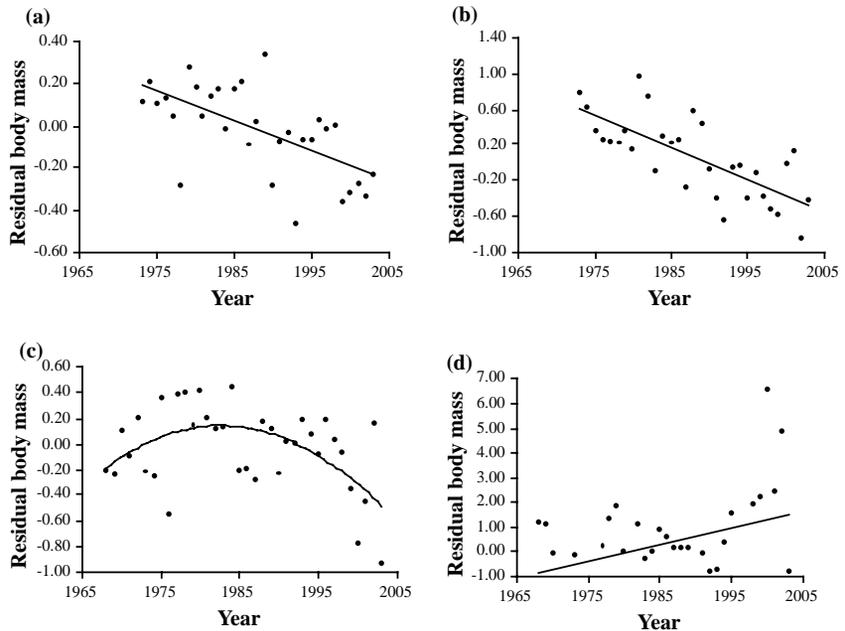
Bird species at different sites therefore varied in the direction and linearity of long-term changes in residual body weight. Many species showed no detectable trend. However, significant linear decreases in residual body weight were apparent at Wicken Fen in bullfinch (residual weight =  $-0.103 + -0.014$  year;  $r^2 = 0.006$ ,  $n = 1248$ ,  $P = 0.005$ ) and at Treswell Wood in blue tits (Fig. 1a: residual weight =  $-0.004 + -0.014$  year;  $r^2 =$

$0.026$ ,  $n = 674$ ,  $P < 0.001$ ), great tits (Fig. 1b: residual weight =  $0.063 + -0.036$  year;  $r^2 = 0.078$ ,  $n = 501$ ,  $P < 0.001$ ) and dunnocks (residual weight =  $-0.058 + -0.013$  year;  $r^2 = 0.008$ ,  $n = 896$ ,  $P = 0.008$ ). Interestingly, three out of four of these linear decreases were very similar at around  $-0.014$  g year<sup>-1</sup>.

There were also non-linear decreases in residual body weight, which showed the greatest declines occurring most recently, at Wicken Fen in reed warblers (residual weight =  $0.063 + -0.007$  year +  $-0.001$  year<sup>2</sup>;  $r^2 = 0.006$ ,  $n = 3437$ ,  $P = 0.012$ ) and blackcaps (Fig. 1c: residual weight =  $0.110 + -0.014$  year +  $-0.001$  year<sup>2</sup>;  $r^2 = 0.012$ ,  $n = 742$ ,  $P = 0.012$ ). Unusually, there was also a linear increase in residual body weight in blackbirds at Wicken Fen (Fig. 1d: residual weight =  $-0.004 + -0.013$  year;  $r^2 = 0.006$ ,  $n = 826$ ,  $P = 0.024$ ).

Mean annual rainfall at Swaffham Prior, near Wicken Fen, increased during the study period, but this increase was not significant ( $F_{1,33} = 1.127$ ,  $r^2 = 0.033$ ,  $P = 0.296$ ). However, these rainfall data did explain changes in blackbird residual body weight at Wicken Fen (residual weight =  $-6.222 + 0.013$  rain;  $r^2 = 0.364$ ,  $n = 34$ ,  $P < 0.001$ ), as well as Treswell Wood (residual weight =  $-4.634 + 0.087$  rain;  $r^2 = 0.249$ ,  $n = 29$ ,  $P = 0.005$ ). The positive effect of rainfall here was probably due to yearly earthworm densities, which represent a main food of

Fig. 1. Examples of long-term changes in residual body weight: (a) blue tits, Treswell Woods; (b) great tits, Treswell Wood; (c) blackcaps, Wicken Fen; and (d) blackbirds, Wicken Fen. Mean values are shown per year with best-fit regression lines.



blackbirds, because here were no such effects in any other species (all  $P$ -values  $>0.05$ ).

### Residual wing length changes

Residual wing lengths did not differ between species at Treswell Wood, but they did at Wicken Fen, which is surprising given that these are residuals from the analyses above involving a species effect (Table 1b). Again, there were no effects of residual variation in daily temperature, and no interaction with species, which is perhaps less surprising here in the case of wing lengths (Table 1b). There were significant effects of year (Wicken Fen only) and year<sup>2</sup> (both sites) and, as with residual body weights, there were significant interaction terms between species and year in both Wicken Fen and Treswell Wood, and between species and year<sup>2</sup> in Wicken Fen (Table 1a). So, wing lengths increased at faster than linear rates, but both the rates of this change and the non-linearity differed according to the species and the site involved.

There were linear increases in residual wing length at Wicken Fen for 7 of the 11 species: reed buntings (Fig. 1a: reed buntings residual wing =  $0.383 + 0.076$  year;  $r^2 = 0.041$ ,  $n = 732$ ,  $P < 0.001$ ), reed warblers (residual wing =  $0.428 + 0.059$  year;  $r^2 = 0.087$ ,  $n = 3421$ ,  $P < 0.001$ ), blackcaps (residual wing =  $0.159 + 0.049$  year;  $r^2 = 0.058$ ,  $n = 738$ ,  $P < 0.001$ ), blackbirds (Fig. 2b: residual wing =  $0.414 + 0.064$  year;  $r^2 = 0.028$ ,  $n = 824$ ,  $P < 0.001$ ), bullfinch (residual wing =  $0.248 + 0.033$  year;  $r^2 = 0.021$ ,  $n = 1247$ ,  $P < 0.001$ ), robins (residual wing =  $0.222 + 0.057$  year;  $r^2 = 0.085$ ,  $n = 446$ ,  $P < 0.001$ ) and dunnocks (residual wing =  $0.340 + 0.050$

year;  $r^2 = 0.047$ ,  $n = 870$ ,  $P < 0.001$ ). At Treswell Wood, however, the increase in residual wing length was more likely to be non-linear with an accelerating increase per year in blackbirds (residual wing =  $-0.192 + 0.028$  year +  $0.003$  year<sup>2</sup>;  $r^2 = 0.006$ ,  $n = 882$ ,  $P = 0.034$ ), dunnocks (Fig. 2c: residual wing =  $-0.271 + 0.013$  year +  $0.003$  year<sup>2</sup>;  $r^2 = 0.015$ ,  $n = 898$ ,  $P = 0.001$ ), and wrens (residual wing =  $0.230 + -0.008$  year +  $-0.003$  year<sup>2</sup>;  $r^2 = 0.015$ ,  $n = 909$ ,  $P = 0.001$ ).

There were also some trends in the opposite direction, with linear decreases in residual wing lengths at Wicken Fen willow warblers (residual wing =  $-0.198 + -0.056$  year;  $r^2 = 0.016$ ,  $n = 331$ ,  $P = 0.020$ ), and at Treswell Wood for blue tits (Fig. 2d: residual wing =  $-0.007 + -0.022$  year;  $r^2 = 0.014$ ,  $n = 687$ ,  $P = 0.002$ ) great tits (residual wing =  $0.034 + -0.020$  year;  $r^2 = 0.010$ ,  $n = 512$ ,  $P = 0.021$ ) and chaffinch (residual wing =  $0.052 + -0.034$  year;  $r^2 = 0.019$ ,  $n = 398$ ,  $P = 0.005$ ). It is possible that these unexpected decreases in residual wing length represent allometric responses to aerodynamic selection pressures in line with the decreases in body weight (Table 1a). Therefore, it is of interest to investigate the long-term proportional changes in body shape, by exploring the interactions between body weight and wing length.

### Residual body weight and wing length relationships

Table 2 demonstrates the significant positive linear relationships between residual body weight and wing length across all species of bird at both sites (Fig. 3). There were also strong interactions between these relationships with species (Table 2), with the allometric

Table 2. The relationship between residual body weight and wing length in different species of bird at Wicken Fen and Treswell Wood. Results of ANCOVAs are presented for residual values of (a) body weight and (b) wing length. All additional interaction terms were NS and so were not included here. Significant P-values are underlined.

	Wicken Fen			Treswell Wood		
	F ratio	df	P	F ratio	df	P
(a) Residual weight						
Residual wing	7.05	1,8290	<u>0.008</u>	71.33	1,7840	<u>&lt;0.001</u>
Species × wing	24.99	12,8290	<u>&lt;0.001</u>	8.59	12,7840	<u>&lt;0.001</u>
Year × wing	0.24	1,8290	<u>0.622</u>	0.47	1,7840	<u>0.492</u>
Year <sup>2</sup> × wing	0.36	1,8290	<u>0.549</u>	2.71	1,7840	<u>0.100</u>
Temp × wing	2.59	1,8290	<u>0.108</u>	0.82	1,7840	<u>0.365</u>
(b) Residual wing						
Residual weight	0.52	1,8290	<u>0.471</u>	217.19	1,7824	<u>&lt;0.001</u>
Species × weight	3.51	12,8290	<u>0.001</u>	14.30	12,7824	<u>&lt;0.001</u>
Year × weight	0.239	1,8290	<u>0.625</u>	0.09	1,7824	<u>0.771</u>
Year <sup>2</sup> × weight	0.714	1,8290	<u>0.398</u>	3.17	1,7824	<u>0.075</u>
Temp × weight	2.45	1,8290	<u>0.118</u>	0.94	1,7824	<u>0.333</u>

relationships between weight and wing length differing between species (Fig. 3). However, it is also clear from Table 2 that there were no interactions between these relationships and year (or year<sup>2</sup>), indicating that the species-specific allometric relationships did not change as a consequence of the long-term changes reported above in body weight and wing size (Fig. 1, 2, Table 1). So, the long-term changes as a possible result of global warming must have been accompanied by compensatory adjustments in body weights and/or wing lengths in order to maintain each species' allometric requirements.

### Comparisons of relationships between sites

A comparison of changes in body weight and wing length between sites was carried out by recalculating the residuals (Table 1a) for the five species that were present

at both Wicken Fen and Treswell Wood. The long-term species-specific changes in residual body weight and wing length reported above (Table 1) were again evident in the year and year<sup>2</sup> effects and their interactions with species in Table 3. Interestingly, this analyses revealed clear site effects on absolute body sizes. There was a site by species interaction in the ANCOVA on residual body weights (Table 3a), with blackbirds and robins being heavier in Treswell Wood than in Wicken Fen, and blackcaps being heavier at Wicken Fen than Treswell Wood (Fig. 4a). Residual wing lengths were longer in Wicken Fen in four of the five species, as compared to Treswell Wood (Fig. 4b, Table 4b). There were also clear site by year and site by year<sup>2</sup> interactions for residual wing lengths, but not for residual body weights (Table 3). This indicates that the long-term changes in wing length, and the nature of those changes, shown above (Table 1b) differed between the two sites.

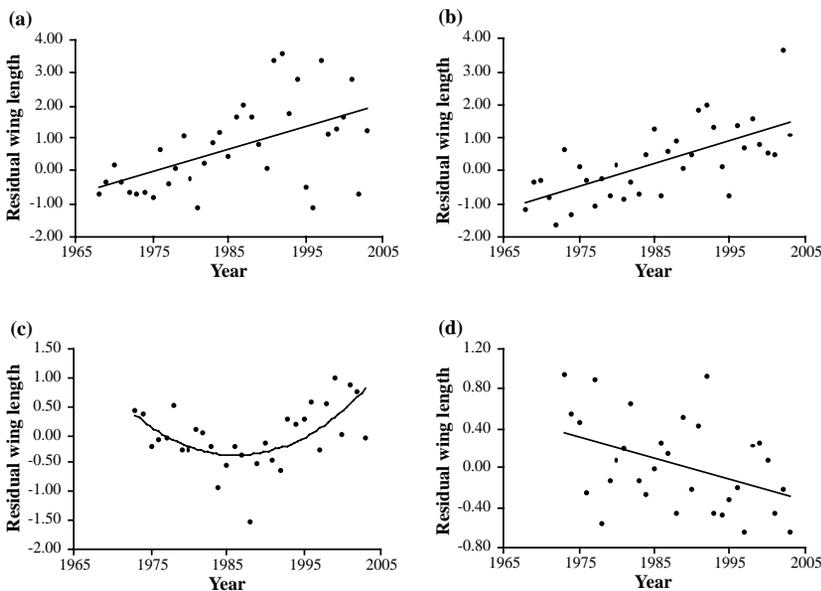


Fig. 2. Examples of long-term changes in residual wing length: (a) reed buntings, Wicken Fen; (b) blackbirds, Wicken Fen; (c) dunnocks, Treswell Woods; and (d) blue tits, Treswell Woods. Mean values are shown per year with best-fit regression lines.

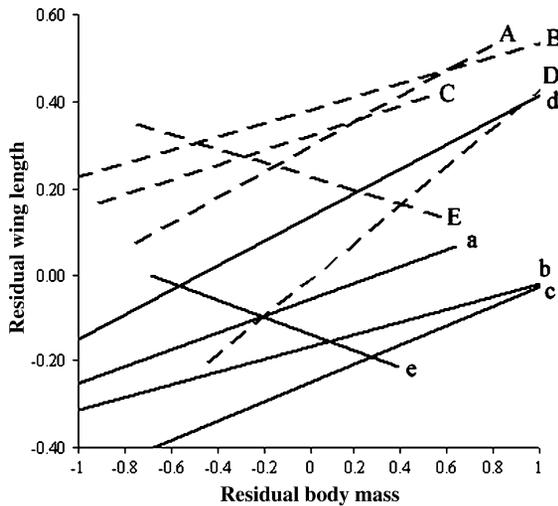


Fig. 3. The relationship between residual body weight and wing length in the five species occurring at both sites. Solid lines and capital letters indicate Treswell Wood and dashed lines and small letters indicate Wicken Fen. Best-fit lines are shown for blackbirds (B:  $y = 0.523 + 0.444x$ ), blackcaps (E:  $y = -0.094 + 0.114x$ ), bullfinches (C:  $y = 0.067 + 0.189x$ ), dunnocks (A:  $y = -0.001 + 0.175x$ ) and robins (D:  $y = 0.056 + 0.139x$ ).

The significant positive effect of residual wing length on residual body weights ( $F_{1,8187} = 351.07$ ,  $P < 0.001$ ) did not differ between sites (wing  $\times$  site interaction:  $F_{1,8187} = 2.82$ ,  $P = 0.093$ ). Likewise, the significant positive effect of residual body weight on residual wing lengths ( $F_{1,8187} = 349.20$ ,  $P < 0.001$ ) did not differ between sites (weight  $\times$  site interaction:  $F_{1,8187} = 1.02$ ,  $P = 0.312$ ).

Table 3. The effects of site (Wicken Fen vs Treswell Wood), year as a covariate (including nonlinear year<sup>2</sup>) and species of bird present at both sites (only blackbirds, blackcaps, bullfinches, dunnocks and robins). Results of ANCOVAs are presented for residual values of (a) body weight and (b) wing length. All additional interaction terms were NS and so were not included here. Significant P-values are underlined.

	F ratio	Df	P
(a) Residual weight			
Site	0.06	1,8231	0.802
Species	0.59	4,8231	0.667
Year	0.83	1,8231	0.364
Year <sup>2</sup>	0.70	1,8231	0.404
Site $\times$ species	8.64	4,8231	<0.001
Site $\times$ year	1.02	4,8231	0.313
Site $\times$ year <sup>2</sup>	1.42	4,8231	0.234
Species $\times$ year	8.58	1,8231	<0.001
Species $\times$ year <sup>2</sup>	2.19	1,8231	0.067
(b) Residual wing			
Site	102.59	1,8227	<0.001
Species	0.67	4,8227	0.610
Year	50.64	1,8227	<0.001
Year <sup>2</sup>	0.01	1,8227	0.932
Site $\times$ species	1.36	4,8227	0.244
Site $\times$ year	17.42	4,8227	<0.001
Site $\times$ year <sup>2</sup>	3.94	4,8227	0.003
Species $\times$ year	40.13	1,8227	<0.001
Species $\times$ year <sup>2</sup>	3.61	1,8227	0.006

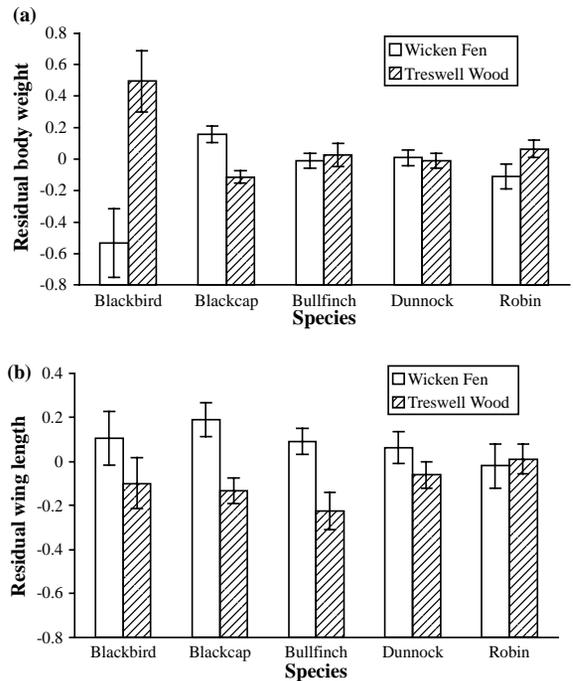


Fig. 4. Mean ( $\pm$ SE) values for: (a) residual body weight; and (b) residual wing length. Data are shown for the five species for which data were available at both Wicken Fen; and Treswell Woods.

Therefore, whilst Wicken Fen and Treswell Wood differed in residual body weights and wing lengths of the five different species, and in the nature of species-specific long-term changes in wing length, these sites did not differ in the allometric relationships between body weight and wing length.

## Discussion

### Body weight, wing length and global warming

Our prediction that body weight would significantly decrease (Bergmann's rule) during the study period was generally confirmed in four species: the dunnock at Wicken Fen, and the great tit, blue tit and bullfinch in Treswell Wood. Non-linear decreases were also found in reed warblers and blackcaps at Wicken Fen, which showed little decline until sizeable decreases in the last few years. Such non-linear declines are not necessarily consistent with the gradual change in temperatures during this period, but may indicate the predicted decline in association with additional selective pressures.

The predicted linear increase in residual wing length was convincingly present for nearly all species examined in Wicken Fen. Again, however, there were non-linear changes as well, this time all the curvilinear increases in wing length occurred in wrens, dunnocks and blackbirds

in Treswell Wood. Allen's rule would certainly predict the gradual linear increases in wing length at Wicken Fen, but perhaps additional factors are needed to explain these changes in the species in Treswell Wood.

This test here of Allen's rule does assume that wing bone length was related in a simple fashion to feather length (Johnston 1969), and that the observed changes in wing length reflected parallel changes in wing bones (i.e. exposed area of wing limbs). There are various reasons why this might not be the case. The close species-specific allometric relationships here between body weight and wing length argue for the importance of aerodynamic consequences for wing shape and wing loading (Rayner 1988). Such effects are likely to depend upon wing bone lengths, but also on changes in feather growth. Differential growth of feathers can change the shape as well as the length of the wing (as measured here) in response to aerodynamic demands. For example, differential flight performance may explain the smaller wing lengths recorded here for species at Wicken Fen, as compared to these same species in Treswell Wood. Perhaps the more cluttered woodland habitat has selected for shorter, and hence rounder, wings in Treswell Wood, or maybe phenotypic flexibility has allowed birds in the woodland habitat to moult and grow appropriately short outer primary feathers.

It is interesting to note that these species-specific allometric relationships were maintained despite the long-term changes in body size and wing length. The relationships between body weight and wing length were also unaffected by the two different habitats for which we have data. All of which argues for aerodynamic adjustments independent of larger-scale effects, such as global warming. However, whilst the long-term changes in body weight were independent of site, wing lengths and the changes in wing length were quite different between sites. This suggests that whilst Bergmann's rule might well apply to the observed long-term body weight decreases, the long-term increases in wing length were not as consistent as we might expect from Allen's rule and that wing length was affected also by an additional factor.

The species that experienced long-term changes in body weight and wing length differ in many of their habits. Some are residents (i.e. the blackbird, chaffinch, dunnock, blue and great tit, robin), while others are summer visitors to Britain (the sedge, reed and willow warblers). Most are insectivorous, but two (the bullfinch and chaffinch) have a largely vegetarian diet. Most breed in open nests, while some (i.e. the blue and great tit) breed in cavities. This variation in life histories and ecology lends support to the hypotheses (i.e. Bergmann's and Allen's rules) that a common environmental factor, such as global warming, affected all of these species (including the migratory ones), rather than any local factor(s). However, it appears that these effects differed

for the different species, especially for wing lengths, which argues against the sole effect of global warming on this character.

We therefore suggest that the most parsimonious explanation for the observed decreases in body weight is that these species were affected by global warming, as predicted from Bergmann's rule. Some species appeared more sensitive than others, because measures of body weight did not always change. Similar decreases in body weight in one rodent and four species of passerines during the second half of the 20th century have been attributed to global warming (Smith et al. 1998, Yom-Tov 2001). Microevolutionary changes in the body size of the bushy-tailed woodrat (*Neotoma cinerea*) during the last 25 000 years have closely reflected past regional temperature fluctuations (Smith et al. 1995). Smith et al. (1995) suggested that changes in body size permit precise quantification of responses to climate changes that have occurred in the past. However, it is clear from these previous studies, and the data presented here that these long-term effects of global warming do not appear universally in all species at all times in any data set. However, it is somewhat unclear what additional short-term and/or local factors might explain any additional variation in body shape in the current study.

The fact that there were no significant relationships between the changes in body weight or wing length and residual temperatures may indicate that conditions close to the date of capture and measurement are unimportant compared to conditions whilst in the nest. This is in accordance with well-established knowledge concerning the effects of nutritional quality early in life and its influence on adult body size in birds (Searcy et al. 2004). Since all our samples were always composed of individuals whose ages differed, and the precise proportion of birds of different ages was not always known. It is therefore impossible here to carry out a more detailed age-related analysis between body weight and wing length and any age-related influences of climate variables.

### Rates of change

The rate of change in body weight observed in this study ( $0.118-0.073\%$  year<sup>-1</sup>) was also similar to the rate observed in Germany between 1981–2003 for the blackbird ( $0.136\%$  year<sup>-1</sup>), the blue tit ( $0.20\%$  year<sup>-1</sup> for adult males), the chiffchaff ( $0.13\%$  year<sup>-1</sup>), and the great tit ( $0.24\%$  year<sup>-1</sup>) (H. Dorsch, pers. comm.). Using the data in Gosler et al. (1995), we calculated the mean rate of change in body weight observed in the great tit in Wytham Wood, England, between 1960–1972 (in the absence of sparrowhawks) and 1981–1993 (after the return of sparrowhawks). The difference in mean

body weight between these periods was 0.81 g, which equals 0.206% per year, reflecting yet again the same magnitude of change observed in this study.

The total calculated decrease in body weight during the 30 years from the start of the study ranged between 0.9–2.2% of initial mean body weight, while increases in wing length were 0.8–2.3% of initial wing length. These changes are comparable to those observed in the medium ground finch (*Geospiza fortis*) after two drought events lasting only 2–3 years each (+1.45% and –1.6% in body weight and +6.6% and –3.5% in wing length; Grant and Grant 1995), but smaller by an order of magnitude than those observed by Yom-Tov (2001) for four species of Israeli passerines (13.4–27.2% increase in body weight during 50 years) and that observed by Smith et al. (1998) for a rodent (14% increase over seven years). Hence, it seems that the selection factor (or factors) operating on the birds in our study was similar in magnitude to those operating on passerines in Germany (H. Dorsch, pers. comm.) and the great tit in Britain (Gosler et al. 1995), but much less severe than those that operated in the other studies.

The rate of increase in wing lengths observed in this study (0.027–0.078% year<sup>-1</sup>) is similar to the rate of decrease in wing length in the red-backed shrike (0.016% year<sup>-1</sup> and 0.024% year<sup>-1</sup> for males and females, respectively) observed by Jakober and Stauber (2000) in Germany. Wing length increases here were also similar in magnitude to those observed in Germany during the last two decades also for the blackbird (0.153% year<sup>-1</sup> and 0.101% year<sup>-1</sup> for females and males, respectively), the blue tit (0.047% year<sup>-1</sup> for males), the dunnock (0.116% year<sup>-1</sup>), and the great tit (0.120% year<sup>-1</sup>) (H. Dorsch, pers. comm.).

### Body weight, wing length and predation

Global warming is a continuous process, but the trends observed in our study were not necessarily linear. Hence, if global warming is a factor driving the observed trends, it cannot be the sole factor. Gosler et al. (1995) have shown that body weight of the great tit was strongly influenced by predation pressure. Lighter body weight and longer wings may enable birds to escape predation better due to smaller wing load and faster take off. On the other hand, short wings enable greater maneuverability. In Wicken Fen, sparrowhawks were rarely observed between 1964–1977, but started to breed close to the Fen in 1987, while in Treswell Wood sparrowhawks returned as a breeding bird only in 1983, bred until 1985 whence it stopped and started to breed again and continue to do so until 2000. In Wicken Fen, 3–10 individual hen harriers (*Circus cyaneus*) wintered regularly during the study period and marsh harriers (*C. aeruginosus*) started to breed there in 1991, and

2–3 pairs breed regularly since 1994. Analysis of pellets of hen harriers in Wicken Fen indicates that they consume many passerines (especially dunnocks, wrens and reed bunting), and about 15% of the prey items in marsh harriers are passerines (R. Clark, pers. comm.).

The observed non-linear linear trends in reed warbler and blackcap body weight decreases at Wicken Fen started between 1985–1988, coinciding with the reappearance of the sparrowhawks as breeding birds. All species studied are potential prey for sparrowhawks. The blackbird and the song thrush are favourable prey for females, whereas the smaller species are taken by the smaller males (Newton 1986, Gosler et al. 1995). This suggests that predation pressure is likely to be another factor behind the observed trends in body weight and wing size.

### Body weight in the blackbird

In Wicken Fen, body weight of the blackbird increased (at a rate of 0.068 g year<sup>-1</sup>), contrary to the prediction from Bergmann's rule. Interestingly, this was half the rate of increase observed in blackbirds in Germany during autumn between 1982–2003 (0.13 g year<sup>-1</sup>; H. Dorsch, pers. comm.). The reason for these increases may lie in the different ways that birds have reacted to global climate change, and supporting evidence for this may come from changes in distribution and abundance. Burton (1995, Appendix 1) provides data on changes in the breeding distribution of European birds since 1850, while Gibbons et al. (1993) provide data for trends in distribution and abundance of breeding birds in the British Isles between the late 1960s and early 1990s. Burton's (1995) data show that all but three of the species in our sample (the robin, the song thrush and the wren) have increased their breeding range in various directions, while the blackbird has increased its range in Europe more than any other passerine. In fact, Williamson (1975) stated, "among the passerines, no bird status has improved more dramatically than the blackbirds". Before 1850, this was considered a shy woodland bird, but by the 1930s it had spread to rural and suburban gardens throughout western Europe, and expanded its range greatly to the north in Finland and Sweden as well as to many of the Scottish islands, including the Shetlands and Faeroes (Burton 1995). It seems that the blackbird has benefited from climate change more than other temperate species, possibly due to the changes in rainfall that have made earthworms, one of its main foods, more available. The significant positive relationship found here between blackbird body weight and annual rainfall supports this hypothesis. A similar increase in body size in the large Japanese field mouse *Apodemus speciosus* during the second half of the last century was attributed to elevated ambient minimal

temperatures, which increased food availability and thus conserved energy (Yom-Tov and Yom-Tov 2004). Similarly, Tornberg et al. (1999), who studied the diet and morphology of Finnish goshawks from 1960s to 1990s, reported a decline in male size and an increase in female size during that period. The authors associated these trends with a reduction of grouse in the diet over the period. Males switched to alternative prey and became smaller, while females, which switched to larger prey (mountain hares *Lepus timidus*), became bigger (Tornberg et al. 1999). However, the increase in body weight observed in the blackbird raises the question of what is the selective advantage for blackbirds in being larger. The answer to this may lay in increased intraspecific competition, which favours larger body size (Adler and Levins 1994).

### Adaptions to habitat

Not all bird species examined here showed the same long- or short-term trends in body weight and wing length. Some species showed the predicted trends, possibly in response to global warming, while others did not. There were also differences in the trends observed between the two localities, especially with regards to wing length, with blackbirds and robins were heavier in Treswell Wood, while blackcaps were heavier in Wicken Fen. These latter differences may be related to habitat preference. Ulfstrand et al. (1981) found that bill and wing length were significantly larger among male great tits inhabiting deciduous in comparison to coniferous forest, and suggested that larger individuals are capable of securing territories in the preferred habitat for this species. The same argument may apply here: the preferred habitat of blackbirds and robins is woodland, whereas blackcaps inhabit more open scrub habitats. In Treswell Wood, wing length was shorter in four of the five species that occur also in Wicken Fen. Shorter, and thus rounder, wings enable higher maneuverability that is required for birds inhabiting woodland (Alatalo et al. 1984). At this stage, we cannot explain the other changes. However, one common pattern seems to be the retention of species-specific body sizes and proportions, perhaps as a result of aerodynamic considerations in association with foraging conditions, predation and inter- and especially intraspecific competition. Such species-specific patterns, along with more specific effects such as in the blackbirds, may explain the non-uniform reactions of different bird species and populations to global warming.

In conclusion, therefore, we found that in several bird species body weight decreased and wing length increased, but in some species these trends were non-linear. These changes could be attributed mainly to global warming, in accordance with Bergmann's rule

regarding body weight, although the claim appears less secure for Allen's rule regarding wing length. Since some of these changes were not linear, and even varied in direction according to the species concerned, it would seem that there might be other contributory factor(s), such as predation and changing land-use and habitat quality (e.g. rainfall, earthworm availability and black-bird body weights). However, it does seem that some of the predicted long-term changes in body size have occurred in birds, and that these might be indicative of long-term environmental changes as a result of global warming.

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