

Global warming and body mass decline in Israeli passerine birds

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Global warming may affect the physiology, distributions, phenology and adaptations of plants and animals. In Israel, minimum summer temperatures increased by an average of 0.26 °C per decade during the second half of the 20th century. Bergmann's rule predicts that, in warm-blooded animals, races from warm regions are smaller than races from cold regions. Numerous studies 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. Using museum specimens, I tested the prediction that the body mass and tarsus length of five resident passerine species in Israel declined between 1950 and 1999. The body mass of four species (the graceful warbler *Prinia gracilis*, the house sparrow *Passer domesticus*, the yellow-vented bulbul *Pycnonotus xanthopygos* and the Sardinian warbler *Sylvia melanocephala*, but not of the crested lark *Galerida cristata*) declined significantly during this period. Tarsus length also declined significantly during this period for two species (the graceful warbler and the house sparrow). Body condition (body mass-to-tarsus length ratio) decreased in the Sardinian warbler, the yellow-vented bulbul and the crested lark. It is suggested that the above declines in body mass and tarsus length are due to global warming and also in accordance with Bergmann's rule. The above explanation does not exclude the possibility that other factors, such as a decrease in food availability, contributed to the decline in body mass. These declines may have serious implications for community structure and competition among bird species and may affect the survival of small passerines.

Keywords: global warming; body mass; tarsus length; Bergmann's rule; Israel; body condition

1. INTRODUCTION

Global mean surface temperatures have increased by 0.3–0.6 °C since the late 19th century (Intergovernmental Panel on Climate Change 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 a review, see Hughes 2000). For example, since 1966 the growing season of plants has advanced by approximately eight days in northern latitudes (Myneni *et al.* 1997), the arrival date of some migratory birds in Britain became significantly earlier between 1974 and 1999 (Jenkins & Watson 2000) and the laying dates of many British birds became increasingly earlier throughout 1971–1997 (Crick *et al.* 1997; McCleery & Perrins 1998). Similarly, Berthold (1991) reported that many bird species in Europe altered their migratory habits and attributed the above 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 American birds (Johnson 1994; Thomas & Lennon 1999). Morphological changes due 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* increased significantly between 1975 and 1993 and several studies have shown that recently collected stomatal densities of plants were significantly lower than in herbarium specimens of the same species collected between 70 and 200 years ago (Beerling & Kelly 1997). Although none of these studies represents a controlled experiment, these trends are more parsimo-

nously explained by a correlation with recent climatic change (Hughes 2000).

Temporal and geographical intraspecific variation in adult body size may be related to several factors, including climate, inter- and intraspecific competition and predation. Bergmann's (1847) rule is probably the best-known rule in zoogeography. It states: 'In warm blooded animals, races from warm regions are smaller than races from cold regions' (Mayr 1970, p. 319). This rule describes a correlation between morphological variation and ambient temperature and tends to be valid for changes in body mass with latitude (Mayr 1970). 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 have provided further support for the importance of ambient temperature in determining the body mass of homoeothermic animals.

Bergmann's (1847) rule has been interpreted as an adaptation to ambient temperature: the relatively larger body surface areas of the smaller races serve as efficient heat dissipators in warm climates, while 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 (see Yom-Tov (1993) for a review). Mass change in homoeothermic animals can occur rather 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 size of the house sparrow *Passer domesticus* correlated positively with the seasonality and annual temperature range

Table 1. Results of ANCOVAs examining the effects of sex and year on the body mass and tarsus length of five species of passerine birds

(Year affected body mass in four species and tarsus length in two species. Body mass or tarsus length did not differ between the sexes in any of the species.)

	crested lark			house sparrow			graceful warbler			yellow-vented bulbul			Sardinian warbler		
	d.f.	<i>f</i>	<i>p</i>	d.f.	<i>f</i>	<i>p</i>	d.f.	<i>f</i>	<i>p</i>	d.f.	<i>f</i>	<i>p</i>	d.f.	<i>f</i>	<i>p</i>
body mass (g)															
sex	1	1.114	0.293	1	1.591	0.209	1	1.458	0.231	1	0.027	0.870	1	0.316	0.576
year	1	1.667	0.199	1	4.687	0.032	1	7.939	0.006	1	7.575	0.007	1	9.542	0.003
sex × year	1	0.363	0.548	1	1.168	0.282	1	1.642	0.203	1	0.102	0.751	1	0.500	0.459
residual	132			144			84			87			76		
tarsus length (mm)															
sex	1	1.045	0.308	1	0.267	0.893	1	0.127	0.723	1	0.468	0.496	1	0.017	0.896
year	1	0.554	0.458	1	6.603	0.011	1	12.337	0.001	1	0.817	0.368	1	3.122	0.081
sex × year	1	1.615	0.206	1	1.002	0.529	1	0.326	0.569	1	1.030	0.313	1	0.018	0.893
residual	144			139			81			86			85		

in both regions (Selander & Johnston 1967; Johnston & Selander 1971; Baker 1980; Lowther & Cink 1992). Similarly, within 50 years of its introduction into New Zealand, the body size of the brushtail possum *Trichosurus vulpecula* correlated with ambient temperature (Yom-Tov *et al.* 1986) as it does in Australia from where it was introduced.

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, the mean body mass of the great tit *Parus major* in England increased following the disappearance of one of its predators, i.e. the sparrowhawk *Accipiter nisus*, and decreased again following its return to the woods (Gosler & Greenwood 1995).

Closely related species sometimes differ in size in sympatry more than they do in allopatry, suggesting that character displacement operates in sympatry as a result of competition (Brown & Wilson 1956; Taper & Case 1992). Changes in size in relation to the number of sympatric competing species may occur rapidly and Yom-Tov *et al.* (1999) showed that, in Pacific islands, skull size (which is highly correlated with body mass) of the kiore (*Rattus exulans*) and the ship rat (*Rattus rattus*) was negatively correlated with the number of other rodents on the same islands. For the ship rat these changes occurred within 100 years or less, while for the kiore they may have occurred over a longer period of time (up to 1000 years).

The above climatic and other man-made changes in Israel (Ben-Gal *et al.* 1999; Yom-Tov & Mendelsohn 1988) may have caused changes in the body mass of birds and the aim of this paper is to examine whether such changes have indeed occurred.

2. METHODS

The Zoological Museum of Tel Aviv University possesses a relatively large collection of passerine skins from which I selected adult specimens of resident species, of which more than 80 specimens were collected continuously during the second half of the 20th century: the crested lark *Galerida cristata*, the house sparrow *Passer domesticus*, the graceful warbler *Prinia gracilis* and

the yellow-vented bulbul *Pycnonotus xanthopygos*. I added the Sardinian warbler *Sylvia melanocephala* to the above species, the population of which comprises both resident and migratory specimens in Israel, although most migrants belong to the same subspecies as the residents (*Sylvia melanocephala momus*). Passerine species in Israel comprising resident, wintering and migrant populations and belonging to more than one subspecies (i.e. the greenfinch *Carduelis chloris*, the goldfinch *Carduelis carduelis* and the Spanish sparrow *Passer hispaniolensis*) were not included in spite of the large sample in the museum.

Birds had been randomly collected for the museum at various times of the year, mostly by shooting, but also by using mist nets and collecting freshly dead birds. There has been no change in the method of collection over the past 50 years. Upon collection, these specimens had been weighed to an accuracy of 0.1–0.5 g and their tarsus lengths measured to an accuracy of 0.1 mm. The effects of year of collection and sex on body mass and tarsus length were examined by using ANCOVAs and regressions. The ratio between body mass and a skeletal measurement is often used as a measure of body condition and was also used in this study.

3. RESULTS AND DISCUSSION

The body masses of the graceful warbler, Sardinian warbler, house sparrow and yellow-vented bulbul (but not of the crested lark) declined significantly between 1950 and 1999 (table 1). The calculated average declines in body mass during this period were 26.8, 27.2, 13.4 and 14.0%, respectively, for the above species and year of collection explained 15.3, 13.4, 4.3 and 7.7%, respectively, of the variation in the body masses of these species (figure 1). During the above period, tarsus length only declined significantly in the graceful warbler and the house sparrow (table 1) and the calculated declines in tarsus length during this period were 15.6 and 8.7% for these two species, respectively, explaining 16.3 and 5.3% of the variation, respectively (figure 2). For the two species in which both body mass and tarsus length declined significantly, the decline in both parameters explained a similar proportion of the variation (for the graceful warbler 15.3 and 16.3% of body mass and tarsus

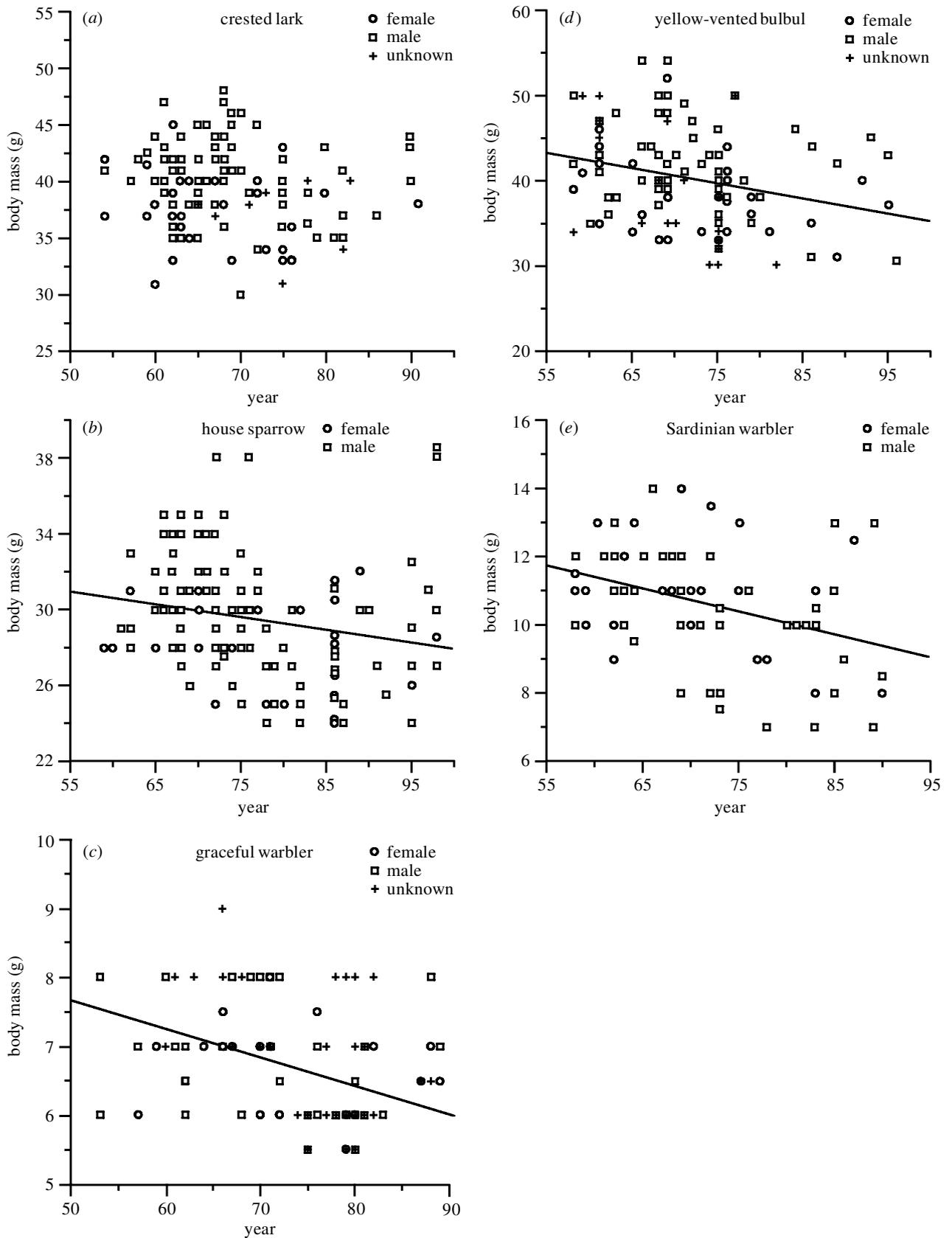


Figure 1. Temporal changes in the body mass of five species of resident passerine birds during the second half of the 20th century. The regression of body mass against year was highly significant for (b) the house sparrow ($R^2 = 0.043$ and $p = 0.011$), (c) the graceful warbler ($R^2 = 0.153$ and $p < 0.001$), (d) the yellow-vented bulbul ($R^2 = 0.077$ and $p = 0.003$) and (e) the Sardinian warbler ($R^2 = 0.134$ and $p = 0.001$), but not for (a) the crested lark ($R^2 = 0.014$ and $p = 0.156$). Circles, females; squares, males; crosses, sex unknown.

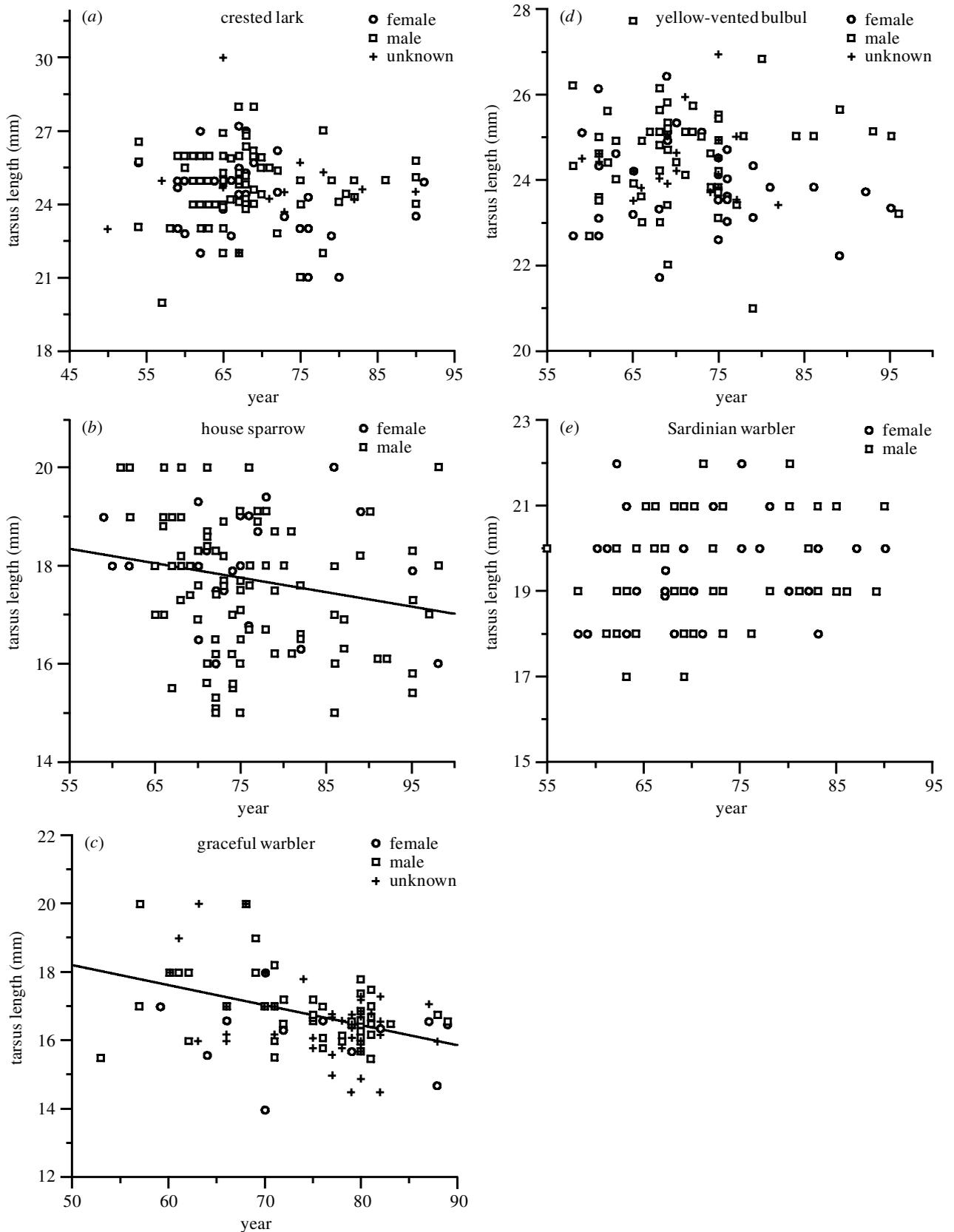


Figure 2. Temporal changes in the tarsus length of five species of resident passerine birds during the second half of the 20th century. The regression of tarsus length against year was highly significant for (b) the house sparrow ($R^2 = 0.053$ and $p = 0.006$) and (c) the graceful warbler ($R^2 = 0.163$ and $p < 0.001$), but not for (a) the crested lark ($R^2 < 0.001$ and $p = 0.848$), (d) the yellow-vented bulbul ($R^2 = 0.007$ and $p = 0.387$) and (e) the Sardinian warbler ($R^2 = 0.039$ and $p = 0.063$). Circles, females; squares, males; crosses, sex unknown.

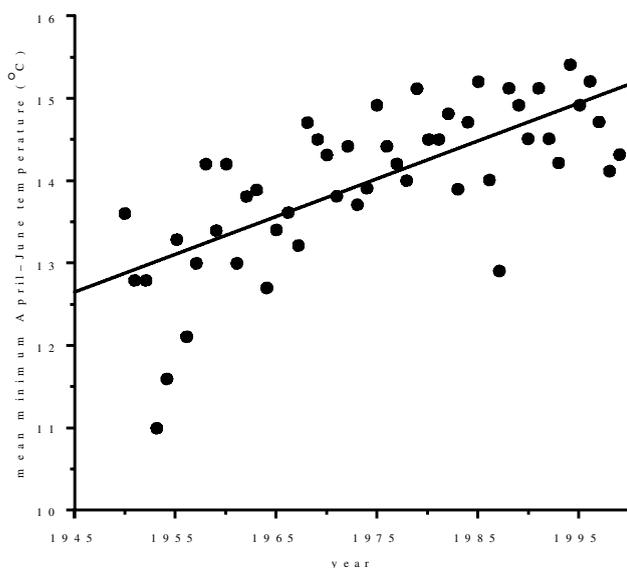


Figure 3. The increase in the average minimum spring (April–June) temperature at Ramat David, Israel, between 1950 and 1999.

length and for the house sparrow 4.3 and 5.3% of these parameters, respectively). However, the decline in body mass was greater than that in tarsus length (1.7 and 1.5 times for the graceful warbler and the house sparrow, respectively). The fact that tarsus length declined at a lower rate than body mass and in only two out of the four species in which body mass declined is probably because a change in a linear measurement such as tarsus length does not fully represent a change in volume or mass.

The ratio between body mass and a skeletal measurement is often used as a measure of body condition (Gorney *et al.* 1999). During the study period, the body mass-to-tarsus length ratio declined significantly in the Sardinian warbler ($R^2 = 0.205$ and $p < 0.0001$), the yellow-vented bulbul ($R^2 = 0.078$ and $p = 0.0042$) and the crested lark ($R^2 = 0.044$ and $p = 0.0107$), but not in the graceful warbler ($R^2 = 0.006$ and $p = 0.485$) and the house sparrow ($R^2 = 0.001$ and $p = 0.708$). The significant decline in the body mass-to-tarsus length ratio in the Sardinian warbler and yellow-vented bulbul indicates that at least part of the observed decline in body mass is due to a decrease in soft tissues. The decrease in body mass in the graceful warbler and house sparrow is due to an equivalent decrease in tarsus length, indicating a decline in both skeleton and soft tissues. In the crested lark, where no decline was observed in either body mass or tarsus length, the body mass-to-tarsus length ratio had decreased significantly, indicating a decrease in soft tissues. Hence, the body mass decline observed in this study is due to either a decrease in soft tissues or a decrease in body size or both.

Since there was a significant negative relationship in Israel between average minimum spring (April–June) temperatures and year from 1950 to 1999 ($F_{1,48} = 46.60$, $p < 0.0001$ and $R^2 = 0.493$) (figure 3), it is reasonable to assume that the declines in body mass and tarsus length of the above species are related to global warming. Such evolutionary changes and phenotypic responses are possible and have been shown to take place rather

quickly. For example, groups of young sibling pigs (*Sus scrofa*), laboratory mice (*Mus musculus*) and chickens (*Gallus domesticus*) that were reared in cold temperatures were heavier than those reared in high temperatures, as expected from Bergmann's (1847) rule (Allee & Schmidt 1951; Weaver *et al.* 1969). Similarly, within 100 years of its introduction into North America and New Zealand, the body size of the house sparrow *P. domesticus* correlated positively with the seasonality and annual temperature range in both regions (Selander & Johnston 1967; Johnston & Selander 1971; Baker 1980; Lowther & Cink 1992). The above explanation does not exclude the possibility that other factors, such as a decline in food availability, contributed to the decline in body mass. However, I have no evidence for a trend in food availability of the above species, as this aspect of their biology has never been studied in Israel.

The above decline in body mass is in contrast to the situation among British passerines where reduced predation pressure by sparrowhawks (*A. nisus*) in woodlands was followed by a body mass increase (and, when the sparrowhawk population recovered, body mass decreased to the previous level) (Gosler & Greenwood 1995) rather than a decrease as observed here. The difference in the trends in body mass between the two countries may be explained by two facts: (i) only one (the Sardinian warbler) of the species studied here inhabits woodland and (ii) the sparrowhawk is a rare summer breeder in Israel and other avian predators of birds are rare in Israel (Shirihai 1996).

Hughes (2000) predicted that species with a short generation time and rapid population growth rates might undergo microevolutionary change *in situ* in reaction to climate change. It seems that the body mass declines of the graceful warbler, Sardinian warbler, house sparrow and yellow-vented bulbul are such a reaction, which may affect the composition and structure of the birds' communities.

Body size influences both food size and interspecific competition and determines which species use which resources and which species can even coexist within an ecological community (Dayan & Simberloff 1998). For example, Snow (1976) and Newton (1972) reported a positive relationship between the beak size of birds (which often correlates with body size) and the size of the fruits and seeds they consume. Yellow-vented bulbuls consume fruits of a certain size, but probably do not compete effectively with smaller frugivorous passerines for smaller fruits. However, as their body mass declines, they may outcompete smaller competitors such as various *Sylvia* species, several species of which migrate through Israel during autumn and consume fruits. Similarly, smaller house sparrows may outcompete various finches (i.e. the greenfinch and the goldfinch). Hence, the reported declines in body mass and tarsus length may have serious implications for community structure and competition among bird species and may affect the survival of small passerines.

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REFERENCES

- Allee, W. C. & Schmidt, K. P. 1951 *Ecological animal geography*. New York: John Wiley & Sons.
- Baker, A. J. 1980 Morphometric differentiation in New Zealand populations of the house sparrow (*Passer domesticus*). *Evolution* **34**, 638–653.
- Beerling, D. J. & Kelly, C. K. 1997 Stomatal density responses of temperate woodland plants over the past seven decades of CO₂ increase: a comparison of Salisbury (1927) and contemporary data. *Am. J. Bot.* **84**, 1572–1583.
- Ben Gal, T., Bitan, A., Manes, A., Alpert, P. & Rubin, S. 1999 Temporal and spatial trends of temperature patterns in Israel. *Theor. Appl. Climatol.* **64**, 163–177.
- Bergmann, C. 1847 Über die Verhältnisse der Wärmeökonomie der Thiere zu ihrer Grösse. *Göttinger Studien* **1**, 595–708.
- Berthold, P. 1991 Patterns of avian migration in light of current global 'greenhouse' effects: a central European perspective. *Acta XX Cong. Int. Ornithol.* **2**, 780–786.
- Brown, W. L. & Wilson, E. O. 1956 Character displacement. *Syst. Zool.* **5**, 49–64.
- Crick, H. Q. P., Dudley, C., Glue, D. E. & Thomson, D. L. 1997 UK birds are laying eggs earlier. *Nature* **388**, 526.
- Dayan, T. & Simberloff, D. 1998 Size patterns among competitors: ecological character displacement and character release in mammals, with special reference to island populations. *Mamm. Rev.* **28**, 99–124.
- Dayan, T., Simberloff, D., Tchernov, E. & Yom-Tov, Y. 1991 Calibrating the paleothermometer: character displacement and the evolution of size. *Paleobiology* **17**, 189–199.
- Gorney, E., Clark, W. S. & Yom-Tov, Y. 1999 A test of the condition-bias hypothesis yields different results for two species of sparrowhawks (*Accipiter*). *Wilson Bull.* **111**, 181–187.
- Gosler, A. G. & Greenwood, J. J. D. 1995 Predation risk and the cost of being fat. *Nature* **37**, 621–623.
- Hughes, L. 2000 Biological consequences of global warming: is the signal already apparent? *Trends Ecol. Evol.* **15**, 56–61.
- Intergovernmental Panel on Climate Change 1995 Summary for policy makers. In *Climate change 1995: the science of climate change* (ed. J. T. Houghton, L. G. Meira Filho, B. A. Callander, N. Harris, A. Kattenberg & K. Maskell), pp. 3–7. Cambridge University Press.
- Jarvinen, A. 1994 Global warming and egg size of birds. *Ecography* **17**, 108–110.
- Jenkins, D. & Watson, A. 2000 Dates of first arrival and song of birds during 1974–1999 in mid-Deeside, Scotland. *Bird Study* **47**, 249–251.
- Johnson, N. K. 1994 Pioneering and natural expansion of breeding distributions in western North American birds. In *A century of avifaunal change in western North America* (ed. J. R. Jehl & N. K. Johnson), pp. 27–44. Lawrence, KS: Cooper Ornithological Society.
- Johnston, R. F. & Selander, R. K. 1971 Evolution in the house sparrow. II Adaptive differentiation in North American populations. *Evolution* **25**, 1–28.
- Lowther, P. E. & Cink, C. L. 1992 House sparrow. In *The birds of North America*, no. 12 (ed. A. Poole, P. Stettenheim & F. Gill), pp. 1–20. Philadelphia/Washington, DC: Academy of Natural Sciences/American Ornithologists' Union.
- McCleery, R. H. & Perrins, C. M. 1998 Temperature and egg-laying trends. *Nature* **391**, 30–31.
- Mayr, E. 1970 *Population, species and evolution*. Cambridge, MA: Harvard University Press.
- Myneni, R. B., Keeling, C. D., Tucker, C. J., Asrar, G. & Nemani, R. R. 1997 Increased plant growth in the northern high latitudes from 1981–1991. *Nature* **386**, 698–702.
- Newton, I. 1972 *Finches*. London: Collins.
- Selander, R. K. & Johnston, R. F. 1967 Evolution in the house sparrow. Intra-population variation in North America. *Condor* **99**, 217–248.
- Shirihai, H. 1996 *The birds of Israel*. London: Academic Press.
- Snow, D. W. 1976 *The web of adaptation: bird studies in the American tropics*. Quadrangle: New York Times Books.
- Taper, M. L. & Case, T. J. 1992 Models of character displacement and the theoretical robustness of taxon cycles. *Evolution* **46**, 317–333.
- Thomas, C. D. & Lennon, J. J. 1999 Birds extend their ranges northwards. *Nature* **399**, 213.
- Weaver, M. E., Douglas, L. & Ingram, I. 1969 Morphological changes in swine associated with environmental temperature. *Ecology* **5**, 710–713.
- Yom-Tov, Y. 1993 Does the rock hyrax, *Procapra capensis*, conform with Bergmann's rule? *Zool. J. Linn. Soc.* **108**, 171–177.
- Yom-Tov, Y. & Mendelssohn, H. 1988 Changes of the distribution and abundance of vertebrates during the 20th century in Israel. In *The zoogeography of Israel* (ed. Y. Yom-Tov & E. Tchernov), pp. 515–548. Dordrecht, The Netherlands: Dr W. Junk Publishers.
- Yom-Tov, Y., Green, W. O. & Coleman, J. D. 1986 Morphological trends in the brushtail possum, *Trichosurus vulpecula*, in New Zealand. *J. Zool. Lond.* **208**, 583–593.
- Yom-Tov, Y., Yom-Tov, S. & Moller, H. 1999 Competition, coexistence and adaptation amongst rodent invaders to Pacific and New Zealand islands. *J. Biogeogr.* **26**, 947–958.