



Relative effects of climate change, isolation and competition on body-size evolution in the Japanese field mouse, *Apodemus argenteus*

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ABSTRACT

Aim This paper examines body size variation in both recent and Quaternary populations of the Japanese field mouse *Apodemus argenteus* in order to assess the relative effects on body size of climate change, isolation and competitive interactions with its congeneric *A. speciosus*. Both temporal (since the Last Glacial Maximum, LGM) and spatial (over the Japanese archipelago) scales are considered.

Location The small field mouse is widespread in Japan, and the specimens examined were collected from 10 localities on islands of widely differing area (from 4 km² to 230,510 km²) and at latitudes ranging from 30.3° N to 45.1° N.

Methods The effects of geographical factors such as latitude and island area on the size variation of *A. argenteus* were investigated, using the lower incisor size. In addition, the size of some specimens from two Quaternary localities was compared with the size of the extant specimens. Evolutionary rates of size change since the LGM were calculated in darwins. Hutchinson size ratios were used to examine the pattern of variation of the size segregation between the two Japanese field mice, *A. argenteus* and *A. speciosus*, in relation to time and space.

Results There was a negative relationship between size and latitude among living *A. argenteus* populations. In addition, there was no effect of island area on body size, especially at higher latitudes. At lower latitudes, *A. argenteus* were larger on smaller islands, although this trend was not statistically significant. Quaternary specimens of *A. argenteus* were smaller in size than their living representatives. The interspecific size ratio between the two Japanese *Apodemus* was larger on smaller islands and at higher latitudes, and there has been a decrease in the size ratio between the two *Apodemus* since the LGM. Lastly, in accordance with the theory of character displacement, the small *A. argenteus* was larger in allopatry than in sympatry, whereas the large *A. speciosus* was smaller in allopatry than in sympatry.

Main conclusions These results indicate that *A. argenteus* does not conform to Bergmann's rule or to the island rule. The variation in size for the small Japanese field mouse at both spatial and temporal scales may be related to climate change, with an additional effect of competition with the large field mouse, especially on smaller islands. The size convergence between the two Japanese *Apodemus* observed over the last 21,000 years may be explained by the diminution of available food resources due to the reduction of land mass areas following the LGM. It may also be the result of an evolution towards an optimal body size; a hypothesis previously proposed to explain the evolution of body size in island mammals. Lastly, the evolutionary rates of body size calculated for *A. argenteus* since the LGM are typical of rates calculated for other Quaternary mainland

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mammals, thus suggesting that the evolution in this species was not particularly rapid, as is often thought for island mammals.

Keywords

Island rule, Bergmann's rule, competition, Hutchinson ratio, body size evolution, *Apodemus*, Japan.

INTRODUCTION

'Despite some progress...we don't understand why mammals have the sizes they do' (Van Valen, 1973).

Island vertebrates, in comparison with their mainland equivalents, often provide remarkable examples of body size evolution. Among mammals, large species tend to evolve towards a smaller size following their isolation, whereas small species show the exact opposite evolutionary size trend (Foster, 1964; Van Valen, 1973; Lomolino, 1985). These typical insular trends of dwarfing of large mammals and gigantism of small mammals, also known as the island rule (Van Valen, 1973), have been documented in a number of species and islands. In particular, island endemic rodents are usually larger in size than their mainland congeners, and there is an abundant literature providing examples of gigantism among island rodents, for both fossil and recent species (review in Millien & Damuth, 2004). In particular, some species of the genus *Apodemus* conform to the hypothesis of gigantism on islands, e.g. *A. sylvaticus* on some Mediterranean islands (Angerbjörn, 1986; Libois *et al.*, 1993; Michaux *et al.*, 2002), on the British islands (Delany & Healy, 1967; Berry, 1969; Delany, 1970; Angerbjörn, 1986), on Iceland (Kurtén, 1959) and in Denmark (Angerbjörn, 1986), *A. flavicollis* in various islands in Europe (Angerbjörn, 1986) and *A. speciosus* in Japan (Millien & Damuth, 2004). The extent of body size change on islands is considered to be positively correlated with the degree of isolation (distance to the mainland or source), and inversely related to island area (Foster, 1964; Case, 1978; Heaney, 1978). Hypotheses explaining body size evolution of island mammals invoke various biological factors, including the absence of predators and/or competitors (Case, 1978; Heaney, 1978; Lawlor, 1982; Angerbjörn, 1986; Damuth, 1993; Dayan & Simberloff, 1998).

However, if the island is large enough, or if an island species is distributed over an archipelago, body size may also be affected by climatic factors. The most commonly reported biogeographical trend is Bergmann's rule, the tendency of individuals within the geographical range of a species to be larger in size at higher latitudes (Mayr, 1956, 1963; Ashton *et al.*, 2000; Meiri & Dayan, 2003). In addition, Bergmann's rule is often interpreted as a response to variation in temperature in space (Mayr, 1963) or in time (review in Millien & Damuth, 2004). For example, the Japanese archipelago extends over a distance of *c.* 2000 km in length,

and ranges from 22 to 45° N in latitude. Such a variation in latitude is characterized by an equally wide range of climatic variation over the entire archipelago, ranging from warm-tropical in the south to cool-temperate in the north. Under such conditions, Bergmann's rule predicts that the Japanese mammals should show some variation in body size related to climatic variation. At least two rodent species are known to be larger at higher latitudes in Japan: the vole *Microtus montebelli* (Kaneko, 1988) and the large field mouse, *A. speciosus* (Millien & Damuth, 2004). In the latter species however, Millien & Damuth (2004) showed that isolation and temperature interacted to affect body size variation on small islands.

In this paper, I will focus on the small Japanese field mouse *A. argenteus*, which is the direct competitor of *A. speciosus*, and is also widely distributed across the Japanese archipelago – taken together, the two *Apodemus* are the most abundant rodents in Japan (Abe, 1994; Sekijima & Sone, 1994). There is some evidence that *A. speciosus* exerts some competitive pressure over *A. argenteus* (Sekijima & Sone, 1994). Classically, the lack of competitors on islands is thought to be a major factor influencing body size evolution of endemic mammals (Angerbjörn, 1986). However, interspecific competition is also a factor promoting size divergence between species on the mainland (Brown & Wilson, 1956) and on islands (Dayan & Simberloff, 1998). The strength of the competition for resources can be assessed through the study of the size divergence of two or more competitors (Simberloff & Boecklen, 1981; Dayan *et al.*, 1989, 1990; Yom-Tov, 1991; Dayan & Simberloff, 1994, 1998; Jones, 1997; Parra *et al.*, 1999; Simberloff *et al.*, 2000). According to Hutchinson (1959), there is a minimum theoretical size ratio of 1.28 between two species necessary for their coexistence. The existence of such a minimum size ratio is controversial (Eadie *et al.*, 1987; Greene, 1987; MacNally, 1988; Ganeshaiah, 1999; Parra *et al.*, 1999). For example, Millien-Parra & Loreau (2000) found no evidence for a minimum size ratio among 11 Japanese rodent assemblages, based on the lower incisor size and shape. Nevertheless, the Hutchinson size ratio is a direct and simple index which allows one to study the size divergence between two species. Here, I will look at the variation in the Hutchinson size ratio between the two Japanese field mice in relation to the biogeography of Japan. In addition, the effect of competition between the two *Apodemus* will be assessed through the comparison of their size variation in sympatry and allopatry. The theory of character displacement operating

in sympatry predicts that competing species are more different in sympatry than in allopatry (Brown & Wilson, 1956; Taper & Case, 1992). Accordingly, the small field mouse *A. argenteus* should be larger in allopatry than in sympatry, whereas the opposite trend should be observed for the large *A. speciosus*.

Lastly, the observations made on recent populations of *A. argenteus* will be compared with data from Quaternary localities, in order to examine the history of evolutionary size change in this species since the Last Glacial Maximum (LGM). Traditionally, body size and morphological evolution are supposed to be faster for island organisms than for their mainland counterparts. The red deer on Jersey island greatly reduced its size in *c.* 6000 years (Lister, 1989), and the dwarf woolly mammoths on Wrangel Island are thought to have evolved in *c.* 5000 years (Vartanyan *et al.*, 1993). On a much shorter time-scale (several decades), Pergams & Ashley (2001) reported microevolutionary rates for three genera of island rodents: *Peromyscus maniculatus* from California Channel Islands (Pergams & Ashley, 1999, 2001), *Mus musculus* from British Channel Islands (Berry, 1964) and *Rattus rattus* in Galapagos Islands (Patton *et al.*, 1975). They concluded that these evolutionary rates were 'extremely high', confirming the general theory of island evolution. Similarly, Kurtén (1959) reported an 'enormously high' rate of evolution for the Icelandic *A. sylvaticus* over *c.* 1000 years. Millien & Damuth (2004), however, showed that the rates of body size evolution since the LGM in Japan in *A. speciosus* were not excessively high, due to the counterbalancing effect of climate change during this period (Millien & Damuth, 2004). Here, I will calculate the rates of body size evolution over the same period of time (21,000 years) for *A. argenteus* and compare them with the evolutionary size rates obtained earlier (Millien & Damuth, 2004) for *A. speciosus*.

A comparison of the patterns of size variation in the two Japanese field mice, at both spatial (over the Japanese archipelago) and temporal (since the LGM) scales will allow an assessment of the relative effects of climate change, isolation and competitive interactions on body size change.

MATERIALS AND METHODS

The Japanese archipelago

The studied specimens were collected from islands differing in area by five orders of magnitude, from 4 km² to more than 230,000 km². In addition, they span a wide range of latitude, from 30.3° N to 45.1° N, and extend over a distance of *c.* 2000 km in length, from south to north.

These islands collectively cover three main climatic zones (Millien-Parra & Jaeger, 1999), with annual mean temperature ranging from 5.3 °C in the north to 19.3 °C in the south (FAO, 1987). Paleoclimatic reconstructions show that the climatic zones that are recognized today in Japan existed during the Quaternary, although they were displaced towards the south during glacial episodes (see reviews in Dobson, 1994; Millien-Parra & Jaeger, 1999).

The drop in temperature during these glacial episodes was accompanied by sea-lowering. All the Japanese islands are land-bridge islands (*sensu* Lawlor, 1986), and the maximum water depth surrounding them does not exceed 130 m. The maximum sea level drop recorded during the glaciations of the Quaternary has been estimated at -140 m (see Millien-Parra & Jaeger, 1999). As a result, the main island of Japan, Honshu and all the surrounding smaller islands have been connected to each other at various times during the Quaternary (see Millien-Parra & Jaeger, 1999). The last connection occurred during the maximum sea-lowering of the LGM, around 21,000 years ago. This low sea-level stand was followed by a transgression, and all the Japanese islands remained isolated from one another until today. It is thus reasonable to assume that the currently observed differences between the small island and Honshu populations have developed since the LGM.

Fossil and recent specimens

The two Japanese field mice, *A. speciosus* and *A. argenteus* are widespread in Japan, and are the most abundant species among the Japanese rodents (Abe, 1994). They are known in Japan from fossil specimens and are thought to have been restricted to the Japanese archipelago since the Middle Pleistocene (Kawamura, 1989; Dobson & Kawamura, 1998).

The material used for this study includes a total of 151 specimens of the extant species *A. argenteus*, the small Japanese field mouse. This species is widely distributed over Japan today, and 10 different localities have been considered here (Table 1). They are located on the main island of Honshu (Mt Hayachine, Mt Goyo, Nikko, Mt Fuji and Mt Odaigahara) as well on some of the smaller surrounding islands (Hokkaido, Sado, Oki, Tsushima and Tane islands). Thirty-three fossil specimens from two Late Pleistocene localities on Honshu were also examined (Table 2). Sample sizes range from three to 37 specimens. All the material is stored at the National Science Museum, Tokyo.

Measurements

The antero-posterior diameter of the lower incisor (AP) is a simple, repeatable measurement that can be taken on both extant and fossil specimens (Millien-Parra, 2000), and it is an unbiased and accurate estimator of body size among rodents ($r = 0.93$, $P < 0.0001$ for the allometric relationship between lower incisor size and body length or body weight; result from Millien-Parra, 2000). The measurement was taken for each specimen studied at the level of the incisor gap, with a drawing tube coupled to a 2-D digitizer, to the nearest 0.01 mm. Only adult specimens were considered (based on the complete eruption of the third molar) for recent specimens, and for fossil specimens for which the incisor was still in connection with the lower jaw. The fossil material also contained isolated incisors, and juvenile specimens were excluded on the basis of the morphology of the tip of the incisor, in particular, the little

Table 1 Mean antero-posterior diameter of the lower incisor (*n*; SD) for *Apodemus argenteus* populations in 10 localities today and estimated mean AP at the LGM

Locality	Geography		Temp. (°C)		AP (mm)		Size evolution		Size ratio with <i>A. speciosus</i> *
	Lat. (°N)	Area (km ²)	Today	LGM	Today	LGM	% Change	Darwins	
Honshu									
Mt Hayachine	39.5	230,510	10.0	1.0	0.994 (6; 0.04)	0.962	+3.29	1.54	1.210
Mt Goyo	39.2	230,510	10.3	1.3	1.065 (6; 0.06)	0.964	+10.49	4.75	–
Nikko	36.7	230,510	12.5	3.5	1.047 (37; 0.07)	0.976	+7.23	3.32	1.224
Mt Fuji	35.4	230,510	13.7	4.7	1.025 (31; 0.07)	0.983	+4.28	1.99	1.132
Mt Odaigahara	34.2	230,510	14.8	5.8	1.053 (15; 0.05)	0.989	+6.47	2.99	1.103†
Small islands									
Hokkaido Isl.	42.7	78,511	–	–	1.016 (14; 0.07)	0.964‡; 0.962§	+5.41‡; +5.57§	2.51‡; 2.58§	1.404
Sado Isl.	38.0	857	–	–	1.039 (9; 0.07)	0.976¶	+6.41¶	2.96¶	1.241
Oki Isl.	36.2	243	–	–	1.094 (3; 0.03)	0.989**	+10.62**	4.80**	1.157
Tsushima Isl.	34.2	698	–	–	1.050 (27; 0.06)	0.989**	+6.17**	2.85**	1.210
Tane Isl.	30.3	446	–	–	1.135 (3; 0.01)	0.989**	+14.76**	6.56**	1.162

*Data for *A. speciosus* from Millien & Damuth (2004). †Compared with the Kisuki-cho population of *A. speciosus* (Millien & Damuth, 2004).

Honshu population used for estimation of AP(LGM) of the small island populations: Mt Goyo‡, Mt Hayachine§, Nikko¶ and Mt Odaigahara**.

Table 2 Mean antero-posterior diameter of the lower incisor (*n*; SD) for *Apodemus argenteus* fossil samples from two Late Pleistocene localities

Locality	Lat. (°N)	AP (mm)	Temporal size trend		Size ratio with <i>A. speciosus</i> *
			% Change	<i>t</i> -test	
Shiriya quarry	41.2	0.989 (13; 0.039)	+0.40‡; +7.57‡	$P = 0.817‡; P < 0.005‡$	1.423
Shiraiwa mine	34.8	0.996 (20; 0.064)	+2.91§	$P = 0.157§$	1.329

*Data for *A. speciosus* from Millien & Damuth (2004). Extant Honshu population used for comparison: Mt Hayachine†, Mt Goyo‡ and Mt Fuji§.

or no wear on the surface of the cutting edge extremity of the incisor.

Statistical analyses

Within each sample, the variable AP was tested for normality with the Kolmogorov–Smirnov test. Comparisons between sexes among each population were conducted using *t*-tests, and as multiple tests were performed, the significance levels were corrected using the Bonferroni method (Sokal & Rohlf, 1995).

In order to study the geographical size trends in living populations, a multiple regression analysis between incisor size (as the dependent variable), and latitude and island area was performed on all individual data. *Post hoc* mean comparisons were performed between different populations (independent *t*-tests), and the significance levels were corrected using the Bonferroni method. In order to remove any latitudinal effect, small island localities were compared with the closest Honshu locality – Hokkaido island with Mt Goyo and Mt Hayachine, Sado island with Nikko, and Oki, Tsushima and Tane islands with Mt Odaigahara. In addition, *t*-tests were conducted to

compare incisor mean size between living and fossil populations.

I used the relationship between present-day temperature and latitude across the Japanese archipelago (Millien & Damuth, 2004), based on averages reported for 131 meteorological stations throughout Japan (FAO, 1987). This relationship was combined with the relationship between incisor size and latitude among extant *A. argenteus* to obtain the relationship between the incisor size and temperature in this species. I estimated the incisor size at the LGM for the different Honshu localities using this latter relationship and assumed that the temperature at the LGM was 9 °C lower than today (Jouzel *et al.*, 1987).

Evolutionary rates are reported in darwins (factors of *e* per million years; Gingerich, 1983) following the formula: $d = (\ln AP_{\text{present}} - \ln AP_{\text{LGM}}) / \Delta t$ (Haldane, 1949), where $\ln AP_{\text{present}}$ and $\ln AP_{\text{LGM}}$ are the natural logarithms of the lower incisor mean size for any given locality today and at the LGM, respectively, and Δt is the time interval in Myr. The time span since the LGM is 21,000 years or 0.021 Myr.

In order to investigate the effect of interspecific competition between *A. speciosus* and *A. argenteus* in Japan, the mean

incisor size ratio between the two *Apodemus* species was computed for each locality where they occur in sympatry. The effect of latitude on the interspecific size ratio was examined with Pearson correlation coefficient. The additional effect of island area on this index of interspecific competition was assessed with a paired *t*-test.

All statistical analyses were performed using Systat software (version 5).

RESULTS

Summary statistics

The normality of the variable AP could not be rejected for any case (Kolmogorov–Smirnov test, all $P > 0.05$), and the absence of sexual size dimorphism was confirmed for all extant populations examined (*t*-test, all $P > 0.05$). Data for both sexes were thus combined in all analyses, and sexual size dimorphism was assumed to be also non-existent in fossil populations.

Geographical trends among living populations

There was no significant relationship between island size and latitude among the 10 Japanese localities (Pearson correlation, $r = 0.25$, $P = 0.49$). The results of the multiple regression analysis on the 151 living *A. argenteus* specimens show that there is a statistically significant relationship between latitude and incisor size, after removing the effect of island size ($t = -2.17$, $P < 0.03$). The incisor size decreases with latitude and there is a *c.* 5% decrease in AP from south to north in Japan ($AP = 1.210 - 0.005 \text{ lat}$).

The analysis also shows that there is no significant relationship between incisor size and island size ($t = -0.99$, $P = 0.32$). Overall, *A. argenteus* individuals are not significantly different (*t*-test, $t = -0.71$, $P = 0.48$) in size on smaller islands (mean AP: 1.047) than on Honshu (mean AP: 1.039). Further mean comparisons show that the locality mean for AP among island populations are not significantly larger than those from the closest Honshu locality (*t*-test, all $P > 0.180$). The only exception is for the Tane island population, from which individuals are significantly larger than individuals from the closest Honshu population of Mt Odaigahara ($t = -2.66$, $P < 0.02$).

Evolutionary size trend

The two Late Pleistocene populations of *A. argenteus* were between 0.4% and 7.6% smaller than extant populations from localities of similar latitude, although this trend is significant in only one case out of the three comparisons made (Table 2).

Figure 1 shows the relative size changes in incisor size since the LGM for islands and the Honshu populations for two ranges of latitude. The evolution in incisor size of *A. argenteus* populations from Oki, Tane and Tsushima islands are depicted with those from Fuji and Odaigahara (all latitudes $< 36.5^\circ \text{ N}$),

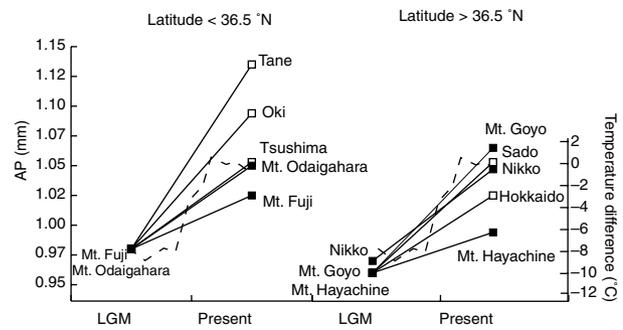


Figure 1 The evolution of the lower incisor size (AP) in *Apodemus argenteus* since the Last Glacial Maximum (LGM). The figure is separated into two latitudinal ranges; left: latitude $< 36.5^\circ \text{ N}$; right: latitude $> 36.5^\circ \text{ N}$. Open squares: small island populations; filled squares: Honshu populations. Sea level was at its lowest stand *c.* 21,000 years ago (LGM), and all the small island populations are believed to have been continuous with the Honshu populations. The incisor size at the LGM has been estimated assuming a temperature 9° C lower than today (Table 1). Each population evolved towards a larger size (solid lines), tracking the temperature change over time (dotted line, modified from Jouzel *et al.*, 1987) since the LGM. This size increase has been more marked on small islands than on Honshu for latitude $< 36.5^\circ \text{ N}$.

whereas the evolution in incisor size of populations from Hokkaido and Sado islands are depicted with those from Mt Hayachine, Mt Goyo and Nikko (all latitudes $> 36.5^\circ \text{ N}$). For latitudes lower than 36.5° N , the temperature effect has been accentuated by the island effect on small islands, resulting in larger individuals on small islands than on Honshu populations. In contrast, there was no additional island effect for populations on small islands at higher latitude (Fig. 1).

Evolutionary rates

Combining the relationship between incisor size and latitude among the 151 *A. argenteus* living specimens ($AP = 1.210 - 0.005 \text{ lat}$) and the relationship between temperature and latitude observed today across the Japanese archipelago ($T = 45.445 - 0.897 \text{ lat}$, Millien & Damuth, 2004), I computed the relationship between incisor size and temperature in *A. argenteus*: $AP = 0.9567 + 0.00567T$. Using this equation, the size at the LGM for various Honshu and small island *A. argenteus* populations was estimated (Table 1). The temperature at the LGM was assumed to be 9° C lower than today, at any given latitude.

The evolutionary rates of incisor size evolution since the LGM for Honshu and small-island populations of *A. argenteus* vary from 1.54 to 6.56 darwins (Table 1). There was no significant difference in the rate of size increase since the LGM between small-island (mean rate: 3.71 darwins) and Honshu (mean rate: 2.92 darwins) populations ($t = 0.89$, $P = 0.40$). The difference in mean evolutionary rate between small islands and Honshu populations is slightly larger for latitudes lower than 36.5° N (mean rate for small islands: 4.73; mean rate for

Honshu: 2.49), but this difference is not statistically significant ($t = 1.90$, $P = 0.163$).

The effect of interspecific competition

When present in sympatry, the mean size ratio between the two living *Apodemus* ranges from 1.103 to 1.404, with a mean value of 1.205 (Table 1). There was a positive significant correlation between the size ratio and latitude ($r = 0.752$, $P < 0.020$). In addition, Hutchinson size ratios were significantly larger on small islands (mean ratio: 1.24) than on the closest Honshu locality (mean ratio: 1.16; $t = 2.90$, $P < 0.03$). There has also been a decrease in the size ratio between *A. argenteus* and *A. speciosus* since the Late Pleistocene. Overall, the size ratio was larger in Late Pleistocene localities (mean ratio: 1.376) than among living *Apodemus* (mean ratio: 1.206, $t = -2.57$, $P < 0.03$). This pattern is also apparent when comparing the values of the size ratios between fossil and living populations occurring at similar latitude (Table 2). When comparing Shiriya to Mt Hayachine and Shiraiwa to Mt Fuji, a paired t -test indicated that the size ratio was larger between the two fossil *Apodemus* than between their living representatives ($t = 25.62$, $P < 0.03$).

For some localities, it was possible to examine the size pattern of interspecific differentiation of the two living *Apodemus* in allopatry. In particular, Mt Goyo and Mt Hayachine are located in the same region, with a very similar latitude (Table 1). In Mt Goyo, where *A. speciosus* is absent (Millien & Damuth, 2004), *A. argenteus* individuals are significantly larger than in Mt Hayachine ($t = 2.39$, $P < 0.04$).

DISCUSSION

The present study has demonstrated a decrease in size from south to north in *A. argenteus*. This result is coherent with the observations made previously on the lower jaw (Renaud & Millien, 2001). This result is not consistent with Bergmann's rule, and is the inverse of the increase in size with latitude observed in *A. speciosus* (Millien & Damuth, 2004). A number of recent studies have discussed the validity of Bergmann's rule (review in Meiri & Dayan, 2003). Even among other living species of *Apodemus*, *A. argenteus* may not be the only exception to Bergmann's rule, as a trend of decreasing size with latitude, although very small, was also observed in *A. sylvaticus* in Europe, based on a composite morphometrical index of size of the lower jaw (Renaud & Michaux, 2003). Other similar examples of an opposite response to the same latitudinal gradient in sympatric species has also been observed among Australian marsupial carnivores (Jones, 1997), and among two canids in Chile (Fuentes & Jaksic, 1979).

Overall, there was no effect of island area on size in *A. argenteus*, in particular for small islands at higher latitude. At lower latitude, individuals were always larger on small islands than on Honshu, but the tendency of insular gigantism in *A. argenteus* was not marked enough to be statistically significant. There are other exceptions to the island rule

documented among rodents (Foster, 1964; Case, 1978; Lomolino, 1985), and *A. argenteus* specimens studied here would be another example to the list. Thus, *A. argenteus* does not conform to Bergmann's rule or to the island rule.

However, the observation of geographical differentiation observed today among islands of differing areas should not be sufficient to refute the island rule (e.g. in this particular case, the gigantism of small mammals). The pattern of size differentiation observed today is just the result of a long history of successive size changes that may not necessarily have operated in a constant direction (Hendry & Kinnison, 1999). In the case of the Japanese field mice, however, the hypotheses formulated from the observation of living populations were tested against data obtained from fossil material (Millien & Damuth, 2004, for *A. speciosus*, and this study for *A. argenteus*). A comparison of the fossil material with recent specimens of *A. argenteus* showed that Late Pleistocene individuals were smaller in size than their living representatives. The evolutionary size increase in *A. argenteus*, which accompanied the climate warming following the LGM, thus conforms to the geographical trend observed today of decreasing incisor size with decreasing temperature in this species.

Figure 2 depicts a model of the evolution in size since the LGM in various situations for both small island and Honshu populations. Millien & Damuth (2004) made the hypothesis that the net evolutionary size change in the congeneric species *A. speciosus* since the LGM was the product of both the island effect (positive effect on size) and temperature increase (negative effect on size). In the case of *A. speciosus*, isolation had a positive effect on size, whereas climate change had a negative effect on size (Fig. 2). For the small island populations, the temperature effect has been greater than the island effect, resulting in a net decrease in size since the LGM (Fig. 2c). The situation is very different in the case of *A. argenteus*, for which we observed a negative relationship between incisor size and temperature. We also observed a small effect of isolation for small island populations at latitudes lower than 36.5° N. At lower latitudes, the size evolution in *A. argenteus* is thus the result of the addition of temperature increase (positive effect on size) and, albeit to a much lesser extent, isolation (positive effect on size, Fig. 2e). At higher latitude, the size evolution in *A. argenteus* is the result of the single climate effect (positive effect on size), with no additional effect of isolation on small islands (Fig. 2f). Again, the evolutionary size increase in *A. argenteus* since the Late Pleistocene is opposite to the evolutionary size decrease observed in *A. speciosus* over the same period (Millien & Damuth, 2004).

The evolutionary rates calculated over the last 21,000 years for *A. argenteus* are typical of evolutionary size rates for other Quaternary mainland mammals (Gingerich, 1983). In other words, the size evolution in *A. argenteus* was not accelerated, as often supposed for island mammals (Pergams & Ashley, 1999). Millien & Damuth (2004) made a similar conclusion based on evolutionary size rates calculated for *A. speciosus* in Japan over the same period of time. The evolutionary rates for the lower

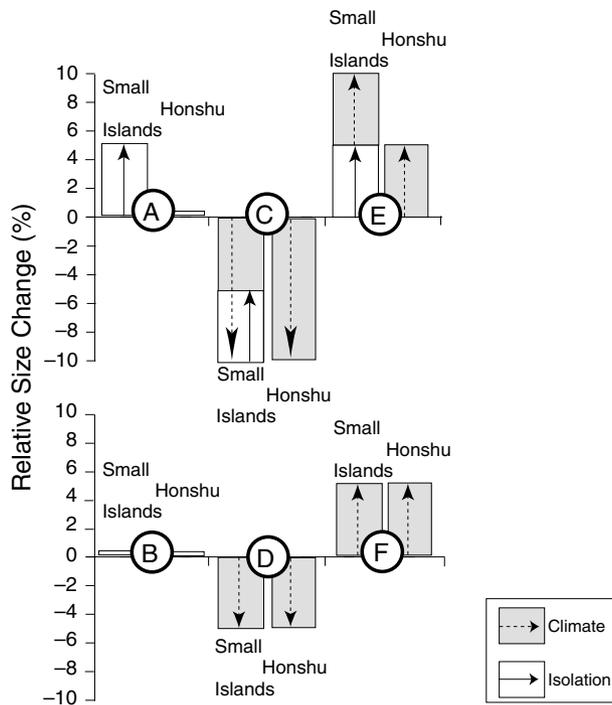


Figure 2 A theoretical model of body size evolution for *Apodemus* in Japan since the LGM. The net evolutionary size change is the result of the island effect (no effect: B, D and F; positive effect: A, C and E), and temperature change (no effect: A and B; negative effect: C and D; positive effect: E and F); temperature change effect: dotted arrow, isolation effect: solid arrow. For each situation (A to F), the left bar refers to small islands and the right bar refers to Honshu. The situation C was observed for *A. speciosus*, whereas *A. argenteus* conforms to situation E for latitudes lower than 36.5°N, and to situation F for latitudes higher than 36.5°N.

incisor size ranged from 0.83 to 7.01 in *A. speciosus* and these rates are not significantly different than those for *A. argenteus* ($t = -0.01$, $P = 0.99$). There is however a notable difference between the meanings of these evolutionary rates for the two *Apodemus* species. Millien & Damuth (2004) found that evolutionary size rates were significantly smaller on the smaller islands than on Honshu, and in order to explain this difference they described a model of evolutionary change in *A. speciosus* where the general trend of size reduction due to climate change was counteracted by isolation on small islands. The size evolution in *A. speciosus* in response to a warming climate was thus *decelerated* because of isolation. In contrast, no significant difference in evolutionary rates could be seen in the present study between the small islands and Honshu for *A. argenteus*. The evolutionary rates in this species would thus just be the result of a normal 'continental' size evolution due to climate change, with no effect of isolation. In summary, according to this model of size evolution, *A. argenteus* shows typical mainland evolutionary rates, whereas *A. speciosus* shows decelerated island rates. However, the rates are not different in the two *Apodemus* species, thus suggesting that there is no significant difference between rates of evolution on islands and

rates of evolution on mainland for this genus. This is not in accordance with the conclusions of some recent studies on microevolution among rodents (Pergams & Ashley, 1999, 2001), and further comparisons between island and mainland mammals need to be made in order to clarify this controversy. In particular, there is an important need to include fossil data in such studies, when available.

Another important finding of the present work is that the two Japanese *Apodemus* respond differently to the same biogeographical changes, in both space and time. The two species showed opposite size trends with latitude, as well as opposite evolutionary size trends since the LGM. In addition, the amount of size variation was also different for the two species, *A. speciosus* being much more varied in both space and time than *A. argenteus*.

The two species have similar feeding behaviours and are largely granivorous, although they can include in their diet some insects (Saitoh & Nakatsu, 1997), and there is no obvious difference in food preference between the two species (Doi *et al.*, 1978). Both species are found in various habitat throughout Japan, although there are some differences between them, as *A. argenteus* is a semi-arboreal mouse which occurs mostly in forests, whereas *A. speciosus* is mostly terrestrial and its habitat ranges from open fields to forests (Kaneko, 1982; Abe, 1986; Sekijima & Sone, 1994; Sekijima, 1999). Similarly, Doi *et al.* (1978) found higher densities of *A. speciosus* at lower altitude and secondary forests, whereas *A. argenteus* was more abundant in stable natural forest areas of Kyushu. It seems that there is a spatial segregation between the two field mice. However, the two *Apodemus* species occupy the same habitat in many forests (Oka, 1992), and when they co-occur, there is some experimental evidence suggesting that the two species interact with each other. Sekijima & Sone (1994) demonstrated, by removal experiments, the existence of competition between the two species. In particular, they detected a higher competitive ability of *A. speciosus*, which may be linked with its larger size and its broader ecological niche. This hypothesis is consistent with several field studies showing that *A. argenteus* is a more specialist species in regard to its micro-habitat use (Doi *et al.*, 1978; Abe, 1986; Sekijima & Sone, 1994; Sekijima, 1999). In addition, this hypothesis could also explain the larger variation in size observed for *A. speciosus*, both in space and in time. In other words, there is one dominant species, the larger *A. speciosus*, which responds to a greater extent to climate change and isolation, whereas the small *A. argenteus* varies to a much lesser extent in both space and time. Lastly, the ecological dominance of *A. speciosus* over *A. argenteus* is confirmed by the observation that the latter is absent from the smallest islands, where there may not be enough resources.

The existence of size segregation is also suggested by the geographical variation of the Hutchinson lower incisor size ratio between the two *Apodemus* across the Japanese archipelago. These ratios ranged from 1.1 to 1.4, and are similar to the values obtained for the two Japanese *Apodemus* in Renaud & Millien (2001), based on the size of the mandible (from 1.25 to

1.44). More importantly, the range of values obtained in the present study also equals the range (1.1–1.4) proposed by Hutchinson (1959). This suggests that there is an effective size segregation between the two Japanese field mice. In addition, there is an increase in the Hutchinson size ratios from south to north, indicating that the two *Apodemus* species are more distinct in size in the most northern localities from Japan (Table 1). They are also more distinct in size on smaller islands, where the size ratios are larger (Table 1). This last result is in accordance with the conclusions of Millien-Parra & Loreau (2000) which showed that there was a better size segregation of species on smaller islands, when considering all the Japanese rodents (between two and five coexisting species from two rodent subfamilies).

Further evidence for the existence of competitive interactions between the two Japanese field mice is provided by their variation in size in allopatry. I showed that *A. argenteus* is larger in Mt Goyo where *A. speciosus* is absent. Similarly, *A. argenteus* is absent from Rishiri island, a very small island located north-west of Hokkaido, and from Shikine island, another small island located south of Honshu. The *A. speciosus* individuals were significantly smaller in Rishiri island than in Hokkaido island, whereas they were not significantly different in size on Shikine island compared to on Mt Fuji (Millien & Damuth, 2004). In agreement with the hypothesis of character release, *A. argenteus* is larger in allopatry than in sympatry and *A. speciosus* is smaller in allopatry than in sympatry.

Lastly, there was a decrease in the size ratio from Late Pleistocene to the present, which illustrates the evolutionary size convergence between the two species. This evolutionary size convergence between the two Japanese *Apodemus* could be explained by the diminution of available resources due to the reduction of land mass areas since the LGM, in particular on smaller islands. Alternatively, two models, based on the premise of an optimal body size, have been proposed to explain the evolution of island mammals. The first is based on the relationship between body size and mammalian population density (Damuth, 1993) and predicts that there is an optimal body mass of 1 kg for mammal species. The second is based on the existence of a compromise between the rate of resource acquisition and resource conversion among mammals (Brown *et al.*, 1993) and suggests an optimal body size of 100 g. The two Japanese *Apodemus* could have converged towards an optimal body size since the LGM. The body mass of *A. speciosus* today ranges from 20 g to 60 g, and those of *A. argenteus* ranges from 10 g to 20 g (Abe, 1994). In both species, body mass has converged since the LGM to a value of 20 g, which is much lower than values proposed in the two models of optimal body size (Brown *et al.*, 1993; Damuth, 1993). The hypothesis of an evolution towards an optimal body size among the two Japanese field mice may still be valid, although in this particular case the theoretical value would be much smaller than those proposed earlier. This observation may be linked to the absolute quantity of available resources on small islands which may lower the theoretical values of optimal body

sizes based on physiological and ecological characteristics of the species (Case, 1978).

CONCLUSION

This study suggests that there is still much to learn about body size evolution in island mammals. It also highlights the fact that two closely related species may respond in an entirely opposite manner to the same climate variation, both in space and time. We have seen that factors such as isolation and climate change, which are usually considered separately, may act in concert. The ultimate effect of these factors depends upon the ecological context, here the presence or absence of competitors.

Lastly, it is suggested that evolutionary rates of island rodents may not be as rapid as usually expected from the theory of island evolution. More comparisons between island and mainland species need to be conducted in order to confirm the validity of the hypothesis of rapid evolution of island organisms.

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BIOSKETCH

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