Climatic change and body size in two species of Japanese rodents

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Using museum specimens, we studied temporal changes in skull size in two species of Japanese rodents, the large Japanese field mouse (Apodemus speciosus) and Pratt’s vole (Eothenomys smithii = E. kageus) during the 20th century. We used the greatest length of the skull (GTL), zygomatic breadth (ZB), narrowest width of the skull across the interorbital region (IC) and the length of the upper cheek teeth row (M) as indicators to such changes. We found that GTL and ZB (but not IC and M) increased during the study period in mice, and that IC and M (but not GTL and ZB) increased marginally in voles. We attribute these changes to elevated ambient minimal temperatures, which increased food availability and energy savings for the mice, and required diet change in the voles. © 2004 The Linnean Society of London, Biological Journal of the Linnean Society, 2004, 82, 263–267.

ADDITIONAL KEYWORDS: Apodemus speciosus – Eothenomys smithii – Japan.

INTRODUCTION

Global climate change is apparent at many levels of ecological organization, including life-history parameters, shifts in geographical range, species composition of communities, and changes in structure and function of ecosystems (McCarty, 2001). Global mean surface temperatures have risen by 0.6°C since the late 19th century (IPCC, 1995). Global climate change may affect animals in opposite ways, as an increase in ambient temperature may have opposite effects on animal size. Bergmann’s rule states: ‘In warm blooded animals, races from warm regions are smaller than races from cold regions’ (Mayr, 1970). Bergmann’s rule was 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, and the relatively small body surface area of larger races may help in heat conservation in cold climates. 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, Browning & Shepherd, 1998). Although neither of these studies represents a controlled experiment, these trends are explained most parsimoniously by a correlation with recent climatic change (Hughes, 2000). An additional aspect is that elevated ambient temperature during winter and spring may enhance plant growth and food availability for animals, and improved food availability may consequently influence various life-history parameters. Hence, elevated ambient temperature may cause improved body condition and increased body size. For example, an advance of 6 days per generation in the timing of breeding of the North American red squirrel (Tamiasciurus hudsonicus) in the Yukon region, Canada, has been attributed to a large increase in the availability of food to female squirrels that followed an increase of ambient temperature (Reale et al., 2003). Conditions experienced during early development affect growth and ultimately body size (Henry & Ulijaszek, 1996; Lindstrom, 1999). This is exemplified by the observations that during the last two centuries body height and weight in human populations have increased significantly (secular trend), predominantly in European and European-origin populations. The prime determinants of this trend are considered to be improved nutrition and availability of public health services (Ulijaszek, Johnston & Preece, 1998). Similar phenomena have been observed in animals. For example, in harbour porpoises (Phocoena phocoena) increased prey avail-

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ability (presumably due to hunting pressure and a decrease in population density) resulted in an increase in body length of calves and earlier sexual maturity of females (Read & Gaskin, 1990). A recent increase in skull size among red foxes (Vulpes vulpes) and Eurasian badgers (Meles meles) in Denmark, and in body length among several species of carnivores in Israel has been attributed to an improved diet (Yom-Tov, Yom-Tov & Baagøe, 2003; Yom-Tov, 2003).

In this article we examined two hypotheses: (1) increased food availability positively affects skull size, and by implication, also body size; (2) global warming negatively affects skull size (and, by implication, also body size), as expected from Bergmann’s rule. We selected two species of common Japanese rodents for the study – the large Japanese field mouse (Apodemus speciosus) and Pratt’s vole (Eothenomys smithii = E. kageus). These two species, which have been collected continuously throughout much of the 20th century and are well presented in the National Science Museum, Tokyo, therefore provide a good model to examine the above hypotheses.

MATERIAL AND METHODS

SPECIES

Apodemus speciosus is an endemic Japanese rodent with a mass of 40–60 g (Abe, 1986; Abe, Shida & Saitoh, 1989). It inhabits mixed, broad-leaved and coniferous forests and forest plantations, but prefers natural forest (Bjornstad, Stenseth & Saitoh, 1999; Saitoh, Bjornstad & Stenseth, 1999), and is found also in fields (Kaneko, 1982). It is granivorous (45% of its diet) and insectivorous (45%) (Ota, 1984). This species displays morphological plasticity, with increased size on small islands, but there is no size variation within Honshu Island (Renaud & Millien, 2001).

Eothenomys smithii is an endemic Japanese rodent with a mass of 20–35 g (http://noah.ees.hokudai.ac.jp/~iwasa/E_smithii.html). It inhabits wooded hills and mountains, meadows and fields, and feeds mainly on green plants including moss, fruits and nuts as seasonal foods (Kaneko, 1982; Y. Kaneko, pers. comm.).

MUSEUM MATERIAL

Skulls of 150 adult field mice and 166 voles that had been collected on Honshu Island between 1949 and 1989 (Apodemus) and 1920 and 1989 (Eothenomys) were measured at the National Science Museum, Tokyo. Adults were defined as such through tooth wear and the fusion of the cranium bones. For each skull, we noted (from its label or museum catalogue) its sex, locality and date of collection, and when available also body and tail lengths. Using digital calipers, four measurements were taken from each skull to an accuracy of 0.01 mm: greatest length (GTL), zygomatic breadth (ZB), narrowest width of the skull across the interorbital region (IC) and the length of the upper cheek teeth row (M).

Data on mean monthly minimum and maximum temperatures for a representative meteorological station of Honshu Island (Fukushima, 37.75°N, 40.47°E) for the studied period were obtained from the following website: http://climate.geog.udel.edu/~climate/html_pages/download.html#ghcn_T_P_clim

In order to test whether skull size of A. speciosus and E. smithii had undergone any change during the studied period we carried out regression tests on skull characters against year of collection and ambient temperatures. Preliminary tests indicated that in both species males were significantly larger than females, and all analyses on skull characteristics were performed on residuals controlled for sex.

RESULTS

SKULL SIZE, YEAR OF COLLECTION AND AMBIENT TEMPERATURE

For field mice, both GTL and ZB were seen to have increased significantly along the studied period, and year of collection explained 13.3% and 17.7% of the variation in GTL and ZB, respectively (Fig. 1). The calculated increase from 1949 to 1989 was 5.16% and 6.20% for GTL and ZB, respectively. Both GTL and ZB were significantly related to body length (GTL: $F_{1,142} = 84.380, R^2 = 0.373, P < 0.0001$; ZB: $F_{1,142} = 41.468, R^2 = 0.226, P < 0.0001$) and to tail length (GTL: $F_{1,154} = 53.069, R^2 = 0.256, P < 0.0001$; ZB: $F_{1,154} = 23.147, R^2 = 0.130, P < 0.0001$). However, there was no trend of change in size of IC ($F_{1,140} = 0.887, P = 0.3477$) and M ($F_{1,142} = 3.509, P = 0.0313$), total body length ($F_{1,142} = 3.509, P = 0.0631$) or tail length ($F_{1,164} = 2.363, P = 0.1266$). There were no significant relationships between any of the skull characters and mean minimum or maximum annual temperatures in the year of collection.

For voles, there was a significant but marginal decrease in residual (after controlling for sex) IC ($IC = 0.258–0.004 \times year; F_{1,164} = 6.228, R^2 = 0.037, P = 0.0136$) and M ($M = 0.286–0.004 \times year; F_{1,164} = 4.696, R^2 = 0.028, P = 0.0317$). Year of collection explained only 3.7% and 2.8% of the variation in IC and M, respectively. These results, although statistically significant, seem to have little biological significance. There was no trend of change in GTL ($F_{1,164} = 3.460, P = 0.0647$) and ZB ($F_{1,164} = 0.132, P = 0.7163$), total body length ($F_{1,154} = 0.003, P = 0.9858$) or tail length ($F_{1,150} = 0.005, P = 0.9460$). There were no significant relationships between any of
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the skull characters and mean minimum or maximum annual temperatures in the year of collection, apart from a marginal relationship between mean minimum annual temperature and IC ($F_{1,164} = 4.973, P = 0.0271$) that explained only 2.9% of the variation.

**AMBIENT TEMPERATURES DURING THE 20TH CENTURY**

Between 1900 and 1990 mean annual temperature ($T_a$) on Honshu Island significantly and linearly increased by 1.53°C ($T_a = 0.017 \times \text{year} - 19.532$; $F_{1,164} = 63.910, R^2 = 0.418, P < 0.0001$). This increase was mainly due to an increase of minimal temperatures (2.07°C) rather than maximal temperatures (0.99°C) during this period. The increase in mean minimal temperature was 2.07, 1.67, 2.13 and 2.67°C during winter (December–February), spring (March–May), summer (June–August) and autumn (September–November), respectively, whereas mean maximal temperature increased only by 1.47, 1.50, 0.77 and 0.50°C during the above seasons, respectively.

**DISCUSSION**

Our results indicate that in the field mice GTL and ZB significantly increased along the studied period, total body length also increased, but not significantly, and IC and M did not change. By contrast, skull size in the voles hardly changed. We also found that minimal temperatures in Japan had increased significantly during the same period, particularly minimum temperature during autumn, summer and winter. Low ambient temperatures inhibit plant growth, and elevated temperatures, particularly minimum temperatures during winter, spring and autumn, enhance plant growth and prolong the growing period, thus increasing food availability to herbivorous animals. Hence, *A. speciosus* did not conform with Bergmann’s rule, and its skull size increased during the 20th century. We suggest that the observed increase in skull size (and, by implication, body size) in the field mouse is a reaction to warmer autumn, summer and winter. The elevated ambient temperatures may affect the mice in two ways: by enabling them to save energy on metabolism, and by lengthening the growing season of plants, thus making food available for longer periods. The energy savings to field mice due to elevated temperature can be calculated using data from Haim, McDevitt & Speakman (1995). These authors found that oxygen consumption of short-day acclimated Scottish *Apodemus sylvaticus* increased by 0.186 mL O₂/(g.h°C), and their minimal oxygen consumption was 1.92 mL O₂/(g.h). Hence, an increase of 1°C in ambient temperature saves an amount of energy that equals 9.7% at the lowest critical point, or 19.4% for an increase of about 2°C (the observed increase in minimal temperature on Honshu Island during the 20th century). Assuming that *A. speciosus* is similar to its congener *A. sylvaticus*, and because *A. speciosus* is nocturnal and is exposed to the low temperatures of the night, these animals save a large amount of energy as a result of global warming. Potentially, a mouse can divert these savings to increase in body size, and this seems to be the cause for the observed increase in skull size of *A. speciosus*. Similar phenomena were observed in other studies: the length of the plant growing season in some areas of the globe has increased by

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up to 3.6 days per decade over the past 50 years (Menzel & Fabrian, 1999; Menzel & Estrella, 2001); and increasingly warm winters have affected the development and fecundity of the red deer (Cervus elaphus) and the Soay sheep (Ovis aries) in Norway (Post et al., 1997) and the UK (Forchhammer et al., 2001), respectively.

If the above explanation (increased food availability) is correct, two further questions may be raised. Why did IC and M in mice not increase in parallel with GTL and ZB, and why was there no similar change in GTL and ZB in voles? Both IC and M are closely associated with diet: the molars are used for grinding food, and the space between the interorbital constriction of the skull and the zygomatic breadth indicate the size of the masseter muscle. Hence, whereas the increase in GTL and ZB indicate an increase in skull size (and, by implication, body size), apparently due to increased food availability, the stability of IC and M sizes indicates that it was the composition (rather than the quantity) of the diet of this species that did not change during the studied period.

We suggest, as an answer to the second question (no change in GTL and ZB in voles), that the difference between the two species might be due to their different sensitivity to cold. Although both species occur sympatrically in many areas of Japan, A. speciosus is more abundant in lowlands in comparison with E. smithii, which occurs at a higher elevation in central Honshu (Kaneko & Morii, 1976; Y. Kaneko, pers. comm.). In fact, E. smithii does not occur below 400 m above sea level (H. Endo, pers. comm.). This distribution may indicate that A. speciosus is more sensitive to cold than E. smithii. Hence, the elevated ambient temperatures during the 20th century affected A. speciosus more than E. smithii. This effect may have been due to energy saving during warmer growing seasons, which enabled the mice to divert energy from maintenance to growth. If this explanation is correct, it may also explain the marginal decrease in IC and M in E. smithii. The elevated temperatures may have affected the composition of its diet, resulting in a decrease in these two skull parameters, which are related to diet.

In summary, we found that GTL and ZB increased during the study period in mice, and IC and M increased in voles. We attribute these changes to elevated minimal ambient temperatures, which increased food availability and energy savings for mice, and required diet change in voles.

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