

Recent increase in body size of the American marten *Martes americana* in Alaska

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Using museum specimens, we studied recent changes in skull size of the American marten *Martes americana*, in continental Alaska. In Alaska, global warming has resulted in milder winters that may contribute to an improved food supply in the wild. In the present study, we tested the hypothesis that body size of the marten had increased during the second half of the 20th century, in response to global warming. We found that skull size, and by implication body size, increased significantly during the second half of the 20th century, possibly due to an improved food supply and/or lower metabolic demands in winter. Improved food availability in winter may result from the improved nutritional conditions for prey, and/or from increased access to prey resulting from a longer snow-free season. Longitude had a significant positive effect on skull size and a significant negative effect on teeth size. In Alaska, the climate is milder along the western coast and becomes harsher inland. Hence, the milder climate was associated with larger body size providing further support for our prediction that body size of the American marten was influenced by food availability and reduced energy expenditure. The negative relationship between longitude and teeth size may indicate a trend towards a larger prey in inland marten populations, but we have no data to support or refute this hypothesis. © 2008 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2008, **93**, 701–707.

ADDITIONAL KEYWORDS: food availability – global warming – skull size.

INTRODUCTION

Intraspecific geographical variation in body size of both homeotherms and ectotherms is a common phenomenon (Blackburn, Gaston & Loder, 1999; Ashton, Tracy & de Queiroz, 2000; Ashton, 2002a, b; Freckleton, Harvey & Pagel, 2003; Meiri & Dayan, 2003; Millien *et al.*, 2006) and has been related to many factors, including inter- and intraspecific competition, food availability, and reaction to ambient temperature in accordance with Bergmann's rule. Changes in body size may occur rapidly (i.e. within decades or even a few years) and, during the past few decades, numerous studies have reported recent significant changes in body size of several species of birds and mammals (Millien *et al.*, 2006). For example, body weight of the great tit *Parus major* Linnaeus in Britain has changed in accordance with predation pressure

(Gosler, Greenwood & Perrins, 1995); body weight and wing length of the Galapagos medium ground finch (*Geospiza fortis*) has changed following two drought periods of only 2–3 years each (Grant & Grant, 1995); skull size of the great Japanese wood mouse *Apodemus speciosus* Temminck and the masked shrew *Sorex cinereus* Kerr in Alaska has increased during the second half of the 20th century, apparently due to an improved diet (Yom-Tov & Yom-Tov, 2004, Yom-Tov & Yom-Tov, 2005); body size of several species of passerine birds (Yom-Tov, 2001; Yom-Tov *et al.*, 2006a) and a rodent (Smith, Browning & Shepherd, 1998) has decreased within several decades, apparently as a reaction to global warming; and body size of three species of rodents introduced into Pacific islands has changed, apparently due to inter- and intraspecific competition (Yom-Tov, Yom-Tov & Moller, 1999).

Global climate change may have an effect on body size. Global temperatures increased on average by

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0.6 °C from the late 19th century to 1994 (Houghton *et al.*, 2001). At high latitudes, the increase is greater than average, and minimum temperatures increased at approximately twice the rate of maximum temperatures (Houghton *et al.*, 2001). Global warming may affect the physiology, distribution, phenology, and adaptation of plants and animals (Hughes, 2000). Recent morphological changes in animals have also been attributed to global warming. For example, 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). On the other hand, recent increases in body size of several species of mammals have been attributed to increased food availability due to the indirect effects of global warming (Yom-Tov & Yom-Tov, 2004, 2005).

Mainland Alaska is a vast area (approximately 1.5 million km²) stretching between 54.5–71.5°N and 130–168°W (142–168°W after excluding the south-eastern panhandle) comprising Arctic tundra in the north, conifer and boreal forest further south and south-east, and rainforest along the West Pacific coast. North of the Arctic Circle, the region experiences constant daylight in the summer, but remains in darkness for much of the winter. As a result, the north–south temperature gradient is large. For example, mean monthly temperatures of the coldest (January) and warmest (July) month in the extreme south of Alaska at Ketchikan (55°20'N, 131°38'W) are 0.9°C and 14.3°C, respectively and, on the coast of the Arctic Ocean at Barrow (71°18'N, 156°43'W) they are –25.4 °C and 4.7 °C, respectively (The Alaska Climate Research Center; <http://climate.gi.alaska.edu>).

In north-western North America, and particularly in Alaska, average warming since 1950 has been approximately 2 °C and almost twice as much in the interior in winter, and the growing season has lengthened by more than 14 days (Parker *et al.*, 1994; <http://www.usgcrp.gov/usgcrp/Library/nationalassessment/overview>). In the Arctic, the increase during the last 30 years was 2 °C per decade (ACIA, 2004). Tape, Sturm & Racine (2006) found an increase in shrub cover over the past 50 years in northern Alaska and related this to the increase in ambient temperatures during this period. These authors argue that such a change in vegetation may have a fundamental impact on animals.

The American marten *Martes americana* (Turton) is a common carnivore in the coniferous and mixed forests of North America, distributed from New England, Minnesota, and New Mexico in the south to northern Alaska and Canada in the north. The marten is widespread and abundant in Alaska, where it is extensively harvested for its fur, and many specimens have been deposited in museums (Clark *et al.*,

1987). Season lengths and restrictions on the use of motorized vehicles for trapping in easily accessible areas (areas with many roads) have been established to reduce the opportunity for overexploitation (Kirchhoff, 2000; <http://www.adfg.state.ak.us/pubs/notebook/furbear/marten.php>).

The marten is an opportunistic feeder whose a varied diet includes rodents (especially voles, but also tree and flying squirrels), snowshoe hares (*Lepus americanus* Erxleben) and a large variety of other animals, as well as fruits in season (Clark *et al.*, 1987; Buskirk *et al.*, 1994; Small, Stone & Cook, 2003). Data on the diets of marten from 22 studies throughout the USA and Canada summarized by Martin (1994) indicate that diet diversity declines from south to north, and the two studies carried out in Alaska had the lowest diversity, with 66% (Buskirk & MacDonald, 1984) and 73% (Lensink, Skoog & Buckley, 1955) of the diet composed of voles. Population size, reproduction, survival, and winter range have been shown to be determined largely by food availability (Weckwerth & Hawley, 1962; Soutiere, 1979; Clark, 1984).

The shape and size of an animal's body influence energy demand (Casey & Casey, 1979). The elongated small body of the marten determines its relatively high surface area to volume ratio that, together with its short fur, is associated with a high metabolic rate (Harlow, 1994). American martens have a relatively high mass-specific basal metabolic rate, low thermal efficiency, they do not undergo deep torpor, and their locomotor efficiency is low compared to other animals (Harlow, 1994). These characters make them sensitive to changes in ambient temperature, and imply that the martens' food consumption is high.

The present study aimed to examine whether body size of the American marten inhabiting Alaska had changed during the second half of the 20th century. Because ambient temperatures in Alaska increased significantly during this period, especially during winter, we hypothesized that body size would have changed accordingly. Two opposite trends could be predicted: (i) body size will have decreased, as predicted by Bergmann's rule and (ii) body size will have increased due to reduced metabolic demands in warmer climate, coupled with increased food availability.

MATERIAL AND METHODS

Skulls of 434 American martens were measured at the University of Alaska Museum of the North, in Fairbanks. A list of the specimens measured and their details (sex, longitude, latitude and year of collection) were taken from the museum records (see Supplementary Material). The specimens were adults of

known sex and with data on latitude, longitude, and year of collection. Skulls of young specimens (with open sutures between the bones of the skulls or whose teeth had not fully erupted) were not measured. Martens attain adult size during the first year of life and, as far as we know, there are no published data on their longevity in Alaska. The age of the studied specimens was unknown. For each year of collection, we aimed for a sample of approximately 20 specimens. Most of the specimens had either been donated by over 50 different hunters or collected by various scientists and staff of the Alaska Department of Fish and Game during the period 1949–1998. Collection effort was not uniform throughout the study period, and the skulls had been deposited in the museum during the 1950s, in 1978–1979, and in the 1990s. Body and tail length of some marten specimens had been recorded by the collectors and are used in the present study to calculate the relationships between skull parameters and total body length. Using digital calipers, four measurements were taken from each skull to an accuracy of 0.01 mm: greatest length (GTL), zygomatic breadth (ZB), the length of the largest upper cheek teeth – the shearing upper premolar (carnassial, PM4) and diameter of the upper canine (C). In most cases, the right tooth was measured. In carnivores, all four parameters are associated with diet: GTL is associated with the size of the temporal muscles, which are important to overcome the resistance of prey to occlusion; the zygomatic arch is closely related to the size of the masseter muscle that pulls the jaw forward and upward; and both muscles are important for chewing. The size of the canines is generally associated with prey size (Ewer, 1973). Larger canines enable a predator to take and handle larger prey items, whereas larger premolars and molars enable it to crush larger prey, or to grind grain and other hard food items (Romer, 1962). In mammals, skull and body parameters are related. For example, Creighton (1980) showed that tooth size of 123 species of mammals was significantly related to body size, and Johnston (1991) showed that, in the weasel *Mustela frenata*, cranial length and mass, as well as zygomatic breadth, were significantly related to body size.

Our sample included specimens collected in mainland Alaska, but not from the Alaska Panhandle. The reason for this is that the latter region comprises many islands, peninsulas, and inlets, and island populations of many mammals differ from those of the adjacent mainland. Moreover, this region is distinguished from the rest of Alaska by its mild, maritime, and humid climate that supports a dense forest of Sitka spruce (*Picea sitchensis* Bongard) and western hemlock (*Tsuga heterophylla* Raf.), whereas the forests and tundra of mainland Alaska exist in a

much harsher climate and are dominated by white spruce (*Picea glauca* Moench) on well drained and south-facing slopes and black spruce (*Picea mariana* Miller) on north-facing slopes. Accordingly, island martens are larger than their mainland counterparts (Nagorsen, 1994), as predicted by the island rule (Foster, 1964). This race has also been described as subspecifically distinct, and is likely a separate genetic lineage (Stone & Cook, 2002).

Net primary production (NPP) is an indicator of food availability for both herbivores and their predators. NPP data (g carbon m⁻² year⁻¹ for 1° squares for the 20th century) were kindly provided by Dr Mark Lomas (University of Sheffield). To test the relationship between skull size and NPP for the presumed year of growth, we fitted annual NPP value for each specimen according to its locality and year of collection. However, because the age of the specimens was unknown, the NPP data used were more likely to represent a trend of change rather than actual NPP at the growth period of a specific specimen. We also used NPP data at the centre of distribution of our specimens' data (64.5°N, 149.5°W) to calculate the change in NPP that had occurred during the study period.

We used principal component analysis (PCA, based on correlation matrix) to combine the information of the four skull parameters (GTL, ZB, PM4, and canine, all log-transformed) into principal components. We examined the effects of year of collection, sex (dummy variable), latitude, longitude, and NPP and their interactions (but not interactions with NPP) on the principal component scores by running multiple regressions using JMP (version 5.1; SAS Inc.). As far as we are aware, there are no measured ambient temperature data for each of the localities and years from where and when our specimens were collected. Thus, the factor 'year' represents a combination of environmental factors including ambient temperature in the year of collection

RESULTS

All four skull parameters were significantly related to body length (for GTL: $R^2 = 0.859$, $F_{1,15} = 91.507$, $P < 0.0001$; ZB: $R^2 = 0.720$, $F_{1,15} = 38.520$, $P < 0.0001$; PM4: $R^2 = 0.719$, $F_{1,15} = 38.291$, $P < 0.0001$; canine: $R^2 = 0.812$, $F_{1,15} = 64.647$, $P < 0.0001$), indicating that marten skull size accurately reflects body size.

PC1 clumped the two skull measurements (GTL and ZB) and PC2 the two teeth measurements (PM4 and canine) into two variables. Eigenvalues were 2.903 and 0.789, and the proportions of variance explained by these factors were 72.6% and 19.7%, respectively.

Table 1. Effect of sex, year, latitude, longitude and net primary production (NPP) and their interactions (excluding interactions with NPP) on PC1 and PC2

Term	PC1		PC2	
	<i>t</i> -ratio	<i>P</i> > <i>t</i>	<i>t</i> -ratio	<i>P</i> > <i>t</i>
Intercept	-5.42	< 0.0001	2.58	<u>0.0103</u>
Sex	21.91	< 0.0001	7.05	< 0.0001
Year	6.43	< 0.0001	-0.69	0.4936
Sex × Year	0.59	0.5544	0.40	0.6904
Latitude	-0.35	0.7253	-1.37	0.1713
Sex × Latitude	0.09	0.9297	-1.53	0.1263
Year × Latitude	1.36	0.1758	0.54	0.5924
Sex × Year × Latitude	0.29	0.7752	1.58	0.1157
Longitude	3.10	<u>0.0021</u>	-4.06	< 0.0001
Sex × Longitude	0.13	0.8986	-1.68	0.0947
Year × Longitude	-1.39	0.1659	2.04	<u>0.0418</u>
Sex × Year × Longitude	-0.03	0.9787	0.87	0.3841
NPP	-0.42	0.6761	0.19	0.8530

The full factorial model (PC1: $F_{12,376} = 56.2$, $P < 0.0001$; PC2: $F_{12,376} = 9.2$, $P < 0.0001$) accounted for 64.2% and 22.6% of the variance in PC1 and PC2, respectively. Significant results are underlined.

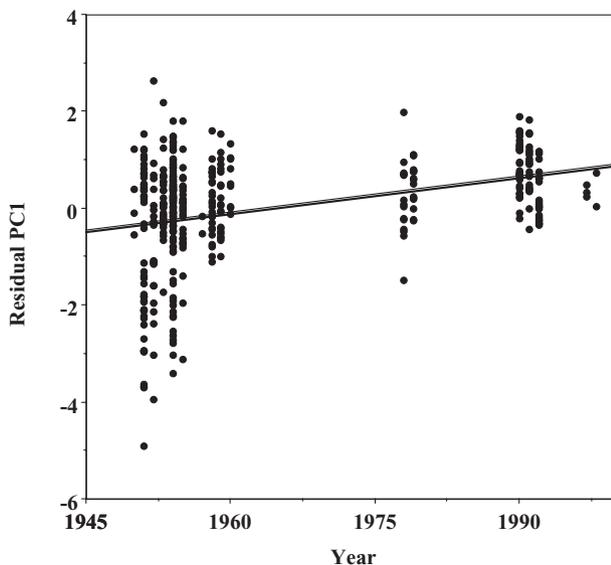


Figure 1. The effect of year of collection on PC1 (corrected for sex, latitude, and longitude net primary production (NPP) and their interactions as well as NPP). $F_{1,387} = 52.885$, $P < 0.0001$, $R = 0.120$.

Results of multiple regressions (Table 1) indicated that males were significantly larger than females, and longitude had a significant effect on both PC1 and PC2. Year had a significant effect on PC1 (but not on PC2) indicating that body size (but not the teeth) increased during the study period (Fig. 1). Latitude, NPP, and all interactions but one were not significant. The only significant (marginally so: $P = 0.0418$)

interaction was year × longitude in relation to PC2. Removal of NPP did not change the proportion of the variation explained.

The calculated annual rate of change in GTL for a hypothetical female and a male marten collected at 60°N, 150°W in 1950 and 2000 were 0.036% and 0.032%, respectively.

Annual NPP at the centre of distribution of our sample (64.5°N, 149.5°W) increased significantly during the second half of the 20th century [$NPP_{(g\ carbon\ m^{-2}\ year)} = 1.17 \times year - 1962$; $F_{1,49} = 6.137$, $P = 0.017$; ZB: $R^2 = 0.111$]. The calculated increase in NPP (58.5gC) equals about 18% over a period of 50 years. For our sample specimens, NPP was positively related to longitude ($F_{1,431} = 316.135$, $P < 0.0001$; $R^2 = 0.423$) and negatively to latitude ($F_{1,431} = 70.517$, $P < 0.0001$; $R^2 = 0.141$).

DISCUSSION

The results of the present study show that skull size and, by implication, body size of the American marten increased during the second half of the 20th century. Considering the relatively short period over which the change took place, it is reasonable to assume that this is a plastic change and not heritable; only future research can clarify this.

Although we do not know the reason for the observed increase in body size of the marten, we suggest that food availability and/or energy conservation in a mild climate have a strong influence on it. It has been suggested that population size, reproduc-

tion, survival, and winter range of the marten are all determined largely by food availability (Weckwerth & Hawley, 1962; Soutiere, 1979; Clark, 1984), and we suggest that food availability also determines its body size. Recent increases in body size have been attributed to increased food availability, either due to changes in agricultural practices (Yom-Tov, Yom-Tov & Baagoe, 2003), fish farming (Yom-Tov *et al.*, 2006b), increased availability of organic garbage (Yom-Tov, 2003), or increase in NPP (Yom-Tov & Yom-Tov, 2004, 2005). The first three factors are unlikely to affect food availability for the marten in Alaska. This state has practically no agriculture, and human population there is relatively small (less than two-thirds of a million during the study period; Times Atlas, 1999). Such a small population is unlikely to affect food availability for the marten, particularly considering that most of our sample was taken from interior Alaska where very few people live.

We suggest that the observed increase in body size is an indirect result of global warming affecting food availability. Mean annual ambient temperatures in Alaska have increased by about 2 °C during the last 50 years and almost twice as much in its interior; winter precipitation has increased by 10%; and the growing season has lengthened by more than 14 days (<http://www.usgcrp.gov/usgcrp/Library/nationalassessment/overview>). Tape *et al.* (2006) reported that, during the last 50 years, there has been an increase in shrub (alder, willow, and dwarf birch) cover in the Alaskan tundra. These authors argue that similar changes occurred in Canada, Scandinavia, and parts of Russia, and that this evidence suggests that a pan-Arctic vegetation transition is underway and may alter the fundamental architecture an function of this ecosystem, with important ramifications for the climate, the biota, and humans.

Shorter and warmer winters in Alaska have extended the growing season of plants, and in turn resulted in an increase in annual NPP. This increase probably led to larger populations of primary consumers such as rodents and hares, which form the majority of the martens' diet. Warmer winters also have shorter periods of snow coverage during which rodents can hide from their predators. This higher food availability, as well as the marten diverting some of the energy formerly used for maintenance in winter into growth, probably enabled the observed increase in size. Although this suggestion is speculative, the above circumstantial evidence provides some support and can be added to the existing evidence that body size of animals is strongly affected by food availability (Millien *et al.*, 2006).

Large body size is considered to be of physiological advantage under stressful conditions and for both inter- and intraspecific competition (Brown, 1995).

However, an increase in food availability may in turn lead to an increase in population size, which will ultimately balance out at a higher level. Under these new conditions, there will be no further increase in body size because food will be a limiting factor.

PC2 was not affected by either year or NPP, indicating that teeth size did not change during the study period (Table 1). Yom-Tov *et al.* (2007) have shown that, although body size of the Canadian lynx (*Felis lynx* Linnaeus) in Alaska changed in accordance with its population cycles, the canines did not change, and they assumed that this was due to the lynx being conservative in its selection of prey. In many carnivores, especially felids and mustelids, teeth size is related to prey size (Ewer, 1973). We suggest that this also applies to the marten, whose body size changed during the study period, whereas its teeth did not. However, only a future experimental study can support or refute this assumption.

In the present study, the average rate of increase for GTL was 0.03% per year, in the same order of magnitude as in Danish red foxes, *Vulpes vulpes* Linnaeus (0.07% per year) and Danish Eurasian badgers, *Meles meles* Linnaeus (0.0275% per year) (Yom-Tov *et al.*, 2003), but smaller than the average 0.14% per year increase among the greater Japanese wood mice, *Apodemus speciosus*, during the second half of the 20th century (Yom-Tov & Yom-Tov, 2004) and approximately 1.5% per year decrease of body mass in woodrats (Smith *et al.*, 1998) within 8 years. Schmidt & Jensen (2003) used old records of body length from Denmark to study changes in size among various mammals, and suggested that, during the last two centuries, the body size of the pine and stone marten (*Martes martes* and *Martes foina*, respectively) has decreased at a rate of approximately 0.15% per year.

We found that longitude had a significant positive effect on PC1 and a significant negative effect on PC2. In Alaska, the climate is milder along the west coast and becomes harsher inland towards the east (i.e. ambient temperatures in winter are positively related to longitude, but summer temperatures are negatively related to it; Alaska Climate Research Center: <http://climate.gi.alaska.edu>). In accordance with these data, in Alaska, NPP is positively related to longitude. Hence, the milder climate is associated with a larger body size, providing further support for our contention that the body size of the American marten is influenced by food availability and energy conservation.

Although PC1 was positively related to longitude, PC2 was negatively related to it, indicating a trend towards a larger prey in inland marten populations, but we have no data to support or refute this hypothesis.

Finally, we expected that NPP would be significantly related to body size, but the findings of the present study refute this prediction. We suggest that the lack of a significant relationship between NPP and body size was due to the fact that we did not know the ages of our specimens, and thus could not fit NPP data of birth year to any of them. However, the year effect may represent environmental changes of several factors, including ambient temperature and NPP.

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SUPPLEMENTARY MATERIAL

The following supplementary material is available for this article:

Table A1. A list of American marten specimens measured in the present study.

This material is available as part of the online article from:

<http://www.blackwell-synergy.com/doi/abs/10.1111/j.1095-8312.2007.00950.x>

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