

# MAMMALS EVOLVE FASTER ON SMALLER ISLANDS

Virginie Millien<sup>1,2</sup>

<sup>1</sup>Redpath Museum, McGill University, 859 Sherbrooke Street West, Montreal (QC) H3A 2K6, Canada

<sup>2</sup>E-mail: virginie.millien@mcgill.ca

Received September 24, 2009

Accepted February 1, 2011

Island mammals often display remarkable evolutionary changes in size and morphology. Both theory and empirical data support the hypothesis that island mammals evolve at faster rates than their mainland congeners. It is also often assumed that the island effect is stronger and that evolution is faster on the smallest islands. I used a dataset assembled from the literature to test these assumptions for the first time. I show that mammals on smaller islands do indeed evolve more rapidly than mammals on larger islands, and also evolve by a greater amount. These results fit well the theory of an evolutionary burst due to the opening of new ecological opportunities on islands. This evolutionary burst is expected to be the strongest on the smallest islands where the contrast between the island and the mainland environments is the most dramatic.

**KEY WORDS:** Body size, Darwins, evolutionary rates.

Ever since Darwin's first observations of Galapagos finches and mockingbirds, islands have been recognized as natural laboratories for the study of evolution (Mayr 1967; Berry 1996). The study of island species has, for example, helped to demonstrate the importance of isolation for speciation and for adaptive radiation (Losos and Ricklefs 2009). In mammals, isolation on islands often leads to significant changes in body size and sometimes the evolution of very peculiar morphologies (Foster 1964; Van Valen 1973; Lomolino 1985, 2005; Sondaar 1991; Lister 1996). Foster (1964) first noted the tendency of small mammals, such as rodents, to be larger on islands when compared to their closest relatives on the mainland. Large mammals, such as deer and elephants, are often much smaller on islands than on the mainland (Foster 1964; Sondaar 1977, 1991; Lister 1996). This tendency for small mammals to become larger and large mammals to become smaller on islands has come to be known as the island rule (Van Valen 1973; Lomolino 1985, 2005).

In addition to phylogenetic affinities or body size of the island species, island area and the degree of isolation have been considered to be correlated with the main factors driving morphological and size evolution on islands (Heaney 1978; Lomolino 1985; Angerbjörn 1986; Berry 1996, but see Meiri et al. 2005).

Based on his observations on the tri-colored squirrel (*Callosciurus prevosti*) in southeast Asia and a review of the literature, Heaney (1978) proposed a qualitative model of size evolution in island mammals. His model included four causal factors: food limitation, predation, interspecific competition, and physiological efficiency. The model did not, however, take into consideration the local climate, time of isolation, or other selective pressures that could occur on a specific island. According to Heaney (1978), the relative importance of each factor in his model was related to island area, which thus determined body size of a given species on a given island. Although this model was mainly derived from observations of one species, Heaney proposed that it could be applied to all island mammals, potentially explaining the differential trends in body size between large and small mammals on islands. Later Filin and Ziv (2004) supported Heaney's hypothesis through a theoretical model linking the direction of body mass change, the rate of change, and the area of the island. Using demographic parameters, allometric laws, and the hypothesis of an optimal body mass, the model predicts that the selection pressures for body size change are stronger on smaller islands. This was due to the inverse relation between island area and the change in population growth rate, which is also affected by the shape of the island and

dispersal ability of the species. Filin and Ziv (2004) predicted that (1) organisms on smaller islands experience a faster change in body mass than those on larger islands, and (2) the change in body mass, either increasing or decreasing, is proportional to the inverse of island area.

Although not restricted to island mammal fauna (see Millien 2006 for a review), some evidence exists for rapid evolution, sometimes within only a few decades, in some isolated species of mammals (Kurtén 1959; Yom-Tov et al. 1986, 1999; Pergams and Ashley 1999, 2001; Simberloff et al. 2000, but see Meiri et al. (2009) who found no evidence for rapid evolution in some island carnivores over the last 200 years). The fossil record also suggests that island species evolve rapidly following isolation (Sondaar 1991; Lister 1996). The trend for more rapid evolution on islands was confirmed in a literature review comparing the rates of morphological evolution of mammals from islands versus the mainland (Millien 2006). This result held for various morphological traits, and under a wide range of time intervals, from a few decades up to several thousands of years. However, Millien (2006) did not address the effect of island size on the rate of evolution, and this hypothesis has not previously been subject to quantitative analysis. Here, using a dataset assembled from the literature on evolutionary rates in island mammals (see Millien 2006), I tested the following predictions: (1) evolution is faster on smaller islands, and (2) the absolute amount of change is greater on smaller islands. I also examined the effect of body mass on the rate and magnitude of evolutionary change.

## Material and Methods

The dataset consists of 72 populations of mammal species or evolutionary lineages belonging to five orders and 21 species from 44 islands from the Atlantic and Pacific oceans, as well as from the Mediterranean and Japan seas (Appendix 1). Most data were for rodent species (55 out of the 72 samples). This reflects in part the fact that Rodentia is the most speciose order of mammals, but also the fact that rodents are very successful at colonizing and establishing on islands and are thus a common member of most insular mammalian faunas. The time interval over which evolutionary changes took place ranged from 21 years to 47,000 years. Island area ranged from 0.6 to 979 sq. km, and was obtained from various sources in the literature and from the United Nations Environment Program Islands website (<http://islands.unep.ch/>). These raw data are provided in a supplement (Table S1), and were obtained from the sources cited in Millien (2006).

Only allochronic rates of evolution, as defined by Hendry and Kinnison (1999), were used. These rates are based on the comparison of a trait of a species or evolutionary lineage from the same point in space, but at different points in time. Allochronic rates thus pertain to actual trait temporal changes and reflect rates

of actual evolution. In contrast, synchronic rates are based on the comparison of two extant populations that share a common ancestor and are found at different places (e.g., mainland-island comparisons). Consequently, synchronic rates reflect rates of divergence that do not provide a direct measure of the rate of evolution (i.e., Fig. 1 in Hendry and Kinnison 1999), and so were not used.

The “darwin” (Haldane 1949) was used as a measure of evolutionary rate as  $(d) = (\ln x_2 - \ln x_1) / (\Delta T)$ , where a character evolved from  $x_1$  to  $x_2$  over a time ( $\Delta T$ ) in millions of years. When more than two datapoints for a character were available within a lineage, evolutionary rates were estimated by the slope of a linear model between  $\ln(\text{rate})$  and  $\ln(\text{area})$  (Millien 2006). Rates in darwins can easily be calculated from mean values published in the literature and are readily available for fossil species. Rates in darwins are proportional to the dimensionality (Gingerich 1993), and so only linear measurements were considered here, such as teeth, skull, long bones, or body-length measurements. The absence of effect of the type of trait used on the value of the evolutionary rate was further tested with an ANOVA. When several types of measurements were available for one species (e.g., a tooth measurement and a long bone measurement), the average rate value was used to avoid overweighting of replicated data (Millien 2006). Evolutionary rates in darwins are also correlated with the time intervals over which they are calculated (Gingerich 1983; Hendry and Kinnison 1999), and this correlation was taken into account in the interpretation of results. Rate (darwin), island area (square km), and time intervals (Million years) data were log-transformed (base e) prior to analyses. A hierarchical variance partitioning approach was used to assess the variance contribution of each explanatory variable (time and area) with rate as the dependent variable (Chevan and Sutherland 1991; Mac Nally 2000). This method accounts for the collinearity between the explanatory variables by obtaining the contribution of each of these variables, both independently and jointly, to the total variance (Mac Nally 2000, 2002). The  $R$  squared was used to estimate the goodness of fit. The  $Z$ -score and a randomization procedure that randomizes the data and computes the distribution of independent effects of each explanatory variable (1000 randomizations for area and time, see Mac Nally 2002 for further details) were used to evaluate the statistical significance of these effects (Mac Nally 2002).

The amount of evolutionary change was expressed as percent change:  $\% \text{change} = ((x_2 - x_1) / x_1) \times 100$ . The relation between the percent change and the rate in darwin is as follows:  $\% \text{change} = ((\exp(\text{rate} \times \Delta T) - 1) \times 100)$ .

The relation between rates of evolution of morphological linear traits and body mass was also examined. I used the average body mass for the species, which was supposed to represent the mass of the mainland ancestor, assuming no or little evolution of the ancestral species on the mainland. In most cases (19 species out of 22), the body mass used was the median of the range of

values published for the species on the mainland using data from Smith et al. (2003). For the remaining three species, I used the body mass of the endemic island species (e.g., *Apodemus speciosus*, published in Silva and Downing 1995). In two cases, body mass data were not available from the above general sources, and so the data were directly obtained from the source paper (Anderson and Handley 2002, for the mass of *Bradypus pygmaeus* and Millien 2004 for *Apodemus argenteus*) or from the closest mainland relative from the same genus (e.g., *Megaloceros algericus* for *M. giganteus*).

General linear models were used to estimate the effects of time interval, island area, and body mass on the rate of evolution and the amount of change of morphological linear characters. For all linear models, the interaction terms between explanatory variables and quadratic terms of all explanatory variables were first included in the model. They were then sequentially removed (interaction terms first, then quadratic terms) when not significant. A logistic regression model was used to test whether the probability of positive versus negative change was dependent on island area and on body mass.

Pagel's lambda (Pagel 1999) was used to assess the phylogenetic signal in the data, based on the phylogeny described in Millien (2006). Pagel's lambda varies between 0 (phylogenetic independence of the data) and 1 (more closely related species have closer trait values). The advantage of this parameter is that it is robust even when the phylogeny is not well resolved (Freckleton et al. 2002). Branch lengths in million years were obtained from Bininda-Emonds et al. (2007), using the "best dates" in the tree file provided in this reference. There were two extinct species in the data for which no divergence time was readily available from Bininda-Emonds et al. (2007). The divergence date of *Cervus* was thus used for the genus *Megaloceros* as there is very little divergence between these two genera (Kuehn et al. 2005). The divergence between the genera *Mammuthus* and *Elephas* was dated at 5.8 to 7.7 Ma (Rohland et al. 2007), and the median value of 6.75 Ma was thus used for the divergence time of *Mammuthus*. Each tip of the phylogenetic tree represented a single population for a given species, and the relation between these populations was not resolved in most cases (resulting in a number of polytomies). The phylogeny is presented in Appendix 1.

Generalized least square (GLS) models fit by maximizing the restricted log-likelihood (REML) were calculated to estimate the effects of time interval, island area, and body mass on the evolutionary rate and the amount of change, while taking into account the phylogenetic structure in the data (Freckleton et al. 2002). The use of GLS methods requires the specification of a correlation structure for the linear model. Both a Pagel correlation structure, which is derived from a Brownian model of evolution by multiplying the covariance by  $\lambda$  (Freckleton et al. 2002), and a simple Brownian motion model were used.

All the analyses were carried out in R statistical software version 2.9.2 (R Development Core Team 2010).

## Results

### EVOLUTIONARY RATES

Rates calculated ranged from 0.7 to 1435.8 darwin, which overlaps with values reported for fossil vertebrates (0.11–32 darwin) in Gingerich (1983) and for contemporary animals (0–395,880 darwin) in Kinnison and Hendry (2001).

An analysis of covariance (ANCOVA) with  $\ln(\text{time})$ ,  $\ln(\text{area})$ ,  $\ln(\text{mass})$ , and the type of variable used (teeth, skeletal, skull or body length, or a combination of them) as factors and evolutionary rate as the dependent variable showed that there was a significant effect of time interval ( $F = 367.2$ ,  $P < 0.0001$ ), island area ( $F = 7.6$ ,  $P < 0.007$ ), and body mass ( $F = 19.6$ ,  $P < 0.0001$ ) on the evolutionary rate value, whereas the effect of the type of variable was not significant ( $F = 0.8$ ,  $P = 0.59$ ).

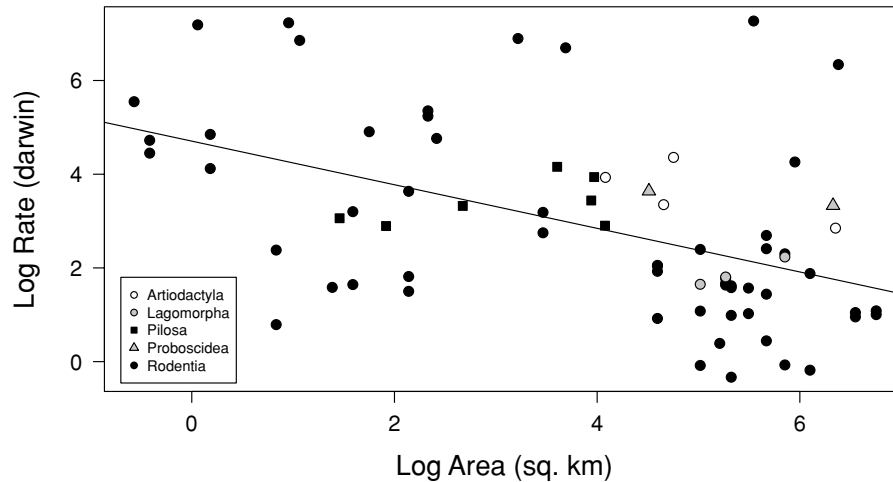
There was a strong correlation in the data between evolutionary rate and time interval ( $r = -0.89$ ,  $P < 0.0001$ ), a relation that has been reported elsewhere (Gingerich 1983; Hendry and Kinnison 1999; Millien 2006).

There was a positive relation (Pearson correlation coefficient,  $r = 0.42$ ,  $P < 0.001$ ) between  $\ln(\text{area})$  and  $\ln(\text{time})$ . This correlation has no obvious biological rationale and may be solely due to a sampling bias. The correlation between the time interval and island area violates the assumption of a lack of colinearity between the independent variables. A variance partitioning analysis was thus used to evaluate both the independent and joint contribution of each explanatory variable (time interval, island area, and body mass) to the variation in rates of evolution. The analysis with  $\ln(\text{area})$ ,  $\ln(\text{time})$ , and  $\ln(\text{mass})$  as the explanatory variables and  $\ln(\text{rate})$  as the dependent variable indicated that  $\ln(\text{time})$  explained in total 79.7%,  $\ln(\text{area})$  24.5%, and  $\ln(\text{mass})$  1.4% of the variance in  $\ln(\text{rate})$ . The independent contribution of each variable was 80.6% for  $\ln(\text{time})$  ( $Z = 36.23$ ,  $P < 0.05$ ), 15.8% for  $\ln(\text{area})$  ( $Z = 6.81$ ,  $P < 0.05$ ), and 3.5% for  $\ln(\text{mass})$  ( $Z = 0.81$ ,  $P > 0.05$ ).

Overall, evolutionary rates ranged from 4.8 darwin on the largest island to 144.2 darwin on the smallest island and were thus over 30 times greater on the smallest islands in the data (Fig. 1).

Rates of evolution were negatively related to island area and positively related to body mass (Table 1, Fig. 2). Overall, rates of evolution were much more variable in small species, mostly rodents. Rates for this order ranged from 0.72 darwin, the lowest value in the entire dataset to 37.90 darwin, one of the largest rates calculated for the entire data.

Pagel's  $\lambda$  indicated a strong phylogenetic structure in the data with a value of 0.90. The analyses were thus repeated with



**Figure 1.** The relation between the rate of evolution and island area. The line is the regression line between Log Rate and Log Area.

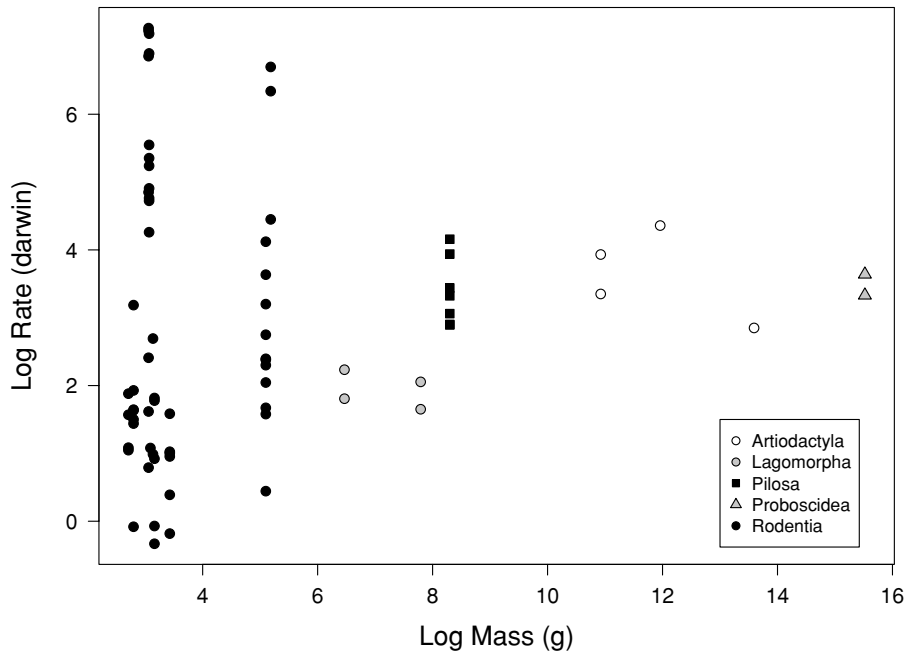
a correction for phylogeny using a general least square model that took into account the phylogenetic structure in the data. The results were similar (Table 1) to those obtained with a simple linear model. Rates of evolution were negatively related to island area and the effect of body mass on evolutionary rate was significant and positive when using a Pagel’s correlation structure for the

linear model. However, an AIC criterion indicated that a simple Brownian model of evolution was more adequate for the data, and the effect of mass on evolutionary rates was not significant with this model. Lastly, a small but significant effect of the quadratic term  $Area^2$  was found with this last model (Table 1). However, the coefficients of the model as indicated in Table 1 imply that the

**Table 1.** Results from linear models with rate of evolution, the percent change, or the absolute value of percent change as the dependent variable. There was a positive relation (Pearson correlation coefficient,  $r=0.42$ ,  $P<0.001$ ) between  $\ln(\text{area})$  and  $\ln(\text{time})$  and a variance partition analysis was used to evaluate the actual contribution of each variable to the model (see text for details). The analyses were performed with and without taking into account phylogenetic structure in the data. For all models, the interaction terms between explanatory variables and quadratic terms of all explanatory variables were first included in the model. They were then sequentially removed (interaction terms first, then quadratic terms) when not significant.

Dependent variable	Predictor	Nonphylogenetic Slope ( $\beta$ )	Phylogenetic <i>Pagel</i> Slope ( $\beta$ )	Phylogenetic <i>Brownian</i> Slope ( $\beta$ )
Log rate	Intercept	-2.15***	-2.16***	0.88 <sup>ns</sup>
	Area	-0.15**	-0.15***	-0.27***
	Mass	0.13***	0.13***	-0.04 <sup>ns</sup>
	Time	-0.87***	-0.87***	-0.72***
	$Area^2$	ns	ns	-0.01*
	<i>AIC</i>		188.82	262.97
Percent change	Intercept	8.53 <sup>ns</sup>	7.46 <sup>ns</sup>	-0.38 <sup>ns</sup>
	Area	-0.51 <sup>ns</sup>	-0.45 <sup>ns</sup>	-2.36***
	Mass	-1.32***	-1.19 <sup>ns</sup>	1.36 <sup>ns</sup>
	Time	0.02 <sup>ns</sup>	0.22 <sup>ns</sup>	1.06 <sup>ns</sup>
	$Mass^2$	ns	ns	-0.06***
	<i>AIC</i>		512.78	586.62
Absolute Percent change	Intercept	11.39***	11.37***	41.81*
	Area	-0.79*	-0.81*	-2.63***
	Mass	0.88***	0.90***	-1.05 <sup>ns</sup>
	Time	0.93*	0.95*	1.88*
	<i>AIC</i>		458.78	519.61

\* $P \leq 0.05$ , \*\* $P \leq 0.01$ , \*\*\* $P \leq 0.001$ , <sup>ns</sup> $P > 0.05$ .

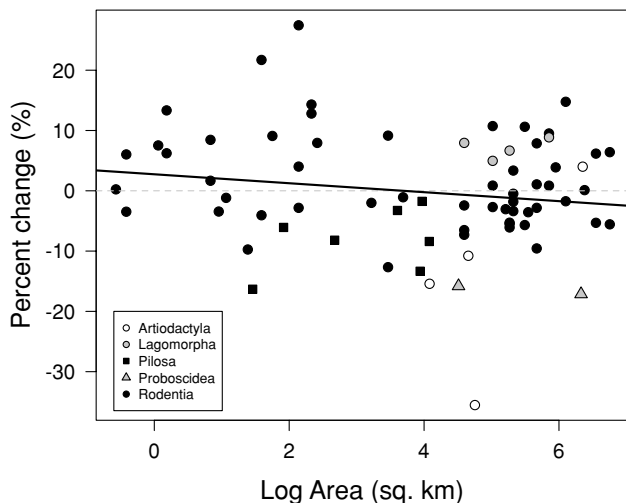


**Figure 2.** The relation between the evolution rate and body mass.

maximum of curvature, calculated when  $\ln(\text{rate})' = 0$ , is found at  $\ln(\text{area}) = -13.5$  ( $\text{area} = 1.3 \times 10^{-6}$  sq. km), a negligible value of island area that falls outside the range of data used. So overall, over the range of data used, the effect of island area on evolutionary rates is negative (Table 1).

**AMOUNT OF CHANGE**

Figure 3 illustrates the relation between the percentage change in the morphological traits considered and island area. The slope was negative, but not significantly different from zero, indicating that the amount of change did not depend on the area of the island.



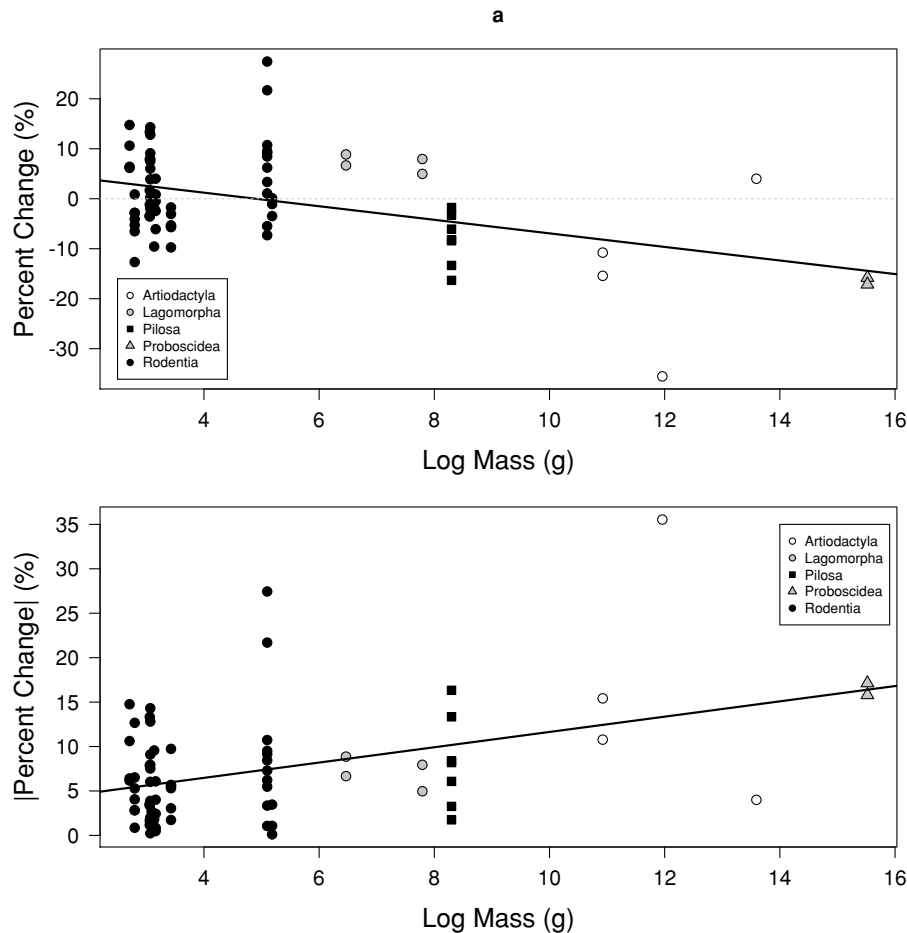
**Figure 3.** The relation between percent change in morphological traits and island area.

Overall, smaller mammals tended to change to a lesser extent than large mammals (Table 1, Fig. 4). A Pagel’s  $\lambda$  of 0.50 indicated the presence of a phylogenetic structure in the data. All the effects of area and mass on percent change were nonsignificant when the phylogenetic structure in the data was accounted for using a Pagel correlation structure for the linear model (Table 1). When using a simple Brownian model of evolution, there was a negative effect of island area on percent change as well as a negative but small effect of  $\text{Mass}^2$  (Table 1).

The absolute (unsigned) value of the percent change was negatively related with island area and positively related with body mass. There was also a positive effect of the time interval on the amount of change (Table 1). A Pagel  $\lambda$  of 0.24 indicated a weak phylogenetic structure in the data. All the effects of area, mass, and time remained unchanged in their direction and significance level when taking into account the phylogenetic structure in the data and using a Pagel’s correlation structure (Table 1). However, the effect of mass was not significant when using a simple Brownian model of evolution.

**DIRECTION OF CHANGE**

Island area had no effect on the direction of size change in island mammals (Fig. 3). A logistic regression model indicated that the probability of positive versus negative change was not dependent on island area ( $z = -0.86, P = 0.39$ ). The negative relation between percent change and body mass observed in Figure 4 illustrates a seeming tendency for smaller species to increase in size and for large species to decrease in size. Overall, however, the trend in Figure 4 was not significant, with a probability of



**Figure 4.** The relation between percent change in morphological traits (A) or the percent of change in absolute value (B) and the average body mass of the species.

positive versus negative change that did not depend upon body mass ( $z = -1.43$ ,  $P = 0.15$ ). Most notably, an equal proportion of rodents displayed either an increase in size ( $n = 28$ ) or a decrease in size ( $n = 27$ ) on islands.

In summary, I found that the first prediction of accelerated evolution on small islands was supported. The second prediction was also supported, as the absolute amount of change in island mammals was negatively related to the area of the island; the smaller the island the greater the amount of change. I also showed that rates of evolution tended to depend on the body mass of the species, with larger species evolving faster on islands. This last relation did not hold when taking into account the phylogenetic structure in the data, a result that should be taken cautiously because this phylogenetic structure was weak. I also found much variability in the direction of change in small mammals.

## Discussion

Altogether, the data presented here showed that rates of evolution are slower over longer time intervals, which could very well be

a mathematical artifact (Sheets and Mitchell 2001). The issue of a spurious correlation between rates of evolution and the time interval over which they were calculated has long been acknowledged (Gould 1984; Sheets and Mitchell 2001). Further, rates in darwin calculated over long time intervals are necessarily lowered, because they average periods of rapid change with periods of slow change or stasis, and they can also include fluctuations in the direction of change (Gingerich 1983; Millien 2007).

There was a significant relation between the time interval and island area in the data assembled here. However, we can conclude that the effect of island area on the rate of evolution and amount of change in isolated mammals is valid and not due to a sampling bias for three reasons. First, despite the strong effect of time interval on the rates of evolution found here, the variance partitioning analysis indicated that a significant portion—nearly a quarter—of the variation in rate is explained by the size of the island. Second, there was no interaction between the time interval and island area in any of the models (although these two factors appeared to be correlated in the data). And lastly, the effect of island area on the rate and amount (both in signed and in absolute



values) of change was significant, even when the time interval was included in the models.

The main finding of this analysis is a negative relationship between the rate of evolution and island area: the smaller the island, the faster the evolutionary change. This result provides the first empirical evidence for early predictions that species on the smallest islands will experience the largest amount and fastest rate of morphological change (Heaney 1978; Filin and Ziv 2004). A number of factors have been identified as drivers of evolution on islands. Some factors are ecological, such as a reduced number of competitors and terrestrial predators or fewer resources on islands. Others factors are demographic, such as higher population densities, higher population growth rates, or reduced dispersal on islands (Case 1978; Heaney 1978; Lawlor 1982; Dayan and Simberloff 1998; Michaux et al. 2002; Palkovacs 2003; Meiri et al. 2005, 2006, 2008; White and Searle 2007). These same factors, probably acting in combination, can also be invoked to explain the more rapid evolution of populations found on islands, and the strength of these factors is likely to be greater on small islands.

The pattern of morphological evolution in island species can be characterized by three components: its direction, magnitude, and speed and below, I now review each of them in the light of the results obtained.

#### **DIRECTION OF CHANGE**

The island rule is supported by empirical data (Foster 1964; Lomolino 1985, 2005) although it has been challenged for carnivores (Meiri et al. 2004), primates (Schillaci et al. 2009), and more generally in mammals (Meiri et al. 2006). The tendency of small species to become larger and of large species to become smaller is not apparent in the data assembled here. In particular, smaller species sometimes increased and sometimes decreased in body size on islands. However, the fact that some of the small island species exhibited a decrease in size is not necessarily a refutation of the island rule. The large Japanese field mouse, *A. speciosus*, provides an illustrative example. This species has evolved toward a smaller size in Japan since the Last Glacial Maximum (Millien and Damuth 2004). However, this species is still the largest in the genus *Apodemus*, and it is much larger than any *Apodemus* species found on the Eurasian mainland (Nowak and Paradiso 1999). As a result, although this species has decreased in size over the last 20,000 years, *A. speciosus*' mainland ancestor was of smaller size (Kawamura 1988). Consequently, despite its recent size decrease, *A. speciosus* is still an example of an endemic rodent species that is larger than its closest mainland relatives, in accordance with the island rule (Foster 1964). Previous reviews on the island rule in mammals were based on island–mainland comparisons that could be qualified as “synchronic,” whereas the data described here only refer to “allochronic” patterns, with the comparison of successive

evolutionary forms from a given lineage on a single island. The data assembled here are thus not suited to conduct a formal test of the island rule.

#### **AMOUNT OF CHANGE**

I found much variability in both the direction and amount of size change in mammals evolving on islands, especially for small mammals. This variability may be linked to a shift toward a more generalist and opportunistic ecology following their isolation on islands. It is precisely those species that have the potential to adapt in a flexible way to the local conditions in their new environment that have an increased chance of survival on islands. This supports the view that, while the ancestral body size of a taxon is important for determining size change on an island, an essential role is played by many other factors, such as diet, behavior, trophic level, life history, or community-wide patterns (Case 1978; Heaney 1978; Lawlor 1982; Dayan and Simberloff 1998; Michaux et al. 2002; Palkovacs 2003; Meiri et al. 2005, 2006, 2008; White and Searle 2007). Moreover, the patterns and strength of body size change in island mammals are likely to be altered by other environmental factors known to influence body size evolution in mammals, such as climate change or fragmentation of the habitat (e.g., Millien and Damuth, 2004; review in Millien et al. 2006).

Heaney (1978) suggested that body size evolution in island mammals was the result of an interaction between island area and body size. In his verbal model of evolution on islands, resource limitation was the main factor causing body size decreases in large mammals, whereas reduced predation and competition were the main factors causing body size increases in small mammals. Heaney (1978) expected these effects to be strongest on small islands. Lomolino (2005) also concluded that the island rule should be the most apparent on the smallest islands, but these results were challenged by Meiri et al. (2005) and Schillaci et al. (2009), who found no effect of island area on the body size of some isolated mammals. The dataset assembled here for island mammals does not support this latter view, as the amount of size change was dependent on island area. Island species tended to change to a greater extent on smaller islands.

#### **RATE OF CHANGE**

The most striking examples of island evolution come from the fossil record, including dwarf elephants and hippopotamuses (Sondaar 1977, 1991; Lister 1996), deer (Lister 1996), and maybe humans (Brown et al. 2004). Why, though, are dwarf island mammals less common today? One possibility is that most of them would not have survived hunting pressure, competition with introduced species, or diseases associated with humans colonizing islands (Sondaar 1987, 1991; Alcover et al. 1998). Meiri et al. (2008) also suggested that the island rule could be expressed

only over longer time scales, and they also found no pattern of faster evolution on islands in carnivores over the last two centuries (Meiri et al. 2009). This assertion is not in accordance with previous studies on the pace of evolution in island mammals (Sondaar 1991; Millien 2006), in which (1) most morphological evolution happens very rapidly following isolation, and (2) island mammals evolve at similar rates to their mainland counterparts over longer time scales. Evolution on islands occurs following either colonization on a newly formed island, or following differential extinctions on a relict island that was once connected to the mainland. The species found on islands have the opportunity to exploit a full new range of resources, in an environment often free of terrestrial predators and with a limited number of competitors due to the different abilities of species to colonize or survive on the island. This ecological opportunity then results into an evolutionary burst with accelerated rates of diversification and/or differentiation of the island species (Losos and Ricklefs, 2009). Moreover, this evolutionary burst is assumed to occur rapidly, at least faster than in mainland situations. Here, I found that species tended to evolve faster on smaller islands. This result fits well the theory of an evolutionary burst due to the opening of new ecological opportunities on islands as described in Losos and Ricklefs (2009). Indeed, one should expect that the smaller the island the more dramatic the ecological contrast between the mainland and the island environment should be (in terms of species diversity, but also abiotic environment), thus potentially leading to accelerated rate of adaptation of species to this new environment. But more importantly, demographic factors that should favor rapid evolution (mainly smaller population size) are likely to be more predominant on the smallest islands where stronger intraspecific competition for limited resources is also expected to occur.

## Conclusion

Many features of the environment of an island, both physical and biological, depend upon its surface area. For example, the largest islands host more diversified habitats and higher mountains, and are less susceptible to natural disturbances than the smaller islands (Whittaker 1995). Moreover, the biological environment of an island is also linked to its surface area. The larger an island, the more species diverse it is (MacArthur and Wilson 1967). As a direct consequence of the link between island area and species diversity, the intensity of predation and interspecific competition pressures are altered on smaller islands. For example, small islands are characterized by the lack of terrestrial mammalian predators (Sondaar 1977; Alcover and McMinn 1994). However, a smaller area also implies limited resources, and a relative increase in intraspecific competition (Adler and Levins 1994). Clearly, the large number of factors affecting the evolution of island mammals (review in Dayan and Simberloff 1998) makes it challenging to characterize

quantitatively and even qualitatively the relation between morphological changes in island species and the surface area of the island. Every isolated population is subjected to a whole suite of selection pressures that vary in their nature and intensity. Each isolated biological assemblage is the result of different colonization histories, with varied times of isolation for each of its constituent. Nevertheless, the number of species, and hence number of competitors and predators on an island, the resource availability, the complexity of the environment and potential ecological niche that can be exploited on an island are all factors related to island area. The smaller an island is, the more “island-like” it is. It is thus not too surprising that both the theory and the empirical data presented here support the hypothesis of accelerated evolution on the smallest islands.

In conclusion, islands remain exceptional “laboratories for the study of ecology and evolution” (Mayr 1967; McNab 2002) and can help us to understand the evolutionary potential of species in the face of rapid and drastic change in their environment. A better understanding of the adaptive response of species in a changing environment is of theoretical and practical importance within the current context of accelerated climate warming and natural habitat destruction and fragmentation through human activities.

## ACKNOWLEDGMENTS

The research was funded by a grant from the Fond Québécois de la Recherche sur la Nature et les Technologies (FQRNT) # 118967. I thank A. Gonzalez for his comments and for suggesting the hierarchical partitioning analysis, J. Davies for advice with the phylogenetic analysis, A. Hendry, S. Meiri, the editors and two anonymous reviewers for their comments on this manuscript.

## LITERATURE CITED

- Adler, G. H., and R. Levins. 1994. The island syndrome in rodent populations. *Q. Rev. Biol.* 69:473–490.
- Alcover, J., and M. McMinn. 1994. Predators of vertebrates on islands. *Bioscience* 44:12–18.
- Alcover, J. A., A. Sans, and M. Palmer. 1998. The extent of extinctions of mammals on islands. *J. Biogeogr.* 25:913–918.
- Anderson, R. P., and C. O. Handley Jr. 2002. Dwarfism in insular sloths: biogeography, selection, and evolutionary rate. *Evolution* 56:1045–1058.
- Angerbjörn, A. 1986. Gigantism in island populations of wood mice (*Apodemus*) in Europe. *Oikos* 47:47–56.
- Berry, R. J. 1996. Small mammal differentiation on islands. *Philos. Trans. R. Soc. Lond. B* 351:753–764.
- Bininda-Emonds, O., M. Cardillo, K. E. Jones, R. D. E. MacPhee, R. M. D. Beck, R. Grenyer, S. A. Price, R. A. Vos, J. L. Gittleman, and A. Purvis. 2007. The delayed rise of present-day mammals. *Nature* 446:507–512.
- Brown, P., T. Sutikna, M. J. Morwood, R. P. Soejono, Jatmiko, E. W. Saptomo, and R. A. Due. 2004. A new small-bodied hominin from the Late Pleistocene of Flores, Indonesia. *Nature* 431:1055–1061.
- Case, T. J. 1978. A general explanation for insular body size trends in terrestrial vertebrates. *Ecology* 59:1–18.
- Chevan, V., and M. Sutherland. 1991. Hierarchical partitioning. *Am. Stat.* 45:90–96.



- Dayan, T., and D. Simberloff. 1998. Size patterns among competitors: ecological character displacement and character release in mammals, with special reference to island populations. *Mammal Rev.* 28:99–124.
- Filin, I., and Y. Ziv. 2004. New theory of insular evolution: unifying the loss of dispersability and body-mass change. *Evol. Ecol. Res.* 6:115–124.
- Foster, J. B. 1964. Evolution of mammals on islands. *Nature* 202:234–235.
- Freckleton, R. P., P. H. Harvey, and M. Pagel. 2002. Phylogenetic analysis and comparative data: a test and review of evidence. *Am. Nat.* 160:712–726.
- Gingerich, P. D. 1983. Rates of evolution: effects of time and temporal scaling. *Science* 222:159–161.
- . 1993. Quantification and comparison of evolutionary rates. *Am. J. Sci.* 293-A:453–478.
- Gould, S. J. 1984. Smooth curve of evolutionary rate: a psychological and mathematical artifact. *Science* 226:984–985.
- Haldane, J. B. S. 1949. Suggestions as to quantitative measurement of rates of evolution. *Evolution* 3:51–56.
- Heaney, L. R. 1978. Island area and body size of insular mammals: evidence from the tri-colored squirrel (*Callosciurus prevosti*) of southeast Asia. *Evolution* 32:29–44.
- Hendry, A. P., and M. T. Kinnison. 1999. Perspective: the pace of modern life: measuring rates of contemporary microevolution. *Evolution* 53:1637–1653.
- Kawamura, Y. 1988. Quaternary rodent faunas in the Japanese islands (Part 1). *Memoirs of the Faculty of Science, Kyoto* LIII:31–348.
- Kinnison, M. T., and A. P. Hendry. 2001. The pace of modern life II: from rates of contemporary microevolution to pattern and process. *Genetica* 112–113:145–164.
- Kuehn, R., C. J. Ludt, W. Schroder, and O. Rottmann. 2005. Molecular phylogeny of *Megaloceros giganteus* – the giant deer or just a giant red deer? *Zool. Sci.* 22:1031–1044.
- Kurtén, B. 1959. Rates of evolution in fossil mammals. *Cold Spring Harbor Symposia on Quantitative Biology* XXIV:205–215.
- Lawlor, T. E. 1982. The evolution of body size in mammals: evidence from insular populations in Mexico. *Am. Nat.* 119:54–72.
- Lister, A. M. 1996. Dwarfing in island elephants and deer: processes in relation to time of isolation. *Symp. Zool. Soc. London* 69:277–292.
- Lomolino, M. V. 1985. Body size of mammals on islands: the island rule reexamined. *Am. Nat.* 125:310–316.
- Lomolino, M. V. 2005. Body size evolution in insular vertebrates: generality of the island rule. *J. Biogeogr.* 32:1683–1699.
- Losos, J. B., and R. E. Ricklefs. 2009. Adaptation and diversification on islands. *Nature* 457:830–836.
- MacArthur, R. H., and E. O. Wilson. 1967. *The theory of island biogeography*. Princeton Univ. Press, Princeton, NJ.
- Mac Nally, R. 2000. Regression and model building in conservation biology, biogeography and ecology: the distinction between and reconciliation of ‘predictive’ and ‘explanatory’ models. *Biodivers. Conserv.* 9:655–671.
- . 2002. Multiple regression and inference in ecology and conservation biology: further comments on identifying important predictor variables. *Biodivers. Conserv.* 11:1397–1401.
- Mayr, E. 1967. The challenge of island faunas. *Aust. Nat. Hist.* 15:369–374.
- McNab, B. K. 2002. Minimizing energy expenditure facilitates vertebrate persistence on oceanic islands. *Ecol. Lett.* 5:693–704.
- Meiri, S., N. Cooper, and A. Purvis. 2008. The island rule: made to be broken? *Proc. R. Soc. Lond. B* 275:141–148.
- Meiri, S., T. Dayan, and D. Simberloff. 2004. Body size of insular carnivores: little support for the island rule. *Am. Nat.* 163:469–479.
- . 2005. Area, isolation and body size evolution in insular carnivores. *Ecol. Lett.* 8:1211–1217.
- . 2006. The generality of the island rule reexamined. *J. Biogeogr.* 33:1571–1577.
- Meiri, S., D. Guy, T. Dayan, and D. Simberloff. 2009. Global change and carnivore body size: data are stasis. *Global Ecol. Biogeogr.* 18:240–247.
- Michaux, J. R., J. G. D. Bellocq, M. Sara, and S. Morand. 2002. Body size increase in insular rodent populations: a role for predators? *Global Ecol. Biogeogr.* 11:427–436.
- Millien, V. 2004. Relative effects of climate change, isolation and competition on body size evolution in the Japanese field mouse *Apodemus argenteus*. *J. Biogeogr.* 31:1267–1276.
- . 2006. Morphological evolution is accelerated among island mammals. *PLoS Biol.* 4:e321.
- . 2007. Spurious or island effect? A response to J. A. Pérez-Claros and J. C. Aledo’s comment on “Morphological evolution is accelerated among island mammals”. *PLoS Biol.* 5:e176.
- Millien, V., and J. Damuth. 2004. Climate change and size evolution in an island rodent species: new perspectives on the island rule. *Evolution* 58:1353–1360.
- Millien, V., S. K. Lyons, L. Olson, F. A. Smith, A. B. Wilson, and Y. Yom-Tov. 2006. Ecotypic variation in the context of global climate change: revisiting the rules. *Ecol. Lett.* 9:853–869.
- Nowak, R. M., and J. L. Paradiso. 1999. *Walker’s mammals of the world*. The Johns Hopkins Univ. Press, Baltimore and London.
- Pagel, M. 1999. Inferring the historical patterns of biological evolution. *Nature* 401:877–884.
- Palkovacs, E. P. 2003. Explaining adaptive shifts in body size on islands: a life history approach. *Oikos* 103:37–44.
- Pergams, O. R. W., and M. V. Ashley. 1999. Rapid morphological change in island deer mice. *Evolution* 53:1573–1581.
- . 2001. Microevolution in island rodents. *Genetica* 112–113:245–256.
- R Development Core Team. 2010. *R: a language and environment for statistical computing in R*. Foundation for Statistical Computing, Vienna, Austria.
- Rohland, N., A. S. Malaspina, J. L. Pollack, M. Slatkin, P. Matheus, and M. Hofreiter. 2007. Proboscidean mitogenomics: chronology and mode of elephant evolution using mastodon as outgroup. *PLoS Biol.* 5:e207.
- Schillaci, M. A., E. Meijaard, and T. Clark. 2009. The effect of island area on body size in a primate species from the Sunda Shelf Islands. *J. Biogeogr.* 36:362–371.
- Sheets, H. D., and C. E. Mitchell. 2001. Uncorrelated change produces the apparent dependence of evolutionary rate on interval. *Paleobiology* 27:429–445.
- Silva, M., and J. A. Downing. 1995. *CRC Handbook of mammalian body masses*. CRC Press, Boca Raton, FL.
- Simberloff, D., T. Dayan, C. Jones, and G. Ogura. 2000. Character displacement and release in the small Indian mongoose, *Herpetes javanicus*. *Ecology* 81:2086–2099.
- Smith, F. A., S. K. Lyons, S. K. M. Ernest, K. E. Jones, D. M. Kaufman, T. Dayan, P. A. Marquet, J. H. Brown, and J. P. Haskell. 2003. Body mass of late quaternary mammals. *Ecology* 84:3403.
- Sondaar, P. Y. 1977. Insularity and its effect on mammal evolution. Pp. 671–705 in M. K. Hecht, and P. C. Goody, eds. *Major Patterns in vertebrate Evolution*. Plenum Press, New-York.
- . 1987. Pleistocene man and extinctions of islands endemics. *Mém. Soc. Géol. France N.S.* 150:159–165.
- . 1991. Island mammals of the past. *Science Progress* 75:249–264.
- VanValen, L. 1973. Pattern and the balance of nature. *Evol. Theory* 1:31–49.
- White, T. A., and J. B. Searle. 2007. Factors explaining increased body size in common shrews (*Sorex araneus*) on Scottish islands. *J. Biogeogr.* 34:356–363.

- Whittaker, R. J. 1995. Disturbed island ecology. *Trends Ecol. Evol.* 10:421–425.
- Yom-Tov, Y., W. Green, and J. Coleman. 1986. Morphological trends in the common brushtail possum, *Trichosurus vulpecula*, in New Zealand. *J. Zool. Lond.* 208:583–593.
- Yom-Tov, Y., S. Yom-Tov, and H. Moller. 1999. Competition, coexistence, and adaptation amongst rodent invaders to Pacific and New Zealand islands. *J. Biogeogr.* 26:947–958.

Associate Editor: G. Hunt

### *Supporting Information*

The following supporting information is available for this article:

**Figure S1.** The phylogeny used to test for a phylogenetic structure in the data.

**Table S1.** Raw dataset.

Supporting Information may be found in the online version of this article.

Please note: Wiley-Blackwell is not responsible for the content or functionality of any supporting information supplied by the authors. Any queries (other than missing material) should be directed to the corresponding author for the article.