



Body size increase in insular rodent populations: a role for predators?

JOHAN R. MICHAUX*†, JOËLLE GOÛY DE BELLOCQ‡, MAURIZIO SARÀ§ and SERGE MORAND‡

*Unité de recherches zoogéographiques, University of Liège, Quai Van Beneden, 22, 4020 Liège, Belgium; †Laboratoire de Paléontologie, cc064, Institut des Sciences de l'Evolution, 34095 Montpellier cedex 05, France; ‡Laboratoire de Biologie Animale (UMR 5555 CNRS), Centre de Biologie et d'Ecologie Tropicale et Méditerranéenne, Université de Perpignan, Avenue de Villeneuve, 66860 Perpignan Cedex, France; §Dipartimento di Biologia Animale, via Archirafi, 18 90123 Palermo, Italy

ABSTRACT

Insular mammalian populations living in areas of small size are often characterized by a drastic change in body mass compared to related continental populations or species. Generally, small mammals (less than 100 g) evolve into giant forms while large mammals (up to 100 g) evolve into dwarf forms. These changes, coupled with changes in other life, behavioural, physiological or demographic traits are referred to generally as the insular syndrome. We tested in this study the relative contribution of three factors — area of island, numbers of competitor species and number of

predator species — to changes in body size of the woodmouse (*Apodemus sylvaticus*) in the Western Mediterranean Sea. Our results, based on a comparative analysis using the phylogenetic independent contrasts method, indicate that the increase in body size is related both to the decrease of island size and to the lower number of predator species. A decrease of competitor species does not seem to have an important effect.

Key words *Apodemus sylvaticus*, body size, comparative analyses, genetic distances, insular syndrome, islands, rodents, predators, Western Mediterranean.

INTRODUCTION

The distribution of animal body size and the changes in body size of insular populations compared to mainland populations have stimulated a large number of theoretical and empirical studies (Case, 1978; Brown, 1984, 1995; Lomolino, 1985; Angerbjörn, 1986; Brown *et al.*, 1993; Damuth, 1993; Adler & Levins, 1994).

Island populations live in small areas isolated from continental populations. The degree of isolation, i.e. the decrease in genetic exchanges, may lead these populations to differentiate greatly from their closely related continental populations, giving rise to new species. The main characteristic of island mammal populations is the often drastic change in body mass compared to that of related continental populations or species. Insular populations of mammals that on continents are smaller than 100 g evolve typically into giant forms, whereas those that are larger than 100 g on continents evolve into dwarf forms (Van Valen, 1973; Lomolino, 1985). Thus,

according to Brown (1995), a single species living on a tiny island should tend to approach the optimum mean body size of 100 g.

Gigantism is observed generally in rodents and insectivores, whereas dwarfism concerns larger species such as artiodactylids or perissodactylids (Thaler, 1973; Vigne *et al.*, 1993). These changes in body mass seem to occur very quickly. Roth (1990) reported that elephants on Sicily and Malta decreased in body mass by an order of magnitude in a few thousand years. In the same way, Atchley *et al.* (1982) showed that it was possible to select giant forms of *Rattus rattus* in only 23 generations in the laboratory. These changes, which involve modifications in life history, behavioural (Gliwicz, 1980; Takada, 1985; Granjon & Cheylan, 1988, 1990; Perret & Blondel, 1993; Adler & Levins, 1994; Blondel, 1995), physiological or demographic (Poitevin, 1984; Blondel *et al.*, 1992; Fons *et al.*, 1995) traits are referred to generally as the insular syndrome. The determinism of these modifications is probably complex and involves numerous factors, which are difficult to dissociate. Nevertheless, several general hypotheses have been proposed to explain these phenomena.

Grant (1985) suggested that founder events, i.e. the colonization by a low number of immigrants, could play an important

Correspondence: Johan R. Michaux, Unité de recherches zoogéographiques, University of Liège, Quai Van Beneden, 22, 4020 Liège, Belgium. E-mail: Johan.Michaux@ulg.ac.be

role in insular differentiation. However, recent genetic studies (Michaux *et al.*, 1996b) have shown that this is not always the case and that ecological factors such as the lower number of competitors or predators may be more important. This hypothesis is corroborated by other studies (Van Valen, 1973; Case, 1978; Lomolino, 1985; Angerbjörn, 1986). In addition, several authors (Carlquist, 1974; Case, 1978; Heaney, 1978; Wassersug *et al.*, 1979; Sarà & Casamento, 1995) have shown that the area size of the island and the degree of isolation of the population from sources of immigrants could also have an important impact on the occurrence of the insular syndrome. This last factor can be estimated by a measure of genetic isolation, i.e. gene flow.

Our aim is to test the relative contribution of three factors: the area size of the island, the number of species of competitors, and the number of species of predators, to changes in body size of the woodmouse (*Apodemus sylvaticus*) in the Western Mediterranean Sea. We used the independent contrasts method in order to take into account the genetic distances among populations.

MATERIALS AND METHODS

Data on woodmouse populations

Genetic distances between populations were obtained from Michaux *et al.* (1996a,b, 1998a,b) (Table 1). Geographic distances among all pairs of islands and peninsulas were obtained from maps (Fig. 1a).

Island populations of woodmice have been considered as giant forms on the basis of cranial morphometric analyses (Michaux, 1996; Michaux *et al.*, 1996b) and of classical morphological data (Felten & Storch, 1970; Kahmann & Niethammer, 1971; Sans-Coma & Kahmann, 1977; Alcover & Gozalbez, 1988; Libois & Fons, 1990; Libois, unpublished

data). Data on body size were obtained from Michaux (1996). Mean body mass of continental populations is approximately 23 g (25 g on Iberian peninsula and 23 g for Italy). In several islands the mean body mass is more than 30 g: Mallorca (35 g), Ibiza (29 g) and Marettimo (30 g) (Fig. 1).

Competitor and predator species account

We used published data from European and national atlases or check-lists, to obtain the numbers of competitor and predator species present in the studied areas (Arnold & Burton, 1978; Schilling *et al.*, 1986; Lo Valvo *et al.*, 1993; Meschini & Frugis, 1993; Yeatman-Berthelot & Jarry, 1994; Michaux *et al.*, 1996b; Hagemeyer & Blair, 1997; Sarà, 1998; Mitchell-Jones *et al.*, 1999). Quantitative data of predation on *A. sylvaticus* were checked in synopses and reviews dealing with the food habits of the European fauna. The main references were: Cramp & Simmons, 1977–1993, Mikkola (1983), Hancock & Kushlan (1984), Gensbøl (1992), Meyburg *et al.* (1998). Only breeding birds and not recently introduced mammals (i.e. *Callosciurus*, *Tamias*) were considered. Some very rare (e.g. *Pica pica* in Sardinia or *Hieraaetus fasciatus* in Calabria) or marginal (e.g. *Microtus savii* in South-eastern France) distributions were not listed. The resulting list of species, interacting as competitors or predators with the wood mouse, is reported in Table 2.

Statistical analyses

Mantel test between geographical distances and genetic distances

Two variables, geographical distance and genetic distance between pairs of *A. sylvaticus* populations were in the form of

Table 1 Genetic distances (%) (Nei & Li, 1979) between insular and continental European populations of woodmice (*Apodemus sylvaticus*). From Michaux *et al.* (1996a,b, 1998a,b)

	Italy	Spain	Corsica	Sardinia	Elba	Sicily	Mallorca	Menorca	Ibiza	Porque- rolles	Port Cros	Marettimo
Italy	—											
Spain	2.6	—										
Corsica	1.37	2.7	—									
Sardinia	1.49	2.45	1.27	—								
Elba	0	2.6	0.84	1	—							
Sicily	3.7	2.9	3.3	3.5	3.7	—						
Mallorca	2.6	1.3	2.7	2.6	2.5	2.9	—					
Menorca	2.3	1.2	2.3	2.4	2.3	2.7	0.5	—				
Ibiza	2.3	1.1	2.3	2.5	2.3	2.8	0.65	0.3	—			
Porquerolles	2.6	1.1	2.5	2.6	2.6	2.7	1.3	1.3	1.1	—		
Port Cros	2.6	1.47	2.7	2.7	2.6	2.5	1.4	1.5	1.45	1.4	—	
Marettimo	3.7	2.9	2.93	2.91	3.7	0	2.9	2.8	2.8	2.9	2.9	—

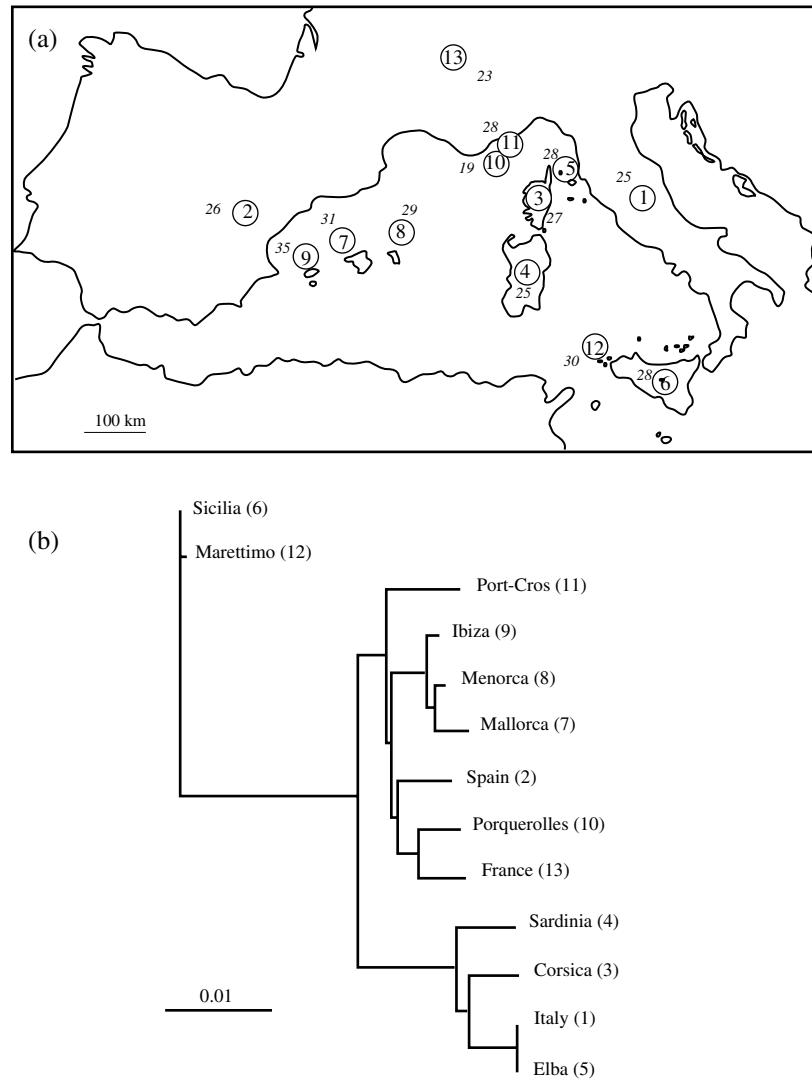


Fig. 1 (a) Geographic origins of sampled populations of *Apodemus sylvaticus*. (b) Tree of genetic distances of sampled populations of *A. sylvaticus* (see Table 2) (numbers in circles refer to location on maps, numbers in *italic* refer to average body size of *A. sylvaticus*, from Michaux, 1996).

matrices. Permutation methods are used widely in population biology (Manly, 1991) and allow one to investigate correlation between distance matrices (Legendre *et al.*, 1994). We used the program *Permute* 3.4 (by P. Casgrain, available at <http://alize.ere.umontreal.ca/~casgrain/>). Correlation was repeated after each of 999 random permutations of the dependent variable (i.e. geographical distance) matrix.

Independent contrasts method

We used the phylogenetically independent contrasts method (Felsenstein, 1985; Harvey & Pagel, 1991; Garland *et al.*, 1992; Harvey, 1996) in order to resolve the problem of non-

independence of data (i.e. traits measured across different populations of the same species). The independent contrasts method is used for interspecific comparative analyses. Populations, like species, are also linked by historical events and it is then necessary to control for genetic information in an intraspecific comparative analysis in order to avoid potential historical confounding effects (i.e. here phylogeography) (see Garland & Adolph, 1994). This can be achieved by taking into account the genetic distances between studied populations.

The genetic distances between pairs of populations were used to obtain a tree (Fig. 1b). We used the CAIC computer application (Purvis & Rambaut, 1995) for independent contrasts analyses. Quantitative data were logarithmically

Table 2 Geographic origins of *Apodemus sylvaticus* populations with island/region area, competitor and predator species. Accidental predators are those reported in single cases or papers to prey upon *A. sylvaticus* with very low frequency (0.01–0.05% of the investigated prey samples). Nomenclature follows Wilson & Reeder (1993) for mammals, Arnold & Burton (1978) for reptiles, and Yeatman-Berthelot & Jarry (1994) for birds

Locations (see map, Fig. 1a)	France (13)	Italy (1)	Spain (2)	Corsica (3)	Sardinia (4)	Elbe (5)	Sicily (6)	Mallorca (7)	Menorca (8)	Ibiza (9)	Porquerolles (10)	Port-Cros (11)	Marettimo (12)
Area (km ²)	500 000	252 000	490 000	8722	23 833	224	25 460	3640	702	541	12.5	6.4	12.1
(a) Competitor species													
<i>Mus spretus</i>	y		y					y	y	y			
<i>Apodemus agrarius</i>		y											
<i>Apodemus flavicollis</i>	y	y	y										
<i>Micromys minutus</i>	y	y	y										
<i>Arvicola terrestris</i>	y	y	y										
<i>Clethrionomys glareolus</i>	y	y	y										
<i>Microtus arvalis</i>	y	y	y										
<i>Microtus agrestis</i>	y	y	y										
<i>Microtus duodecimcostatus</i>	y		y										
<i>Microtus cabreræ</i>			y										
<i>Microtus subterraneus</i>	y	y											
<i>Microtus multiplex</i>	y	y											
<i>Microtus pyrenaicus</i>	y		y										
<i>Chionomys nivalis</i>	y	y	y										
<i>Microtus lusitanicus</i>	y		y										
<i>Microtus savii</i>		y					y						
<i>Microtus gerbei</i>	y		y										
<i>Sciurus vulgaris</i>	y	y	y										
<i>Muscardinus avellanarius</i>	y	y											
<i>Dryomys nitedula</i>		y											
<i>Glis glis</i>	y	y	y	y	y	y	y						
<i>Eliomys quercinus</i>	y	y	y	y	y		y	y	y				
<i>Rattus rattus</i>	y	y	y	y	y	y	y	y	y	y	y	y	y
<i>Mus domesticus</i>	y	y	y	y	y	y	y	y	y	y	y	y	y
(b) Regular predator species													
<i>Vulpes vulpes</i>	y	y	y	y	y		y						
<i>Genetta genetta</i>	y		y					y		y			
<i>Felis silvestris</i>	y	y	y	y	y		y						
<i>Martes martes</i>	y	y	y	y	y	y	y	y	y				
<i>Mustela nivalis</i>	y	y	y	y	y		y	y	y				
<i>Martes foina</i>	y	y	y										
<i>Mustela putorius</i>	y	y	y										
<i>Mustela erminea</i>	y	y	y										
<i>Meles meles</i>	y	y	y										
<i>Herpestes ichneumon</i>			y										
<i>Bubo bubo</i>	y	y	y										
<i>Strix aluco</i>	y	y	y				y						

Table 2 continued.

Locations (see map, Fig. 1a)	France (13)	Italy (1)	Spain (2)	Corsica (3)	Sardinia (4)	Elbe (5)	Sicily (6)	Mallorca (7)	Menorca (8)	Ibiza (9)	Porquerolles (10)	Port-Cros (11)	Marettimo (12)
<i>Asio otus</i>	y	y	y	y			y	y					
<i>Athene noctua</i>	y	y	y	y	y	y	y	y					
<i>Tyto alba</i>	y	y	y	y	y	y	y	y	y	y	y		y
<i>Otus scops</i>	y	y	y	y	y	y	y	y	y				y
<i>Glaucidium passerinum</i>	y	y											
<i>Asio flammeus</i>	y		y					y	y				
<i>Aegolius funereus</i>	y	y											
<i>Buteo buteo</i>	y	y	y	y	y		y						y
<i>Circus gallicus</i>	y	y	y										
<i>Accipiter gentilis</i>	y	y	y	y	y								
<i>Accipiter nisus</i>	y	y	y	y	y		y						
<i>Aquila chrysaetos</i>	y	y	y	y	y		y						
<i>Hieraetus pennatus</i>	y		y					y	y				
<i>Falco tinnunculus</i>	y	y	y	y	y	y	y	y	y	y	y		y
<i>Falco biarmicus</i>		y					y						
<i>Falco naumanni</i>		y	y		y		y						
<i>Falco subbuteo</i>	y	y	y	y	y		y	y					
<i>Milvus milvus</i>	y	y	y	y	y		y	y	y				
<i>Milvus migrans</i>	y	y	y				y						
<i>Elanus caeruleus</i>			y										
<i>Circus cyaneus</i>	y		y										
<i>Burhinus oedicnemus</i>	y	y	y		y		y	y	y				
<i>Lanius excubitor</i>	y		y										
<i>Lanius collurio</i>	y	y	y	y	y	y	y						
<i>Lanius senator</i>	y	y	y	y	y		y	y	y				
<i>Corvus corax</i>	y	y	y	y	y	y	y	y	y				y
<i>Hierophis viridiflavus</i>	y	y	y	y	y	y	y						y
<i>Coluber hippocrepis</i>			y		y								
<i>Malpolon monspessulanus</i>	y	y	y							y			
<i>Natrix natrix</i>	y	y	y	y	y		y						
<i>Coronella austriaca</i>	y	y	y				y						
<i>Coronella girondica</i>	y	y	y										
<i>Vipera aspis</i>	y	y	y			y	y						
<i>Vipera ursinii</i>	y	y											
<i>Vipera berus</i>	y	y											
<i>Vipera latasti</i>		y											
<i>Vipera seoanei</i>				y									
<i>Elaphe scalaris</i>	y		y						y		y		
<i>Elaphe situla</i>		y					y						
<i>Elaphe quatuorlineata</i>		y											
<i>Elaphe longissima</i>	y	y	y		y		y						

Table 2 continued.

Locations (see map, Fig. 1a)	France (13)	Italy (1)	Spain (2)	Corsica (3)	Sardinia (4)	Elbe (5)	Sicily (6)	Mallorca (7)	Menorca (8)	Ibiza (9)	Porquerolles (10)	Port-Cros (11)	Marettimo (12)
(c) Accidental predator species													
<i>Lynx pardinus</i>			y										
<i>Canis lupus</i>	y	y	y	y									
<i>Circus aeruginosus</i>	y	y	y	y	y		y		y				
<i>Circus pygargus</i>	y	y	y	y	y					y			
<i>Hieraaetus pennatus</i>	y	y	y	y	y		y		y				
<i>Larus cachinnans</i>	y	y	y	y	y	y	y	y	y	y	y	y	y
<i>Larus melanocephalus</i>	y	y	y	y	y			y					
<i>Coracias garrulus</i>	y	y	y		y								
<i>Ciconia alba</i>	y	y	y		y								
<i>Egretta garzetta</i>	y	y	y		y								
<i>Ardea purpurea</i>	y	y	y		y		y	y	y				
<i>Ardea cinerea</i>	y	y	y										
<i>Bulbulcus ibis</i>	y	y	y										
<i>Corvus corone</i>	y	y	y		y								
<i>Pica pica</i>	y	y	y		y		y	y					
<i>Garrulus glandarius</i>	y	y	y		y		y	y					

transformed in order to stabilize variance (Harvey, 1982). All regressions between contrasts were forced through the origin (Garland *et al.*, 1992). In order to verify that contrasts were standardized properly we performed a regression of the absolute values of standardized contrasts vs. their standard deviations (Garland *et al.*, 1992) using CAIC.

RESULTS

We found a significant positive relationship between geographical distances and genetic distances using the permutation test, showing that geographical isolation of *A. sylvaticus* populations was related to a decrease in genetic exchanges ($r = 0.57$, $P = 0.001$). The position of the population of Port-Cros can be noted between the Italian group (Italy, Sicilia, Corsica, Elba) and the Iberian (Spain, Balearics) and French (France, Porquerolles) groups.

Using the whole dataset, we found that *A. sylvaticus* body size is not related to area of source region/island ($r = -0.098$, $P = 0.75$; Fig. 2a). However, this lack of correlation was due to one point (Port-Cros). The regression was statistically significant when this outlier was removed ($r = -0.632$, $P = 0.028$; Fig. 2a). Significant correlations were found between *A. sylvaticus* body size and area ($r = -0.71$, $P = 0.0098$), number of regular predator species and area ($r = 0.94$, $P < 0.0001$), number of occasional predator species and area ($r = 0.98$, $P < 0.0001$) and number of competitor species and area size ($r = 0.95$, $P < 0.0001$) using independent contrasts.

We controlled for body size, total number of predator species (occasional and regular) and the number of competitor species in relation to area by using the residuals of the preceding regressions using independent contrasts. We found a negative correlation between the residuals of body size (controlled for area) and the residuals of the total number of predator species (controlled for area) using independent contrasts ($r = -0.76$, $P = 0.0045$, Fig. 2b). A similar negative relationship was found using the number of regular predator species ($r = -0.74$, $P = 0.0063$). These results suggest that the changes in body size of *A. sylvaticus* depend on predator pressures (irrespective of area of source region/island).

No correlation was found between the residuals of body size (controlled for area) and the residuals of the number of competitor species (controlled for area) using independent contrasts ($r = -0.237$, $P = 0.46$).

When using the raw data (i.e. not controlled for genetic distances), a negative trend (also not statistically significant) was found between the residuals of body size (controlled for area) and the residuals of the number of competitor species (controlled for area) ($r = -0.54$, $P = 0.07$, Fig. 2c).

We confirmed these findings by performing a multi-regression using the permutation method (Legendre & Legendre, 1998). Using a backward procedure, this method allows the selection of a subset of explanatory (i.e. independent)

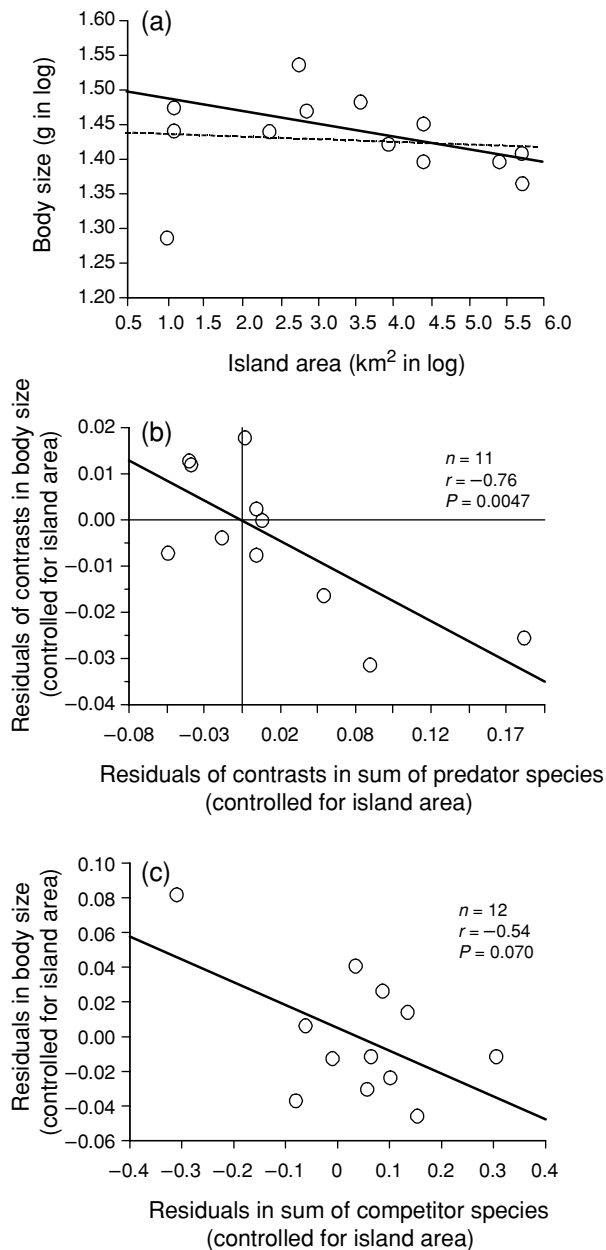


Fig. 2 (a) Relationship between island area and average body size of *Apodemus sylvaticus*. Two regressions were obtained. The significant one (dashed line) was obtained when the outlier Port-Cros (left bottom point) was removed from the analysis. (b) Relationship between the residuals of body size of *A. sylvaticus* (controlled for island area) and the residuals of numbers of predator species (controlled for island area) using independent contrasts. (c) Relationship between the residuals of body size of *A. sylvaticus* (controlled for island area) and the residuals of numbers of competitor species (controlled for island area) using raw data.

variables. These variables were the contrasts in area, the contrasts in total number of predators and the contrasts in total number of competitors. Using the whole dataset, we found that only the total number of predators was correlated with body size ($P = 0.04$). Removing the outlier, we found that both area (partial $P = 0.027$) and total number of predators (partial $P = 0.010$) were correlated with body size ($P = 0.033$).

DISCUSSION

Our comparative analyses using the independent contrasts method show clearly that the increase in body size of *A. sylvaticus* occurred on small islands with a low number of predator species. In general, the explanation for the relationship between increase in body size of small species and island size is not clear. Melton (1982) and Adler & Levins (1994) proposed that on small islands, small-bodied species should have higher population densities than on continents or larger islands. Adler & Levins (1994) suggested that this favours a K -strategy, leading to an increase in life span and to a decrease in the number of offspring. This reduces the overall reproductive effort and results in re-allocation of energy to growth and maintenance and then large body size. However, in the case of woodmouse populations on Mediterranean islands, their densities are often lower than those of continental populations (Sarà & Casamento, 1993; J.R. Michaux, unpublished data). This results probably from competition with the black rat (*Rattus rattus*) and the house mouse (*Mus musculus*), wild populations of both of which are present on many Mediterranean islands at high densities (Granjon & Cheylan, 1988, 1990).

A role for predators

Our analyses indicate that the number of predator species plays a more important role than the number of competitor species. Indeed, Lawlor (1982) and Lomolino (1985), who associated the appearance of insular gigantism with the number of competitor species, based their hypothesis on the fact that, generally, the number of competitor species is lower on small islands than on continents (see also Alcover & Gosálbez, 1988). This leads to 'empty' niche space, which will be more easily filled by individuals having a larger size (Lister, 1976). However, in our case the number of competitor species observed on small islands with large-bodied *Apodemus* is of the same order as those observed on large islands (Corsica, Sicily, Sardinia) where no gigantism is observed (Contoli *et al.*, 1988a,b; Libois & Fons, 1990). Moreover, the densities of the competitor species (principally *R. rattus* and *M. musculus*) currently living on the small Mediterranean islands are drastically high (Granjon & Cheylan, 1988, 1990), which would seem to rule out easy access to the 'free' ecological niche space for the woodmouse.

In contrast, predator pressure is clearly lower on small islands compared to large islands, where it is similar to the continental regions. The relationship between a lower pressure of predators and insular gigantism could be explained by the following scenario. On large islands or on the continent, small mammals have a greater advantage to be as small as possible to escape from predators. On small islands, with fewer predators but also less habitat diversity and low food reserves (Lawlor, 1982; Angerbjörn, 1986; Cirer & Martinez-Rica, 1990), a larger size will have a selective advantage in terms of mechanisms relating to food foraging, territory defence and access to reproduction (Case, 1978; Angerbjörn, 1986). This kind of advantageous character will become fixed if the population size is small and populations are isolated in small areas (Michaux *et al.*, 1996b).

The relationships and the interaction strength between the insular *Apodemus* and particular predator species are likely to differ. Indeed, only one predator species, the weasel *Mustela nivalis*, is absent exclusively on the islands where giant individuals of *Apodemus* are observed. This suggests that the interaction strength between these two species is very considerable and that the absence of the weasel may be a key determinant in the appearance of giant woodmice.

As *A. sylvaticus* colonized the studied Mediterranean islands at least 2000 years before *R. rattus* and *M. musculus* (Reumer & Sanders, 1984; Vigne, 1992; Audouin-Rouzeau, 1994), an additional hypothesis to explain the woodmouse insular gigantism would be that: firstly, its body size may have evolved in the absence of its principal competitors (through the mechanism of decrease of interspecific competition), and secondly, that the current high population levels of *Mus* and *Rattus* may have caused 'unnatural' and very recent depression in the population levels of *Apodemus*. However, prior to the arrival of *Rattus* and *Mus* on the islands, the number of competitor species observed on small islands with large-bodied *Apodemus* was already of the same order as that observed on the large islands where no gigantism is observed (Reumer & Sanders, 1984; Vigne, 1992). We therefore suggest that a decrease of interspecific competition probably had a low role in the appearance of the insular gigantism in the woodmouse during this period and that our predator pressure scenario retains relevance to the period when *Apodemus* was not in competition with *Rattus* and *Mus*.

Finally, our results also highlight the importance of genetic distances, i.e. genetic isolation, as a significant correlation was found using independent contrasts (taking into account the phylogeographical confounding effects), whereas a lack of significant correlation was found using the raw data. A decrease in gene flow seems to be required for selection for increasing body size to occur.

As the number of predator and competitor species are of the same orders in the North Sea islands where giant woodmice are also observed (St Kilda, Rhum and Fair islands)

(Delany & Healy, 1964; Delany, 1970), we can postulate that our hypothesis may be generalized to this region. The same reasoning may also be applied for the garden dormouse (*Eliomys quercinus*) populations from the Mediterranean islands. Indeed, the two islands where giant forms are observed (Lipari and Formentera) are characterized by a significantly lower number of predators, while the number of competitor species is of the same order as on the large Mediterranean islands where no gigantism is observed. Nevertheless, it would be dangerous to extrapolate our hypothesis to other insectivorous or carnivorous small mammals because their predators and competitors are very different.

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BIOSKETCHES

J.R. Michaux is presently working on the phylogeography and conservation biology of different European mammal species.

S. Morand and **J. Goüy de Bellocq** are parasitologists presently working on the effects of isolation in islands on the parasite fauna.

M. Sarà is a mammalogist specializing in the fauna of Sicily.