

CLIMATE CHANGE AND SIZE EVOLUTION IN AN ISLAND RODENT SPECIES: NEW PERSPECTIVES ON THE ISLAND RULE

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Abstract.—As stated by the island rule, small mammals evolve toward gigantism on islands. In addition they are known to evolve faster than their mainland counterparts. Body size in island mammals may also be influenced by geographical climatic gradients or climatic change through time. We tested the relative effects of climate change and isolation on the size of the Japanese rodent *Apodemus speciosus* and calculated evolutionary rates of body size change since the last glacial maximum (LGM). Currently *A. speciosus* populations conform both to Bergmann's rule, with an increase in body size with latitude, and to the island rule, with larger body sizes on small islands. We also found that fossil representatives of *A. speciosus* are larger than their extant relatives. Our estimated evolutionary rates since the LGM show that body size evolution on the smaller islands has been less than half as rapid as on Honshu, the mainland-type large island of Japan. We conclude that island populations exhibit larger body sizes today not because they have evolved toward gigantism, but because their evolution toward a smaller size, due to climate warming since the LGM, has been decelerated by the island effect. These combined results suggest that evolution in Quaternary island small mammals may not have been as fast as expected by the island effect because of the counteracting effect of climate change during this period.

Key words.—*Apodemus*, climate change, evolutionary rates, incisor, island rule, Japan, size.

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Populations that evolve on islands often provide remarkable examples of size evolution. Among island mammals, it is frequently found that small species evolve toward a larger size and large species toward a smaller size (Foster 1964; Van Valen 1973; Lomolino 1985), and this tendency has come to be known as the island rule (Van Valen 1973). The dwarfing of large mammals on island is remarkably well illustrated by Pleistocene elephants (Sondaar 1977; Roth 1992), hippopotami (Simmons 1988), deer (Lister 1989), and sloths (Anderson and Handley 2002). Similarly, the trend toward gigantism of island rodents has been observed in numerous extant species (Hall 1938; Delany 1970; Heaney 1978; Vaughan and Schwartz 1980; Musser 1981; Lawlor 1982; Melton 1982; Davis 1983; Musser and Newcomb 1983; Angerbjörn 1986; Collins and George 1990; Musser and Heaney 1992; Smith 1992; Libois et al. 1993; Vigne et al. 1993; Adler and Levins 1994; Adler 1996; Berry 1996; Ramalhinho et al. 1996; Olmos 1997) as well as among some fossil species (Crusafont-Pairo and Petter 1964; Freudenthal 1976, 1985; Brandy 1978; Mein and Adrover 1982; Daams and Freudenthal 1985; Agusti 1986; Hutterer et al. 1988; Vigne 1992; Biknevicius et al. 1993; Mezzabotta et al. 1996; Michaux et al. 1996; Millien and Jaeger 2001). However, not all island rodent populations show strong body size differences from mainland populations (Foster 1964; Case 1978; Lomolino 1985). The strength of the island effect on size evolution is usually presumed to be roughly inversely proportional to the size of the island (Heaney 1978) and positively related to the degree of isolation from the mainland source of the island population (Foster 1964).

Various selective forces are thought to explain the size increase in island small mammals. In particular, lower predation risk, reduced interspecific competition, or both, rel-

ative to their mainland counterparts, may favor evolution toward larger size in island small mammals (Valverde 1964; Case 1978; Heaney 1978; Angerbjörn 1986; Damuth 1993; Dayan and Simberloff 1998). In addition, under reduced competition and predation pressures, larger size may be advantageous for better exploitation of the limited food resources of island habitats (Case 1978; Smith 1992; Damuth 1993; Brown 1995; Lovegrove 2000).

The physical environment may also exert selective forces on body size, independently of island size or degree of isolation. The body size of individuals within a mammal species' range is often observed to be greater at higher latitudes, a biogeographical trend known as Bergmann's rule (Mayr 1956, 1963; Ashton et al. 2000; Meiri and Dayan 2003). Bergmann's rule is often interpreted as a direct response to temperature (Mayr 1963; Smith et al. 1995), although it may involve other factors such as humidity, seasonal variability, or primary productivity (see reviews in Ashton et al. 2000; Meiri and Dayan 2003) that tend to be correlated with latitudinal gradients. Such a latitudinal trend may be observed in the size of island species if their populations are distributed across a group of islands spanning significant latitudinal range (Kaneko 1988; Yom-Tov et al. 1999). For example, Bergmann's rule has been documented for various skull dimensions in the microtine rodent *Microtus montebelli* in the Japanese archipelago (Kaneko 1988). Size change over time has also been observed in fossil mammal species and interpreted as conforming to Bergmann's rule, because larger size is observed during times when independent evidence suggests that the climate was cooler (Tchernov 1979; Davis 1981; Koch 1986; Klein and Scott 1989; Smith 1992; Bown et al. 1994; Hadly 1997; Smith and Betancourt 1998; Renaud et al. 1999).

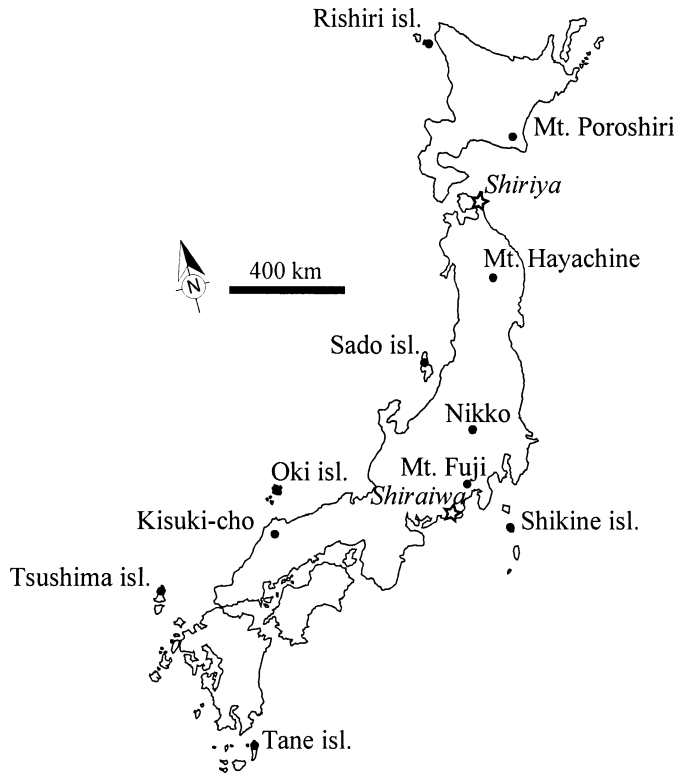


FIG. 1. The 13 localities of extant (dots) and fossil (stars) specimens of *Apodemus speciosus*.

Lastly, it has been proposed that mammal species evolve faster on islands than on the mainland. Among rodent species, rapid morphological evolution has been reported among populations of the house mouse (*Mus musculus*) on the British isles (Berry 1964), among deer mice (*Peromyscus maniculatus*) on the California Channel islands (Pergams and Ashley 1999, 2001), and among rats (*Rattus exulans*, *R. rattus*, and *R. norvegicus*) in New Zealand and other Pacific islands (Yom-Tov et al. 1999).

The Japanese rodent species, the field mouse *Apodemus speciosus*, has been restricted to the Japanese archipelago since at least the Middle Pleistocene and probably earlier (Kawamura 1989; Dobson and Kawamura 1998) and is known in late Quaternary fossil samples from Japan. This species is endemic and widespread in Japan (Corbet 1978; Kaneko 1985; Musser and Carleton 1993; Abe 1994) and is found both on the Japanese mainland (i.e., the very large island of Honshu) as well as on many of the much smaller landbridge islands surrounding Honshu. Most of these islands were connected to Honshu in the Quaternary during periods of lowered sea level (Morley et al. 1986; Millien-Parra and Jaeger 1999). Thus, we have a good knowledge of the approximate time when island populations were separated from the current Honshu (mainland-type) populations.

Because *A. speciosus* is known from both extant and Quaternary localities and from islands at various latitudes and of differing areas, the size variation in this species provides an unusual opportunity to tease apart the joint effects of latitudinal gradients and isolation on small islands. The lower incisor size will be used as an indicator of body size (Millien-Parra 2000) in the analysis of the geographical and evolutionary size variation in this species.

MATERIALS AND METHODS

Fossil and Recent Specimens

The material used for this study includes a total of 206 specimens of the extant species *A. speciosus* that occur in 11 localities (Fig. 1), on islands of differing area by five orders of magnitude, from 4 km² to more than 230,000 km² (Table 1). In addition, they span a wide range of latitude, from 30.3°N to 45.1°N (Table 1). Sample sizes from any given locality range from five to 33 specimens. All the extant specimens studied were collected between 1955 and 1985 and are stored at the National Science Museum, Tokyo, Japan.

Fifty-eight *A. speciosus* fossil specimens from two Late Pleistocene localities (locality 3.2 from Shiriya Quarry and Shiraiwa Mine, Fig. 1) were also examined. All the fossil

TABLE 1. Summary statistics for the antero-posterior diameter of the lower incisor (AP, mm) of *Apodemus speciosus* for each locality and some geographical characteristics of these localities.

Locality	Mean (n, SD)	CV (%)	Latitude (°N)	Island size (km ²)
Extant: Mainland-type (Honshu)				
Mount Hayachine	1.20 (7, 0.13)	11.2	39.5	230,510
Nikko	1.28 (5, 0.07)	5.1	36.7	230,510
Mount Fuji	1.16 (13, 0.13)	10.9	35.4	230,510
Kisuki-Cho	1.16 (15, 0.15)	13.1	35.2	230,510
Extant: Islands				
Rishiri	1.33 (25, 0.11)	8.4	45.1	183
Hokkaido	1.43 (18, 0.09)	6.2	42.7	78,511
Sado	1.29 (31, 0.09)	7.2	38.0	857
Oki	1.27 (33, 0.10)	8.2	36.2	243
Shikine	1.21 (10, 0.09)	7.1	34.2	4
Tsushima	1.27 (29, 0.11)	8.5	34.2	698
Tane	1.32 (20, 0.14)	10.9	30.3	446
Late Pleistocene				
Shiraiwa mine	1.32 (21, 0.11)	8.1	34.8	
Shiriya quarry	1.41 (37, 0.13)	8.9	39.4	

material was collected by Hasegawa and colleagues (Kowalski and Hasegawa 1976; Hasegawa et al. 1988) and 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). AP was measured for each specimen studied. The measurement was taken at the level of the incisor gap, with a drawing tube coupled to a two-dimensional 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 or no wear on the surface of the cutting edge extremity of the incisor.

Statistical Analyses

Descriptive statistics (sample size, mean, and standard deviation) of each sample were computed for the lower incisor size (AP). Within each sample, the variable AP was tested for normality with the Kolmogorov-Smirnov test (Sokal and Rohlf 1995). Sample variability of incisor size for each *A. speciosus* population was estimated by the coefficient of variation (CV = standard deviation \times 100/mean). Among each *A. speciosus* population, *t*-test mean comparison tests between sexes were conducted; because multiple *t*-tests were performed, the significance levels were corrected using the Bonferroni method (Sokal and Rohlf 1995). AP is an unbiased and accurate estimator of body size among rodents ($r = 0.93$, $P < 0.0001$ for the allometric relation between lower incisor size and body length or body weight; result from Millien-Parra 2000).

To study the geographical size trends in living populations, a multiple regression analysis between incisor size (as the dependent variable), and latitude and island size was performed on all individual data. Post hoc *t*-test mean comparisons were performed between different populations, and the significance levels were corrected using the Bonferroni method. *t*-tests were also conducted to compare incisor size between living and fossil populations.

We used the averages reported for 131 meteorological stations throughout Japan (FAO 1987) to compute the relation between temperature and latitude observed today across the Japanese archipelago. This relation was combined with the relation between incisor size and latitude among extant *A. speciosus* to obtain the relation between the incisor size and temperature. We estimated the incisor size at the LGM for the different Honshu localities using this latter relation and assuming that the temperature at the LGM was 9°C lower than today.

Evolutionary rates were computed in darwin (factors of *e* per million years; Gingerich 1983) following the formula:

$$d = (\ln AP_{\text{LGM}} - \ln AP_{\text{present}}) / \Delta t \quad (1)$$

(Haldane 1949), where $\ln AP_{\text{LGM}}$ and $\ln AP_{\text{present}}$ are the

TABLE 2. Multiple regression statistics for the relation between the lower incisor size (AP), latitude, and island size among living populations of *Apodemus speciosus*. The regression has been performed on all individual data. r^2 , coefficient of determination.

Coefficient	Partial regression coefficient	<i>P</i>	<i>N</i>	r^2
Intercept	1.012	<0.0001	206	0.140
Latitude	0.008	<0.0002		
Island size	-3.95×10^{-7}	<0.0001		

natural logarithms of the lower incisor mean size at the LGM, and today respectively, and Δt is the time interval in millions of years. The time span since the LGM is 21,000 years, or 0.021 million years.

All statistical analyses were performed using Systat software (ver. 5.2.1; Systat 1992).

RESULTS AND DISCUSSION

Summary Statistics

Descriptive summary statistics for AP are shown in Table 1 for each locality. The normality of the variable AP could not be rejected for any case (Kolmogorov-Smirnov test, all $P > 0.05$). Values of the coefficient of variation range from 5.1% to 13.1%, which is comparable to values obtained for incisor size in previous studies of both fossil and extant rodent species (Parra et al. 1999; Millien-Parra 2000; Millien and Jaeger 2001). A previous study showed that there was no sexual dimorphism in the size of the lower incisor for six of the populations of *A. speciosus* considered here (Millien-Parra 2000). The absence of sexual size dimorphism was confirmed for the remaining five populations (*t*-test, all probabilities nonsignificant at the $P = 0.05$ level after a Bonferroni correction). Data for both sexes were thus combined in all analyses, and sexual size dimorphism was assumed to be nonexistent in fossil populations.

Geographical Trends among Living Populations

The results of the multiple regression analysis show that there is a small but statistically significant relation between latitude and incisor size, after removing the effect of island size (Table 2). As expected from Bergmann's rule, the incisor size increases with latitude, and there is about an 8% increase in AP from south to north in Japan.

The analysis also shows that there is a significant inverse relation between incisor size and island size (Table 2). Individuals of *A. speciosus* tend to be significantly larger on smaller islands. Overall, *A. speciosus* individuals are significantly larger (Table 3) on islands (mean AP = 1.30) than on Honshu (mean AP = 1.18). *t*-test mean comparisons show that the locality means for AP among island populations are always larger than those from the closest Honshu localities (Table 3), although this trend is not significant in three of the seven islands considered here after correction. Two of these islands (Rishiri and Shikine) are very small (183 km² and 4 km², respectively), and *Apodemus argenteus* is absent from them, whereas it is present on all other islands considered here (Millien-Parra and Loreau 2000). *Apodemus ar-*

TABLE 3. Student *t*-test mean comparisons between island populations and the closer population from Honshu (mainland-type) locality. Because multiple *t*-tests were performed, the significance levels were corrected using the Bonferroni method (Sokal and Rohlf 1995).

Islands	Honshu locality	Relative size of island population	Significant after Bonferroni correction
All islands	All Honshu localities	10.7% ($P < 0.85 \times 10^{-7}$)	yes
Rishiri	Mount Hayachine	10.9% ($P < 0.0135$)	no
Hokkaido	Mount Hayachine	18.5% ($P < 0.00006$)	yes
Sado	Nikko	0.5% ($P = 0.8629$)	no
Sado	Mount Hayachine	7.1% ($P < 0.0499$)	no
Shikine	Mount Fuji	4.6% ($P = 0.2707$)	no
Oki	Kisuki-Cho	8.9% ($P < 0.0081$)	yes
Tsushima	Kisuki-Cho	9.4% ($P < 0.0083$)	yes
Tane	Kisuki-Cho	13.5% ($P < 0.0038$)	yes

genteus is the direct competitor of *A. speciosus* (Sekijima and Sone 1994), and it has been shown that there is a better size segregation between coexisting rodent species in Japan on smaller islands (Millien-Parra and Loreau 2000). In the absence of its competitor, *A. speciosus* may be able to be smaller in body size, thus resulting in an apparent absence of effect of isolation. Finally, the lack of significance for the third island (Sado) may be due to the small sample size for Mount Hayachine ($n = 7$). Overall, the geographical patterns of size variation indicate that recent *A. speciosus* populations conform both to Bergmann's rule and the island rule. This contradicts the conclusions of previous studies (Renaud and Millien 2001; Renaud and Michaux 2003) that found, based on the same material, no obvious effect of insularity or climatic gradient on the size variation in *A. speciosus*. However, size in these studies was estimated by a morphometrical index based on a Fourier analysis of the mandible. This size character may have lower power for body size estimation than the incisor, which has been shown to be an accurate estimator of body size in rodents (Millien-Parra 2000).

Evolutionary Size Trends

The two Late Pleistocene populations of *A. speciosus* were significantly larger than extant populations from localities of similar latitude (Table 4). This result conforms to what one would expect from Bergmann's rule, because late Pleistocene temperatures were lower than those of today. Paleoclimatic reconstructions show that the climatic and vegetation zones that are recognized today in Japan existed during the Quaternary, although they were displaced toward the south during glacial episodes (see reviews in Dobson 1994; Millien-Parra and Jaeger 1999). Unfortunately, an extensive sample of Quaternary localities of differing ages, located at comparable latitudes, and yielding some specimens of *A. speciosus* is not available. Thus, we cannot recover a detailed pattern of evo-

lutionary change in this species. However, assuming that the response of *A. speciosus* to latitude in the present day is a response to differences in mean temperature (or a factor that is reasonably strongly correlated with temperature), we can construct a model of the change of body size in this species in Japan since the LGM (Fig. 2).

The fact that the incisor size in living populations of *A. speciosus* is inversely correlated with temperature across their latitudinal range suggests that at any given latitude *A. speciosus* was at its maximum size during the LGM, approximately 21,000 years ago, when the mean temperature was about 9°C lower than today (Jouzel et al. 1987, 1993). The LGM also corresponds to the lowest sea levels reached during the last glacial cycle (Hearty 1998), and thus the point at which most small islands were most likely to have been connected to the main island of Honshu. Islands such as Oki, Tane, Tsushima, Rishiri, and Hokkaido are separated from Honshu by water depths of no more than 130 m, which is within the range of the maximum drop in sea level estimated for the Japanese archipelago (review in Millien-Parra and Jaeger 1999). In addition, the Japanese islands are in a highly tectonically active region, and at various times significant subsidence is thought to have occurred. Thus, even islands now separated by deeper straits such as Sado and Shikine may have been connected or very close to Honshu for at least a brief period (Millien-Parra and Jaeger 1999). It is thus reasonable to assume that at the LGM the small islands, from which we have samples of *A. speciosus*, were effectively connected with the large island of Honshu and that their populations were potentially continuous with those of Honshu. The currently observed differences between small-island and Honshu populations have developed since the LGM.

Under this hypothesis, size trends in *A. speciosus* since the LGM at any given latitude, both on the small islands and on Honshu, have been toward a smaller size due to the increase in temperature (Fig. 2). The question is why do small-island populations of *A. speciosus* exhibit a larger incisor size than the Honshu populations today? To explain this, we hypothesize that the size decrease in response to climate change has been counteracted by the opposing effect of isolation on small islands. In other terms, the net evolutionary size change since the LGM is the product of both the island effect (positive effect on size) and temperature increase (negative effect on size). For all small islands, the temperature effect has been greater than the island effect, resulting in a net decrease in size since the LGM (Fig. 2).

TABLE 4. Student *t*-test mean comparisons between Quaternary populations and extant populations from the same geographical area.

Quaternary locality	Extant locality	Temporal size trend
Shiriyu	Mount Hayachine	-14.8% ($P < 0.0003$)
Shiraiwa	Kisuki-Cho	-12.2% ($P < 0.0006$)
Shiraiwa	Mount Fuji	-12.4% ($P < 0.0003$)

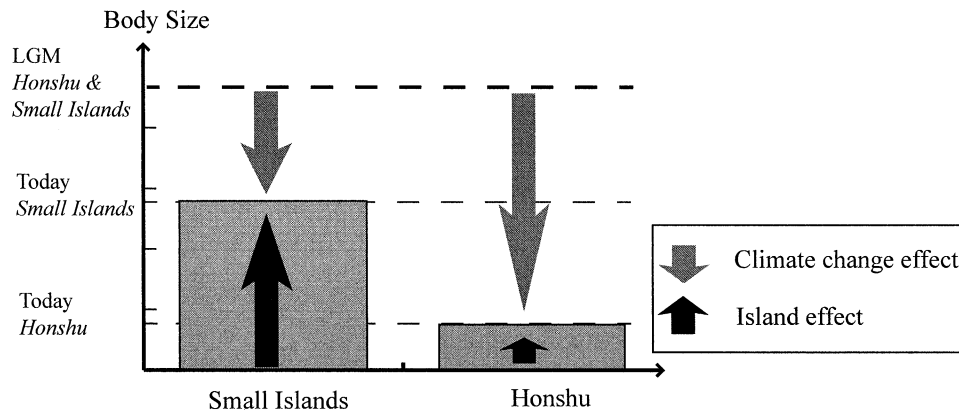


FIG. 2. A theoretical model of body size evolution in small islands and Honshu populations from *Apodemus speciosus* since the last glacial maximum (LGM). The net evolutionary size change since the LGM is the product of both the island effect (positive effect: black arrow) and temperature increase (negative effect: gray arrow). As a result, the body size of small-island populations is larger today than on Honshu.

Figure 3 shows the relative size changes in incisor size since the LGM for islands and the closest Honshu populations for two ranges of latitude. The evolution in incisor size of *A. speciosus* populations from Oki, Tane, Tsushima, and Shikine are compared to those of Fuji and Kisuki-Cho (all latitudes < 36.5°N), whereas the evolution in incisor size of populations from Rishiri, Hokkaido, and Sado are compared to those from Mount Hayachine (all latitudes > 36.5°N). Nikko has been omitted from this figure for simplicity, but would lead to the same representation. In our model, we made the hypothesis that for small islands, the temperature effect has been greater than the island effect, resulting in a net decrease in size since the LGM, and this hypothesis is con-

firmed by our data (Fig. 3). However, a notable departure from this evolutionary size pattern is provided by the population from Hokkaido. On this island, individuals are surprisingly larger than individuals from Mount Hayachine (Honshu) population at the LGM. The evolutionary size trend in individuals from Hokkaido is a net increase in size.

To explain the departure of the Hokkaido population from our model of size evolution, we may have to look at other factors such as the presence/absence of competitors. The small rodent fauna of Hokkaido is indeed substantially different from that of the other more southern islands of Japan (Millien-Parra and Loreau 2000), with the presence of two species of *Clethrionomys* (*C. rufocanus* and *C. rutilus*). *Cleth-*

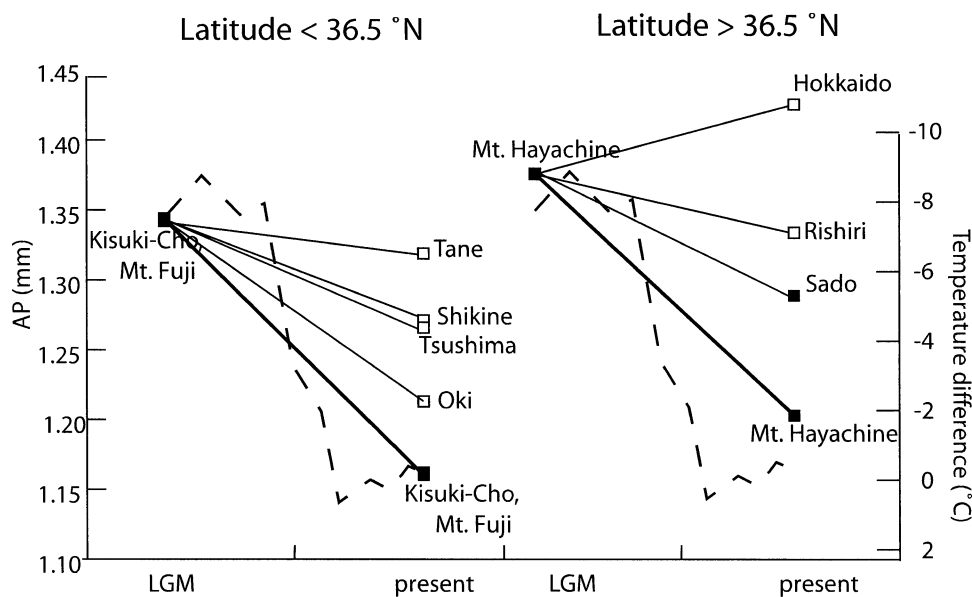


FIG. 3. The evolution of size in *Apodemus speciosus* in Japan since the last glacial maximum (LGM). The figure is separated into two latitudinal ranges: < 36.5°N and > 36.5°N. Open squares, small-island populations; filled squares, Honshu populations. Sea levels were at their lowest stand about 21,000 years ago (LGM), and all the small-island populations are supposed to be continuous with the Honshu populations. The incisor size at the LGM has been estimated assuming a temperature 9°C lower than today (Table 5). With the exception of Hokkaido, each population evolved toward a smaller incisor size (solid line) tracking the temperature change over time (dotted line, modified from Jouzel et al. 1987). This size decrease is less marked on smaller islands than on the large mainland island of Honshu. The Nikko locality has been omitted for simplicity, and the exception of Hokkaido is discussed in the text.

TABLE 5. Estimates of the incisor size (AP) at the last glacial maximum (LGM) for the populations of *Apodemus speciosus* from Honshu. The incisor size at the LGM was estimated using the following relation based on recent specimens: $AP = 1.388 - 0.008 \text{ temp}$; the temperature at the LGM is assumed to be 9°C lower than today.

Locality	Latitude ($^{\circ}\text{N}$)	Temperature ($^{\circ}\text{C}$)		AP (mm)
		Today	LGM	LGM
Mount Hayachine	39.5	10.0	1.0	1.376
Nikko	36.7	12.5	3.5	1.354
Kisuki-Cho	35.4	13.7	4.7	1.343
Mount Fuji	35.2	13.9	4.9	1.342

rionomys rufocanus has a mean incisor size of 1.32, a value that is very close to the mean incisor size of *A. speciosus* on small islands throughout Japan (mean AP = 1.30). The very large size of *A. speciosus* on Hokkaido could thus be the result of size segregation between coexisting species, in addition to the island effect, which together may have been sufficient to counterbalance the effect of climate change.

Evolutionary Rates

We can use our model of size evolution to compute evolutionary rates of size decrease in *A. speciosus* since the LGM. Based on data from 131 meteorological stations (FAO 1987), there is a significant negative relation between temperature and latitude today across the Japanese archipelago ($\text{Temp} = 45.445 - 0.897\text{lat}$, $N = 131$, $P < 0.0001$). This relation was combined with the relation between incisor size and latitude among extant *A. speciosus* ($AP = 0.987 + 0.008\text{lat}$, $N = 206$, $P < 0.0002$) to obtain the following relation between the incisor size and temperature: $AP = 1.388 - 0.008 \text{ temp}$. Using this relation and assuming that the temperature at the LGM was 9°C lower than today provides us with estimates of the incisor size at the LGM for the different Honshu localities (Table 5).

The evolutionary rates of incisor size evolution since the LGM for Honshu and small-island populations of *A. speciosus* vary from 0.83 to 7.00 darwins (Table 6, Fig. 4) and are typical of rates measured over the time span of 21,000 years (Gingerich 1983) for other fossil vertebrates. More importantly, except for the Nikko population, the size decrease of small-island populations has been less than half as rapid as in populations from the large island of Honshu (Fig. 4). The mean value of evolutionary rates is 2.47 darwins for small island populations and 5.72 darwins for the Honshu populations, and these rates are significantly different ($t = -3.448$, $P < 0.006$). The evolutionary size change in *A. speciosus* was thus slower in small-island populations because, according to our model, isolation on small islands had an effect opposite to the effect of climate change that had driven the size evolution in this species since the LGM.

Conclusion

Currently *A. speciosus* shows a typical island-rule pattern of larger body size on smaller islands, as well as conformity with Bergmann's rule of larger size at higher latitudes. However, the evidence suggests that two different selective forces

TABLE 6. Estimates of evolutionary rates (in darwins) for the incisor size (AP, mm) since the last glacial maximum (LGM) for the 11 populations of *Apodemus speciosus* studied. The size at the LGM for the small-island population is equal to the size at the LGM of the closest Honshu population.

Locality	AP (present)	AP (LGM)	% change	Darwins
Okii	1.266	1.342	-5.68	2.786
Tsushima	1.271	1.342	-5.31	2.599
Shikine	1.213	1.344	-9.74	4.878
Tane	1.319	1.342	-1.173	0.833
Sado ¹	1.289	1.378	-6.32	3.111
Sado ²	1.289	1.354	-4.8	2.345
Hokkaido	1.426	1.376	3.63	1.699
Rishiri	1.334	1.376	-3.05	1.476
Mount Fuji	1.160	1.344	-13.68	7.006
Kisuki-Cho	1.162	1.342	-13.43	6.868
Mount Hayachine	1.203	1.376	-12.57	6.399
Nikko	1.282	1.354	-5.32	2.604

¹ Sado was compared to Hayachine.

² Sado was compared to Nikko.

had opposite effects on body size evolution in this species since the LGM. As a result, the small-island populations responded slower in the face of selection for smaller size associated with the climate warming since the LGM. Rather than causing a net increase in size, the island effect in this case seems to have partly counteracted the general postglacial trend of decrease in body size. This is still consistent with the hypothesis that there is a selection for larger size in small species on islands, but the degree of gigantism of *A. speciosus* on small islands observed today is less than expected based on the consideration of the island effect alone. The body size evolution of *A. speciosus* was thus primarily a response to the same climate change, operating both on small islands and on the large island of Honshu, which may also explain why apparently only normal (i.e., mainland type) evolutionary rates are observed in this species. Further quantitative comparisons between island and mainland mammals need to be made to assess the validity of the idea of accelerated evolutionary rates of island organisms.

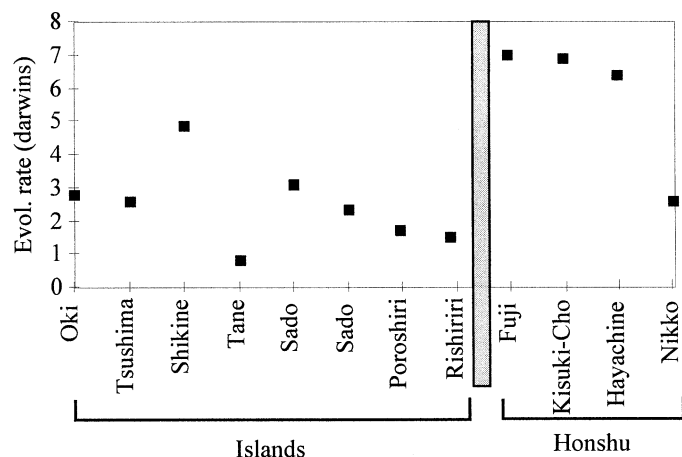


FIG. 4. Evolutionary rates (in darwins) of the incisor size in *Apodemus speciosus* in Japan since the last glacial maximum. Except in one case (Nikko), these rates are smaller for small-island populations than for those from the large island of Honshu.

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