

DWARFISM IN INSULAR SLOTHS: BIOGEOGRAPHY, SELECTION, AND EVOLUTIONARY RATE

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Abstract.—The islands of Bocas del Toro, Panama, were sequentially separated from the adjacent mainland by rising sea levels during the past 10,000 years. Three-toed sloths (*Bradypus*) from five islands are smaller than their mainland counterparts, and the insular populations themselves vary in mean body size. We first examine relationships between body size and physical characteristics of the islands, testing hypotheses regarding optimal body size, evolutionary equilibria, and the presence of dispersal in this system. To do so, we conduct linear regressions of body size onto island area, distance from the mainland, and island age. Second, we retroactively calculate two measures of the evolutionary rate of change in body size (haldanes and darwins) and the standardized linear selection differential, or selection intensity (*i*). We also test the observed morphological changes against models of evolution by genetic drift. The results indicate that mean body size decreases linearly with island age, explaining up to 97% of the variation among population means. Neither island area nor distance from the mainland is significant in multiple regressions that include island age. Thus, we find no evidence for differential optimal body size among islands, or for dispersal in the system. In contrast, the dependence of body size on island age suggests uniform directional selection for small body size in the insular populations. Although genetic drift cannot be discounted as the cause for this evolution in body size, the probability is small given the consistent direction of evolution (repeated dwarfism). The insular sloths show a sustained rate of evolution similar to those measured in haldanes over tens of generations, appearing to unite micro- and macroevolutionary time scales. Furthermore, the magnitude and rate of this example of rapid differentiation fall within predictions of theoretical models from population genetics. However, the linearity of the relationship between body size and island age is not predicted, suggesting that either more factors are involved than those considered here, or that theoretical advances are necessary to explain constant evolutionary rates over long time spans in new selective environments.

Key words.—*Bradypus*, body size, darwins, haldanes, island, selection differential, selection intensity.

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Islands have long attracted biologists' attention as windows into evolution and community ecology (e.g., Darwin 1859; Wallace 1880; MacArthur and Wilson 1967; Brown and Lomolino 1998). Usually relatively depauperate in species richness, insular faunas undergo a shuffling of community composition as species are lost due to extinction or gained through immigration and speciation (MacArthur and Wilson 1967; Simberloff 1974; Heaney 1986, 2000; Lomolino 1986, 2000). The community ecology of islands isolated from continental areas by rising sea level—landbridge islands—is typically dominated by extinction (faunal relaxation), rather than by a more even equilibrium of extinction and colonization, as on oceanic islands (Lawlor 1986; Paterson and Atmar 1986).

Following isolation, many mammals surviving on landbridge islands undergo evolutionary changes in physiology, behavior, and morphological features, such as size, cranial and dental characteristics, and coloration (e.g., Heaney 1978; Lomolino 1985; Kalko and Handley 1994). Models from population genetics can predict morphological shifts in quantitative characters (e.g., such as body size) under changing environmental conditions such as mainland versus insular environments (Lande 1980, 1986; Kirkpatrick 1982). Differentiation in body size, one of the most important predictors of life-history characteristics in mammals (Marquet and Ta-

per 1998), follows a strikingly consistent pattern: Large species generally become dwarfed on islands, whereas small mammals commonly evolve larger size.

Reviews differ in which and how many mechanisms drive that change in body size and under what circumstances each is relevant. Some (Lomolino 1985; Roth 1992; McNab 1994) conclude that insular populations of small species become larger to use broader resource bases in the absence of former competitors (competitive release of Lomolino 1985), and large mammals are often resource-limited on islands, favoring smaller size (resource limitation of Lomolino 1985). Recently, Marquet and Taper (1998, p. 135) suggested that resource limitation may cause both dwarfism in large mammals and gigantism in small ones, due to changes in intraspecific competition that are related to home range size. In contrast, Adler and Levins (1994) put forward models invoking selection for larger body size in small species in response to higher intraspecific competition (see also Crowell 1983). Finally, Heaney (1978) proposed that island area determines which factor drives selection: resource limitation on small islands and competitive release on large islands. General models for the evolution of body size in insular terrestrial vertebrates have been proposed and a few notable exceptions investigated (e.g., Foster 1964; Case 1978; Lawlor 1982; Case and Schwaner 1993; Petren and Case 1997). Thus, while the overall causes of body size evolution in insular situations remain an open area of research, most reviews to date suggest

⁵ Charles O. Handley, Jr. passed away on June 9, 2000.

that selection for smaller size in large mammals on islands is caused by resource limitation and strong intraspecific competition (Heaney 1978; Lomolino 1985; Roth 1992).

Body size is but one of many morphological traits that have been examined in studies assessing evolutionary rates and selection intensities (Lynch 1990; Gingerich 1993; Hendry and Kinnison 1999; Hoekstra et al. 2001; Kingsolver et al. 2001). In studies where relative fitness, w , is known, the linear selection gradient, β , is defined as the slope of a regression of relative fitness on a continuously varying (quantitative) trait or character, z (Arnold and Wade 1984). In contrast, a selection differential measures evolutionary rate and can be calculated without data regarding fitness (see Materials and Methods). The islands of Bocas del Toro, Panama, provide a superb empirical opportunity to investigate differentiation and rates of morphological evolution in mammals, because the ages of the islands have been estimated, the sequence of their formation is known, and the mammalian fauna is well sampled.

The Islands of Bocas del Toro

The province of Bocas del Toro is located on the Caribbean coast of northwestern Panama adjacent to Costa Rica (Fig. 1). Just off shore lies a group of landbridge islands that formed during the Holocene as a result of postglacial events, including rising sea level and continental submergence (Olson 1993; Kalko and Handley 1994; Anderson and Handley 2001). Rising sea levels isolated hilltops and ridges, first as peninsulae, and then eventually as islands. These islands vary in area, distance from the mainland, depth of surrounding water, and age—all contributing to the degree of isolation of the fauna of each island (Table 1).

Combining ocean-floor topography with studies of pollen and coral cores from the western Caribbean allowed C. O. Handley, Jr. and M. Varn (unpubl. ms.) to determine the sequence of island formation and to estimate the dates of separation for the various islands of Bocas del Toro (for details, see Anderson and Handley 2001). Assuming that the present-day submarine topography of Bocas del Toro is not very different from that of the terrestrial topography 10,000 years ago (before flooding), then the depths of water at which land bridges to various present-day islands disappeared should be apparent from current sea-floor maps. Thus, given estimates of sea level at various time intervals in the past, it is possible to estimate the approximate date of isolation of each island.

C. O. Handley, Jr. and M. Varn (unpubl. ms.) produced maps of bathymetric contours of Bocas del Toro for various depths below present sea level and used three models based on coral and pollen cores taken in the western Caribbean to estimate sea levels over the past 10,000 years. Radioisotope dating of *Acropora palmata*, a coral restricted to the upper 5 m of water, formed the bases of the curves of depth below current sea level versus time produced by Lighty et al. (1982) and Fairbanks (1989). Bartlett and Barghoorn (1973) used the pollen of *Rhizophora mangle* in deep-sea cores from the Gatún Basin in Panama to produce a similar curve. *Rhizophora mangle* is an obligate saltwater species and represents the major component of Neotropical coastal mangrove

swamps. Using a composite curve with years before present and depth below current sea level as axes, Handley and Varn dated each of the bathymetric contours and thus estimated island ages from the dates of disappearance of land bridges between each island and the mainland (Table 1). Even if their absolute dates err in one direction or the other, relative dates of island formation will be correct to the extent that sea-floor contours in this region have remained constant through the Holocene.

Isla Escudo was the first of the islands to be separated from the mainland (Fig. 1). It fragmented from the eastern shore of the Península Valiente about 8900 years ago and is not directly related to any of the other islands. To the northwest of the Península Valiente and Isla Escudo, the islands of the Laguna de Chiriquí are younger (Fig. 1A). They fragmented sequentially from the Península Tierra Oscura, which was once a long, J-shaped peninsula jutting out from the southwestern shore of the Laguna de Chiriquí (Fig. 1B). That peninsula was formed by the opening of the Boca del Drago Pass at the western end of the laguna. The outermost islands of the Laguna de Chiriquí are about 5000 years old: Isla Colón, which was the first to split off of the Península Tierra Oscura (ca. 5200 years ago), and Isla Bastimentos, which separated from the peninsula along with what currently is Cayo Nancy (ca. 4700 years ago). Cayo Agua became isolated from the adjacent mainland (presently part of Isla Popa) about 3400 years ago. In the past 1000 years, Cayo Nancy split from Isla Bastimentos proper, and Isla Popa and Isla Cristóbal each separated from the mainland.

Biological interest in the islands of Bocas del Toro emerged only relatively recently (Handley 1959, 1993; Olson 1993; Kalko and Handley 1994; Anderson and Handley 2001). These studies generally assume that the fauna of the coastal plain of Bocas del Toro was relatively uniform as sea levels rose and populations were stranded on the forming islands. Despite significant climatological fluctuations, palynological data indicate that lowland tropical forests remained intact in Panama during the past 2 million years (Colinvaux 1997), lending support to this premise. Subsequent to isolation, numerous species of mammals, including bats, rodents, felids, and mustelids present on the nearby mainland, were extirpated from some or all of the islands (Handley 1993, unpubl. data). Additionally, a few relictual species are present on one or more of the islands but no longer on the adjacent mainland (Handley 1993; Olson 1993; García-París and Wake 2000). Several species surviving on the islands exhibit marked morphological differentiation from their mainland relatives. For example, a fruit-eating bat, *Artibeus incommittatus*, underwent rapid differentiation on Isla Escudo (Kalko and Handley 1994). Similarly, several populations of three-toed sloths (*Bradypus*) have become dwarfed following insularization (Anderson and Handley 2001), and here we further examine their evolution and biogeography.

Three-toed Sloths

Along with armadillos and anteaters, sloths belong to the Neotropical order Xenarthra (Gardner 1993; or magnorder Xenarthra sensu McKenna and Bell 1997). Two distantly related genera, *Choloepus* (two-toed sloths) and *Bradypus*

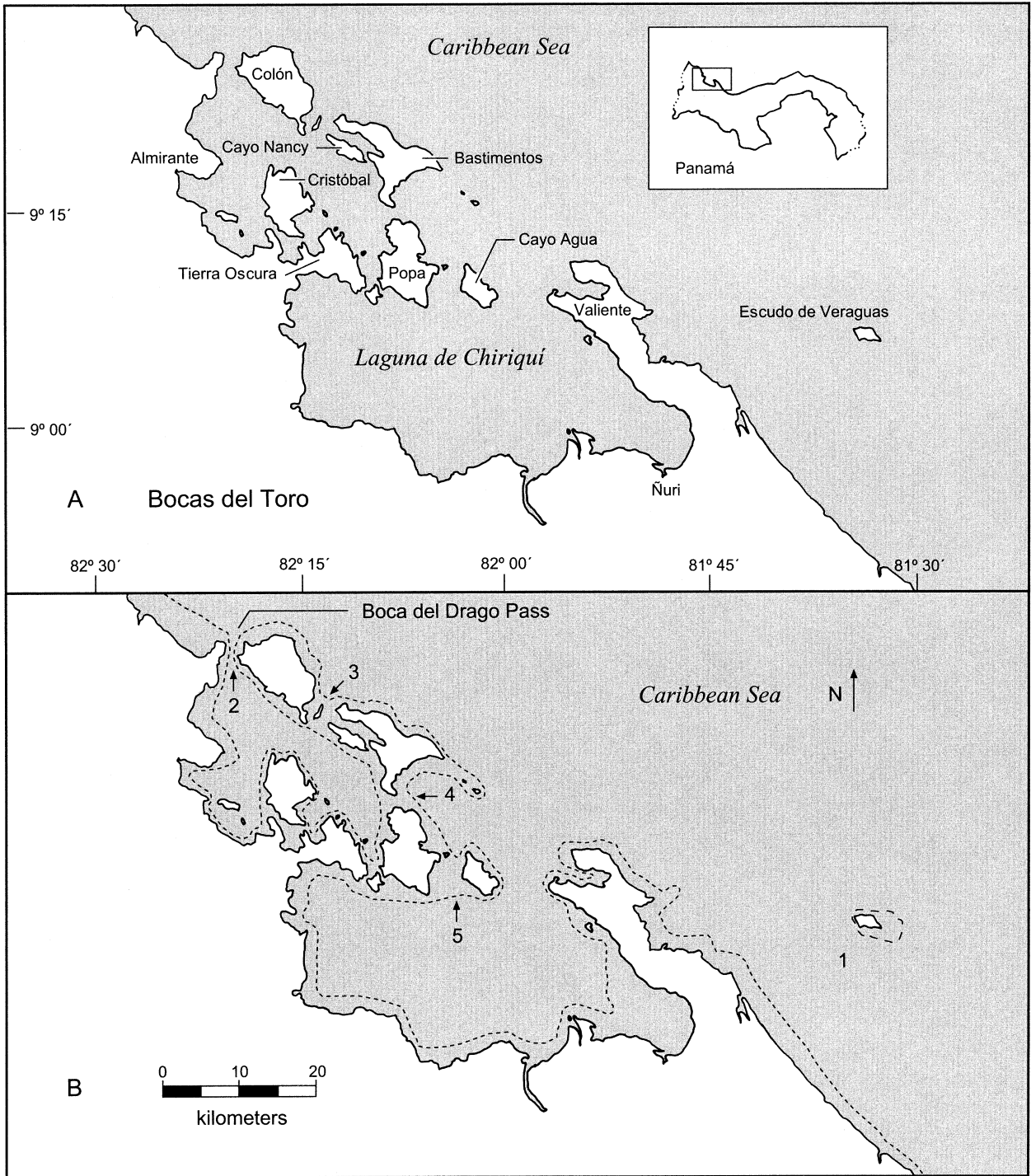


FIG. 1. Maps of Bocas del Toro showing major islands and place names on the mainland (A) and reconstruction of the sequence of island formation (B). In (B), the dashed line approximates sea level at 10 m below present. Major events in the formation of the islands (Anderson and Handley 2001; C. O. Handley, Jr. and M. Varn, unpubl. ms.) are as follows: (1) Isla Escudo separated from the southern coast of the province about 8900 years ago; (2) the Boca del Drago pass opened, creating a J-shaped peninsula in the Laguna de Chiriquí about 6300 years ago; (3) Isla Colón became isolated from the peninsula about 5200 years ago; (4) the superisland Bastimentos-Nancy became separated from what remained of the peninsula about 4700 years ago; and (5) Cayo Agua was formed about 3400 years ago. More recently (in the past 1000 years), Isla Cristóbal and Isla Popa each separated from the mainland, and Cayo Nancy split from Isla Bastimentos.

TABLE 1. Estimated age (since separation from the adjacent mainland), area, and distance from the mainland for the islands of Bocas del Toro, Panama. Data are from the Anderson and Handley (2001).

Island	Age (years ago)	Area (km ²)	Distance from the mainland (km)
Isla Escudo	8900	4.3	17.6
Isla Colón	5200	59.0	1.5
Isla Bastimentos	4700	51.5	6.3
Cayo Nancy	4700	6.8	9.5
Cayo Agua	3400	14.5	6.6
Isla Popa	1000	53.0	1.8
Isla Cristóbal	1000	36.8	0.3

(three-toed sloths), are extant (Webb 1985; Patterson et al. 1992). Here we consider only the three-toed sloths, *Bradypus*. We recently described a new species of *Bradypus* from Isla Escudo (Anderson and Handley 2001), bringing the number of species known in the genus to four (Wetzel and Avila-Pires 1980; Wetzel 1985; Anderson and Handley 2001). This new species, *B. pygmaeus*, is closely related to *B. variegatus*, which is widespread in both Central and South America. The other two species in the genus, *B. tridactylus* and *B. torquatus*, are restricted to South America.

Three-toed sloths are arboreal folivores with low dispersal ability (Carvalho 1960; Montgomery and Sunquist 1975; Chiarello 1998b). Concomitant with their energy-poor diet, they have extremely low metabolic rates and are not fully homeothermic (Britton and Atkinson 1938). Sloths avoid predation largely by avoiding detection, moving very slowly in trees (Brattstrom 1966) throughout small home ranges, which average 1.6 ha (Montgomery and Sunquist 1975; see also Chiarello 1998a). Sloths move even more slowly on the ground than in trees, traveling on average 0.4 km per hour (Britton and Kline 1939; see also Mendel 1985), although they are known to swim well in rivers (Beebe 1926, pp. 7–9; Carvalho 1960). We have found no reference to their swimming in salt water, however; perhaps they have a behavioral aversion to salt water or to rough water and wave action. Their relatively large size, restricted diet, and low dispersal potential make sloths a model system for investigating the effects of isolation on body size in large insular mammals.

Body Size in Sloths from Bocas del Toro

In a morphological and morphometric study of the sloths of Bocas del Toro (Anderson and Handley 2001), we documented a repeated pattern of dwarfism in sloths from several of the islands. The populations of three-toed sloths of the outer (and older, Fig. 1, Table 1) islands of Bocas del Toro—Isla Colón, Isla Bastimentos, Cayo Nancy, Cayo Agua, and Isla Escudo—are significantly smaller in body size than the *Bradypus* from most or all of the four localities on the adjacent mainland (by Tukey's tests of multiple pairwise comparisons with a conservative familywise error rate of $\alpha = 0.05$; from Anderson and Handley 2001; see also Table 2). Furthermore, some of the populations on those five islands themselves vary in mean body size, with that from Isla Escudo clearly being the smallest (Anderson and Handley 2001; Fig. 2; Table 2; see Fig. 3; in addition to the statistical sig-

TABLE 2. Descriptive statistics for greatest length of skull (mm) and scores on the first principal component (PC 1) for adult *Bradypus* from Bocas del Toro, Panama. Measurements and scores are given as the mean \pm two standard errors and the range of minimum to maximum. Sample size is given in parentheses. Data are from Anderson and Handley (2001). Islands are arranged from outermost to innermost; mainland localities from west to east.

Locality	Greatest length of skull	First principal component (PC 1)
Isla Escudo	69.0 \pm 1.34 67.5–72.2 (6)	–0.28 \pm 0.05 –0.35 to –0.22 (5)
Isla Bastimentos	70.4 \pm 1.53 68.3–73.4 (6)	–0.14 \pm 0.07 –0.18 to –0.07 (3)
Cayo Agua	72.5 \pm 1.18 68.7–74.9 (12)	–0.04 \pm 0.03 –0.14–0.02 (11)
Isla Colón	73.4 \pm 2.96 70.5–76.6 (4)	–0.08 \pm 0.12 0.20–0.00 (3)
Cayo Nancy	76.0 \pm 2.60 73.2–80.0 (5)	–0.05 \pm 0.07 –0.15–0.05 (5)
Isla Cristóbal	79.3 \pm 2.00 76.5–82.1 (5)	0.06 \pm 0.08 –0.06–0.13 (4)
Isla Popa	80.0 \pm 1.29 77.7–82.5 (6)	0.11 \pm 0.03 0.09–0.16 (5)
Almirante	79.7 \pm 2.88 75.9–82.5 (4)	0.09 \pm 0.07 0.04–0.15 (3)
Tierra Oscura	80.5 \pm 2.50 76.1–86.0 (7)	0.12 \pm 0.05 0.02–0.19 (7)
Valiente	80.3 \pm 1.99 77.7–83.5 (6)	0.09 \pm 0.04 0.04–0.17 (6)
Ñuri	78.4 \pm 1.13 77.0–80.6 (7)	0.06 \pm 0.03 0.01–0.10 (5)

nificance of the magnitudes of these differences in mean relative to within-group variation, the magnitudes are clearly biologically significant as well). In contrast, the samples from Isla Popa and Isla Cristóbal, young islands close to shore, are not significantly different in body size from any population on the adjacent mainland (Anderson and Handley 2001; Table 2; see Fig. 3).

Although sloths from the five outer islands share small body size, pelage characters indicate similarities between insular and mainland populations that were once contiguous (Anderson and Handley 2001). Several pelage characters evaluated throughout the range of *B. variegatus* in Central and South America show that sloths from Bocas del Toro group most closely with those from nearby samples in central Panama and extreme northwestern Colombia (Anderson and Handley 2001). Furthermore, a few discrete pelage characters vary within Bocas del Toro, with geographically proximate populations there sharing the same character states. For example, there is a west-to-east cline from uniformly colored to blotchy dorsal pelage. Similarly, the only populations in Bocas del Toro with individuals lacking a dorsal stripe are found at Tierra Oscura and the adjacent islands of Isla Cris-

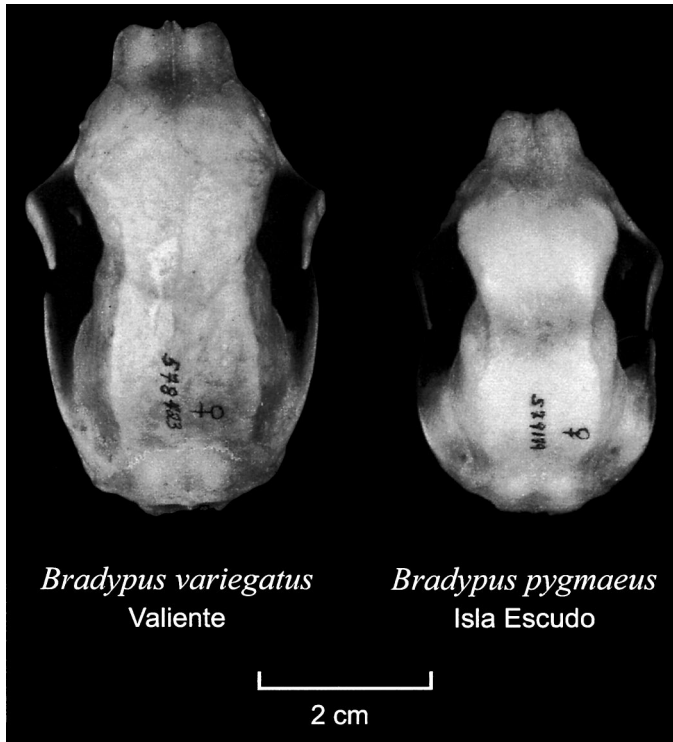


FIG. 2. Skulls of *Bradypus variegatus* from the Península Valiente on the mainland of Bocas del Toro (left) and *Bradypus pygmaeus* from Isla Escudo (right) showing the degree of size divergence of the sloth on Isla Escudo.

tóbal, Isla Popa, and Cayo Nancy (for other examples, see Anderson and Handley 2001).

This pattern of similar pelage traits being present in geographically proximate populations (without regard to whether they are mainland or insular) lies in stark contrast to the striking differences in body size between most insular populations and the nearest respective mainland samples. The few cranial characters common to the small sloths on various islands are all gracile traits associated with size reduction and ontogenetic truncation (e.g., thin zygomatic arches, weakly developed temporal crests). In fact, many cranial traits of adult individuals of the small insular sloths mimic those of immature individuals from the adjacent mainland (Anderson and Handley 2001), suggesting an evolutionary syndrome often described as or attributed to paedogenesis (Reilly et al. 1997). In contrast, the pelage traits provide data independent of size reduction, which is especially predisposed to convergence (Roth 1992). Because of the extreme differences in body size between mainland and insular samples, Anderson and Handley (2001) suggested that the distribution of pelage traits did not represent recent gene flow (via dispersal), but rather the relictual manifestation of previously continuous geographic variation that was subdivided into isolated populations when the islands formed.

This interpretation suggests that populations of *Bradypus* may have evolved smaller size four times subsequent to island formation in Bocas del Toro: independently on Isla Escudo, Isla Colón, and Cayo Agua (each of which formed separately) and once on the superisland Isla Bastimentos—

Cayo Nancy together (they separated from the mainland as a unit and only recently separated from each other; see Fig. 1). Based on several unique cranial features (including some indicative of a divergent pattern of cranial circulation) and extremely small body size (well out of the variation found anywhere in the range of *B. variegatus*), Anderson and Handley (2001) considered that the population on Isla Escudo has evolved to represent a distinct species, *B. pygmaeus*, but that the sloths of other islands remain conspecific with *B. variegatus*, despite their moderate dwarfism. In any case, all insular three-toed sloths in Bocas del Toro are very closely related to populations of *B. variegatus* from the mainland of Panama (see Anderson and Handley 2001 and above). L. E. Olson and R. P. Anderson (unpubl. data) have begun DNA sequencing of part of the mitochondrial genome to elucidate the genetic relationships among populations of *Bradypus* in Bocas del Toro (after Brooks and McLennan 1991; Avise 1994; Matocq et al. 2000). Here, we test several biogeographic hypotheses based on morphological data and physical characteristics of the islands and compare the results with theoretical and empirical values from other evolutionary studies.

MATERIALS AND METHODS

Regressions

Hypotheses based on physical characteristics of the islands

Island area, distance from the mainland, and age represent the major physical variables potentially affecting evolution in insular mammals. Heaney (1978) showed that body size in tri-colored squirrels (*Callosciurus prevosti*) was related to island area (presumably because intra- and interspecific competitive relationships vary with island area and faunal richness, which is a function of area). Thus, in an archipelago with islands varying greatly in area, optimal body size may not be constant among all islands. In contrast, for groups of islands with generally similar areas and selective environments (related to community composition and resource availability) for a particular taxon, island area is not expected to be related to body size (see also Adler and Levins 1994).

Second, distance from the mainland is predicted to affect immigration rates, especially for more vagile taxa (MacArthur and Wilson 1967). Barring differences in ocean currents, prevailing winds, or opportunities for rafting (such as the outlet of a major river) among islands of an archipelago, immigration rates for a particular taxon should be a function of distance. Thus, for taxa and systems with appreciable immigration rates, distance from the mainland will influence rates of morphological evolution by differentially diluting *in situ* evolution on closer islands with colonists from the mainland. In contrast, where immigration is minimal or nonexistent (such as island archipelagos outside the dispersal potential of the species), distance would not be related to body size.

Finally, when directional selection is still occurring on an insular population, the population has not yet reached its optimal body size (evolutionary equilibrium). In such cases, islands of various ages present in the archipelago should show a relationship between body size and island age, with the

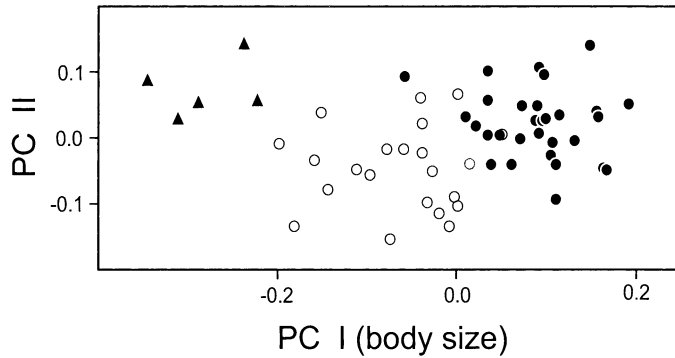


FIG. 3. Plot of specimen scores on the first two axes of a principal components analysis of three-toed sloths (*Bradypus*) from Bocas del Toro, Panama, highlighting the divergence in body size of five insular populations. Specimens from Isla Escudo are marked with solid triangles, those from the four islands of intermediate age (Cayo Agua, Cayo Nancy, Isla Colón, and Isla Bastimentos) are represented by open circles, and specimens from the mainland and from the two youngest islands (Isla Cristóbal and Isla Popa) are denoted by solid circles. The first principal component (PC I) represents a measure of overall body size (Table 3). Data are taken from Anderson and Handley (2001).

most morphological evolution present in the oldest islands. On the contrary, once all insular populations have reached the equilibrium (optimal) body size, island age should no longer be related to body size.

Analyses

To test the above hypotheses regarding optimal body size, dispersal, and evolutionary equilibrium, we conducted a series of regressions. We used scores on the first principal component (PC I; Fig. 3; Table 3) of log-transformed morphological measurements from Anderson and Handley (2001) as a measure of overall body size in the present analyses. We regressed mean PC I scores for insular populations on the following independent physical predictor variables: island area (km²), island distance from the mainland (km), and island age since separation from the mainland of Bocas del Toro (years). Next, for all localities in Bocas del Toro—both island and mainland—we regressed mean PC I scores on the same three predictor variables. In the second set of analyses, years since separation = zero and distance from the mainland = zero for mainland populations; island area was considered a missing value for mainland populations. For both sets of analyses, we conducted multiple linear regressions for those predictor variables that were significant by themselves in simple linear regressions. Likewise, when possible, we subjected significant linear models to lack-of-fit (pure-error) tests (Draper and Smith 1981, pp. 33–42). All statistical analyses were performed in Minitab (1998).

However, not all sloth populations may be considered strictly independent (see Felsenstein 1985). As mentioned above, the geological evidence regarding the sequence of island formation indicates that Isla Bastimentos and Cayo Nancy separated from the mainland together (ca. 4700 years ago) and only recently separated from each other (in the last 1000 years; Anderson and Handley 2001). Thus, if present-day sloth populations derive directly from the founder pop-

TABLE 3. Loadings, eigenvalues, and percent variance explained for the first two axes of a principal components analysis of 57 three-toed sloths (*Bradypus*) from Bocas del Toro, Panama, using the covariance matrix of log₁₀-transformed values of 14 cranial and three external measurements. PC I represents general size, which is uncorrelated with external auditory meatus diameter. Data are taken from Anderson and Handley (2001).

	PC I	PC II
Total length	0.786	0.302
Tail length	0.331	0.788
Hind foot length	0.801	0.141
Greatest length of skull	0.878	0.221
Anterior zygomatic breadth	0.905	0.049
Posterior zygomatic breadth	0.895	-0.010
Postorbital breadth	0.682	0.129
Squamosal process length	0.874	-0.062
Maxillary tooth row length	0.610	0.164
Postpalatal length	0.839	0.269
Palatal breadth	0.712	0.236
Braincase depth	0.794	0.054
Antorbital bar breadth	0.866	-0.092
Descending jugal process length	0.354	0.348
External auditory meatus diameter	-0.044	0.481
Squamosal process breadth	0.689	-0.477
Ascending mandibular ramus breadth	0.842	-0.191
Eigenvalue	0.0164	0.0046
Variance explained	51.2%	14.3%

ulations stranded on the superisland Bastimentos-Nancy when it was formed, then the two populations do not represent independent derivations of dwarfism. Likewise, the four mainland localities represent repetitive estimates of the body size of mainland sloths (which we use as the original body size of the insular sloths at time of isolation).

Considering these issues, we repeated the regression analyses using all geologically independent populations (mainland, Cayo Agua, Isla Colón, Isla Cristóbal, Isla Escudo, Isla Popa, and superisland Bastimentos-Nancy). The mainland and Bastimentos-Nancy represent the two geologically independent populations that are composed of more than one locality. For those two composite samples, we calculated pooled estimates of PC I scores by the grand mean of the constituent populations. For the Bastimentos-Nancy predictor variables, we used the lesser distance from the mainland (that of Bastimentos) and summed the areas of the two islands. These regressions do not assume that the geologically independent populations are independent genetically (i.e., with no current gene flow [dispersal] among them). Given only a moderate number of discrete morphological characters available (Anderson and Handley 2001), molecular analyses are necessary to evaluate that hypothesis from phylogeographic and population-genetic perspectives (L. E. Olson and R. P. Anderson, unpubl. data; see above). Rather, the current, more conservative, approach allows for the possibility of detecting patterns different from those found in the overall regressions of all populations. Furthermore, in the case that the insular populations have been isolated (or effectively so) since separating from the mainland, these analyses permit a more appropriate modeling of their evolution.

Despite its widespread use, simple linear (least-squares) regression is most strictly applicable to cases in which the independent (predictor) variable is measured without error.

Therefore, for those predictor variables that were significant in multiple regressions (i.e., with significant partial sums of squares), we conducted separate reduced-major-axis regressions to produce an unbiased estimate of the slope for further analyses (Sokal and Rohlf 1995).

Furthermore, island area, distance from the mainland, and island age may have nonlinear effects (e.g., Heaney 1978). To consider this possibility, plots of mean PC I scores versus area, versus distance, and versus age for geologically independent populations were examined visually for curvilinear or step (threshold) functions. We did the same for the residuals of regressions onto island age (i.e., plotting residuals from that regression vs. area and vs. distance).

Genetic Drift

Genetic drift, along with mutation, can cause the evolution of quantitative characters in the absence of selection (Lynch 1990; Futuyma 1998, pp. 437–438). To compare the observed differentiation in body size evolution with the maximum phenotypic response expected due to drift, we used a neutral rates test (Lande 1977; Lynch 1990). This test compares observed rates of divergence in quantitative traits with expectations under the null hypothesis of only mutation and drift (for calculations see Lynch 1990; Schluter 2000, pp. 91–92). Using divergence between samples, the number of elapsed generations, and the phenotypic variance, it is possible to calculate an evolutionary rate, Δ , used in such tests. Δ is a per generation ratio of between-species phenotypic variance to within-species phenotypic variance (Lynch 1990). Based on population-genetic theory and empirical data regarding the mutational rate of input of genetic variance, the neutral expectation for Δ lies within the range of 0.01–0.0001 (Schluter 2000). Here we compared divergence in PC I scores for the Isla Escudo population with the grand mean of the four mainland populations.

Complementarily, we then tested for a consistent pattern in the direction of body size evolution by a one-tailed signs test (see Lande 1977, p. 442). We compared the mean PC I score of each of the five insular populations that were significantly different from mainland populations (from Anderson and Handley 2001) with the grand mean of mainland populations, testing whether the sign of change was consistently negative (Zar 1996). Then, we combined Cayo Nancy and Isla Bastimentos into a single datum and repeated the test for the four geologically independent populations with body size significantly different from that of the mainland samples.

Evolutionary Rates and Selection Intensity

To compare the evolution of body size in the sloths of Bocas del Toro with other known cases of rapid evolution under directional selection (which was implicated by the results of the regressions), we conducted a retrospective selection analysis (Lande 1979; Endler 1986, pp. 171–175; Arnold 1988; Hartl and Clark 1989, pp. 441–446). We first calculated the phenotypic change for the population of *Bradypus* on Isla Escudo (*B. pygmaeus*) by subtracting the grand mean of PC I scores for the four mainland populations in Bocas del Toro (z_1) from the mean PC I score for the Escudo population (z_2) and dividing that difference by the pooled

standard deviation (s_p , square root of the mean square error from an ANOVA of the five populations), thus expressing body size change in standard deviation units,

$$\text{body size change} = (z_2 - z_1)/s_p. \quad (1)$$

Dividing phenotypic change (in standard deviation units) by the number of generations (g) produces a common measure of evolutionary rate, the haldane (Haldane 1949; Gingerich 1993; Hendry and Kinnison 1999; see also Lynch 1990). Although age at first reproduction (~ 3 years) and birth frequency (approximately annually) for *Bradypus* are known, data regarding longevity and survivorship remain deficient (Taube et al. 2001 and references therein). Nevertheless, based on available demographic data for *Bradypus* (Montgomery and Sunquist 1978; Hayssen et al. 1993; Pinder 1993; Richard-Hansen and Taube 1997; Taube et al. 2001) and more complete data for *Choloepus* where necessary (summarized in Nowak 1999), we approximated an average generation time of 6 years for *Bradypus* in the wild. We then calculated the number of generations (g) of *Bradypus* since the formation of Isla Escudo (8900 years ago). It follows that,

$$\text{evolutionary rate in haldanes} = \text{body size change}/g. \quad (2)$$

The standardized linear selection differential, or selection intensity (i) is equal to the evolutionary rate in haldanes divided by heritability of the trait (Hendry and Kinnison 1999). Heritability (h^2) of body size typically ranges from 0.2 to 0.7 in mammals (Leamy 1985, 1988; Mavrogenis and Constantinou 1990; Yamaki and Sagae 1991; Ahlborn and Dempfle 1992; Beniwal et al. 1992). Dividing the evolutionary rate in haldanes by h^2 estimates (0.2–0.7) yielded a range of estimates for the average per generation net selection differential (S),

$$i = S = \text{evolutionary rate in haldanes}/h^2. \quad (3)$$

Because we converted to standard deviation units in calculating haldanes, the selection differential (S) is equal to the per generation selection intensity (i ; or standardized linear selection differential) often reported in the literature (e.g., Endler 1986; Kingsolver et al. 2001). These analyses (calculation of haldanes and selection differentials) are based on the following assumptions: (1) constant selection pressure and heritability; (2) a nearly constant body size in mainland populations since the formation of Isla Escudo; and (3) that sloths on Isla Escudo had the same average body size as adjacent mainland populations at the time of isolation.

When time series are present, such as several independent cases of dwarfism, evolutionary rates are best calculated based on the overall relationship between morphological change and time (rather than based only on the endpoints). The rate is estimated from the slope of the regression of morphological change in standard deviation units onto number of generations, following Hendry and Kinnison (1999). This approach takes advantage of all available information and therefore is less vulnerable to errors in estimates of morphological change caused by small sample sizes. Thus, after calculating haldanes and selection intensity for the Escudo population compared with the mainland populations, we recalculated the same values from the slope of the relevant

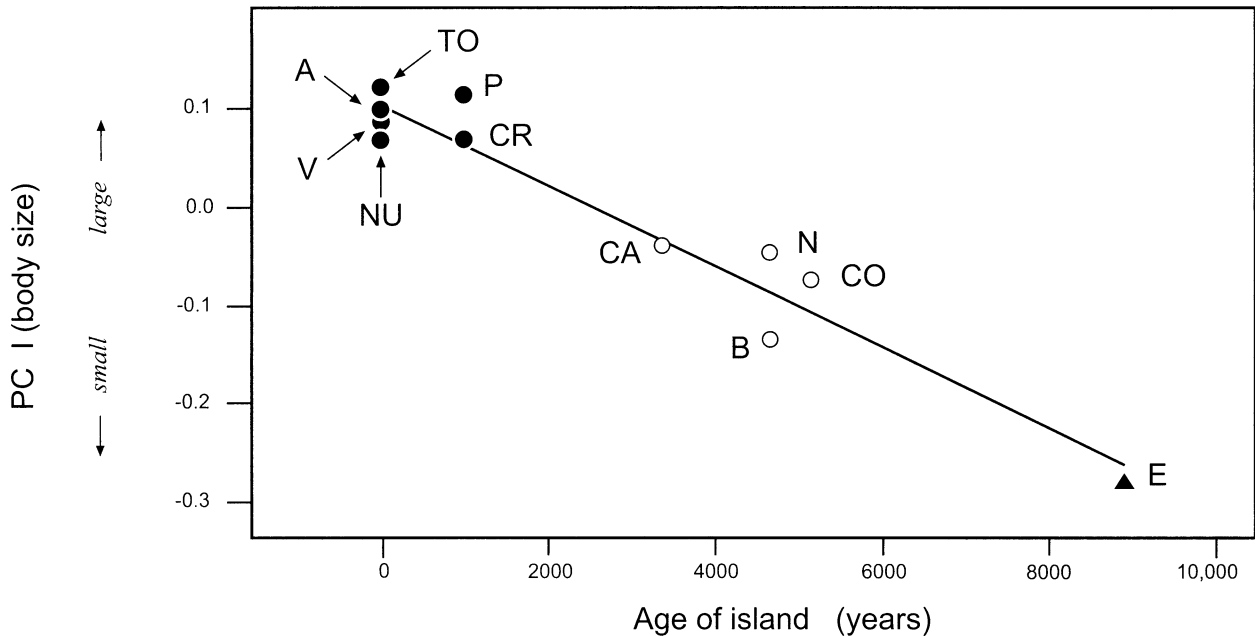


FIG. 4. Regression of general body size (mean PC I score for each locality) on island age (years since isolation) for populations of *Bradypus* from Bocas del Toro, Panama, explaining 94% of the variation in body size among locality means. Isla Escudo is marked with a solid triangle; the four islands of intermediate age (Cayo Agua, Cayo Nancy, Isla Colón, and Isla Bastimentos) are represented by open circles; and mainland localities and the two youngest islands (Isla Cristóbal and Isla Popa) are denoted by solid circles. A, Almirante; B, Isla Bastimentos; CA, Cayo Agua; CR, Isla Cristóbal; CO, Isla Colón; E, Isla Escudo; N, Cayo Nancy; NU, Nuri; P, Isla Popa; TO, Tierra Oscura; V, Península Valiente.

regression of all geologically independent populations (see above).

To compare our results with other examples of evolutionary change where haldanes are not given (e.g., Gingerich 1983), we calculated the evolutionary rate of change of the Isla Escudo population in darwins (Haldane 1949, p. 55; Futuyma 1998, p. 159). In contrast to haldanes, darwins are calculated per years elapsed between samples, rather than by number of generations; furthermore, they are not expressed in standard deviation units. One darwin is equal to a change by a factor of e (2.718) per million years. Over t years elapsed between samples, the rate of evolutionary change of the continuously varying (quantitative) trait z in darwins is equal to $10^6(\log_e z_2 - \log_e z_1)/t$. Despite these drawbacks and special sensitivity to the interval over which it is measured (see Gingerich 1993, 2001; Hendry and Kinnison 1999), the darwin can be used when the standard deviation and generation time are not known (especially common with fossil taxa) and to compare with such cases. For these calculations, we used greatest length of skull measurements as a measure of overall body size (GLS, from Anderson and Handley 2001) instead of scores on PC I because darwins are based on logarithmic ratios and are thus not amenable to negative numbers, such as in standardized principal component scores. Furthermore, darwins cannot be calculated on traits measured on interval scales (where the zero point is arbitrary; Hendry and Kinnison 1999, p. 1644). We again compared the mean for *B. pygmaeus* on Isla Escudo with the grand mean of the four mainland localities in Bocas del Toro.

RESULTS

Regressions

For insular populations, separate regressions of mean PC I scores on island age and on distance from the mainland were significant ($P < 0.001$, $P = 0.019$, respectively), but a regression on island area was not ($P = 0.337$). Of the two significant regressions, the percent of variation explained (R^2) for the regression on island age was much higher (93.8%) than for the regression on distance (70.0%). The regression on island age passed a pure-error (lack-of-fit) test for linearity ($P = 0.892$), whereas the same test for the regression on distance from the mainland could not be performed due to a lack of true repeats (Draper and Smith 1981). In a multiple linear regression of mean PC I scores on both island age and distance from the mainland, island age was significant ($P = 0.017$), but distance was not ($P = 0.793$).

Including both mainland and insular populations, regressions of PC I on island age and distance were each significant ($P < 0.001$). R^2 was once more higher for island age (93.8%) than for distance (78.6%). The regression on area was not significant ($P = 0.337$). The regression on island age passed a pure-error (lack-of-fit) test for linearity ($P = 0.621$), but the regression on distance did not ($P = 0.036$). In a two-variable multiple regression, island age was significant ($P = 0.002$), but distance was not ($P = 0.571$). The linear regression of mean PC I scores on island age (PC I = $0.103 - 0.000041$ [island age]) shows a clear decrease in body size with island age (Fig. 4).

Regressions for all geologically independent populations

showed the same patterns. The regressions of mean PC I scores onto island age and distance from the mainland were significant ($P < 0.001$, $P = 0.006$, respectively), but that onto island area was not ($P = 0.289$). The regression onto island age passed a pure-error test for linearity ($P = 0.726$), in contrast to the one on distance ($P = 0.006$). In the multiple regression, age was significant ($P = 0.005$) but distance was not ($P = 0.245$). The simple linear regression onto age explained 96.9% of the variation among means of independent populations, compared to an R^2 of 81.3% for distance from the mainland. No step functions or curvilinear relationships were evident in visual examinations of PC I scores versus island age, area, or distance from the mainland or between residuals of the regression on island age versus area or distance.

Genetic Drift

The rate Δ calculated comparing mean PC I scores for the Escudo population versus the grand mean of the mainland populations was 0.0055. The range of values under the neutral expectation is 0.01 to 0.0001, bracketing the observed result. Thus, the magnitude of the observed rate could be due to drift. In contrast, regarding the direction of morphological evolution in the five islands with sloth populations different from the mainland on PC I, the probability of all being smaller in body size was significant ($P = 0.0312$; one-tailed binomial). Likewise, the probability of all four geologically independent populations being smaller was of marginal significance ($P = 0.0625$; one-tailed binomial).

Selection Intensity and Evolutionary Rates

The average body size (PC I) of the population of *B. pygmaeus* on Isla Escudo is 7.02 standard deviations smaller than mainland sloths ($z_2 = -0.2811$, $z_1 = 0.0899$, $s_p = 0.0528$). Given an estimated generation time of 6 years and the 8900-year existence of Isla Escudo, that morphological change equals an evolutionary rate of -0.00473 haldanes. Using the slopes of the regressions of body-size change in standard deviation units onto number of generations for the seven geologically independent populations yielded similar estimates. Least-squares regression gave an evolutionary rate of -0.00428 haldanes, and the reduced-major-axis regression produced an estimate of -0.00434 haldanes ($s_p = 0.0604$ for both). The 95% confidence interval for the slope of the least-squares regression did not include zero (lower limit -0.00333 ; upper limit -0.00522). Even a 99.9% confidence interval on the slope (rate in haldanes) failed to include zero, firmly rejecting the hypothesis of no evolution in body size. Using a range of 0.2–0.7 for heritability, these three regression approaches yielded similar ranges for the standardized linear selection differential (i ; average per generation selection intensity) of -0.0068 to -0.0237 (Escudo vs. mainland populations); -0.0061 to -0.0214 (least-squares regression); and -0.0062 to -0.0217 (reduced-major-axis regression) standard deviations.

Body size in *B. pygmaeus* showed a raw change of -10.69 mm in mean GLS measurements (79.72 mm to 69.03 mm; from Anderson and Handley 2001), corresponding to a change of -0.144 in natural-log units ($\log_e 69.03 - \log_e$

79.72). Such a shift over the approximate 8900-year history of Isla Escudo yielded a rate of 16.18 per million years on a natural-log scale, or 16.18 darwins. Using just the specimens for which PC I scores are also available produced a raw change of -11.19 mm in mean (79.59 mm to 68.40 mm), corresponding to a change of -0.152 in natural-log units, or 17.02 darwins.

DISCUSSION

Biogeographic Hypotheses

Island age explained an overwhelming 94–97% of the variation in body size among populations and revealed a linear relationship (e.g., Fig. 4). Although regressions on distance from the mainland were also significant, pure-error tests indicated that the relationship was not linear. Furthermore, multiple regressions showed that distance from the mainland had no independent effect (nonsignificant partial sums of squares). Distance was significant in simple linear regressions (by itself) only because of its high correlation with island age ($r = 0.845$ for insular populations; $r = 0.891$ for all populations; $r = 0.865$ for independent populations). Island area was never a significant predictor of sloth body size. These patterns were consistent for analyses of the insular populations, all populations, and all geologically independent populations.

Thus, we find no evidence for differing optimal body sizes on different islands. No linear, curvilinear, or step functions were evident between body size and island area. This suggests that the islands are similar enough in size that selective environments for sloth body size do not vary appreciably among the islands. The islands of Bocas del Toro possess areas that are similar to the smallest of those examined by Heaney (1978). The empirical values corresponding to his theoretical curvilinear relationship between optimal body size and island area are taxon and system specific, and a large range of island areas would be necessary to detect such a pattern. Thus, although we cannot discount area as a possible predictor of optimal body size in *Bradypus* on hypothetical islands of a larger range of areas, the data do not support its importance in this particular system, simplifying further interpretations.

Likewise, we fail to detect any true effect of distance from the mainland on sloth body size. As mentioned above, the multiple regressions indicate that the significance of distance in linear regressions of body size onto distance derives not from the independent predictive power of distance but rather to its high—although imperfect—correlation with island age. On average, more distant islands tend to be smaller in area, but the exceptions serve to separate the effects of distance and age. For example, Isla Colón (an old island close to the mainland) harbors small sloths, whereas Isla Popa (a young island close to the mainland) has large ones (both are of similar area). Thus, the current data provide no evidence that the evolution of smaller body size in these populations has been diluted by differential immigration of large-bodied sloths from the mainland (more immigration on closer islands). Although the resolution of the available data is not fine enough to reject dispersal events categorically, these results are not consistent with the expectations of a system

with higher immigration rates for closer islands. Dispersal events may occur, but if so, they are evidently rare.

In contrast to the negative results for island area and distance from the mainland, a clear and easily interpretable pattern is revealed regarding island age. Time since isolation seems to explain the evolution of body size in these sloths: Populations on older islands show smaller average body size. The relationship between body size and age is linear and very tight. It explains 97% of the variation in mean body size among geologically independent populations, with similar values for the other regressions (insular populations and all populations).

Arguments for Selection

We interpret that natural selection drove the evolution of these sloths, for several reasons. Although reductions in body size in insular sloths may have begun as “stunting” (sensu Roth 1992), such a purely phenotypic response to insufficient resources cannot explain the magnitude and diversity of dwarfism found on these islands. The Isla Escudo sloth has diverged in body size much more (seven standard deviations) than seems plausible by stunting alone. Furthermore, the strong relationship between island age and sloth size (Fig. 4) is consistent with directional selection—with each geologically independent island representing a snapshot in time. In contrast, a phenotypic response would be evident in even the youngest islands.

Likewise, although genetic drift can cause the evolution of quantitative characters in the absence of selection (Futuyama 1998, pp. 437–438), the uniform direction of the evolution of body size is not predicted by such models. Although the divergence found here lies within the range possible due only to drift and mutation, failure to reject selection using this test provides only weak evidence against it (Hendry and Kinnison 1999, p. 1648). Indeed, many well-known cases attributed to selection fall below the maximum rate possible under neutral (drift) hypotheses (Schluter 2000). Finally, if all five islands with significantly smaller sloths are considered, we can reject the hypothesis that the consistent direction of body size change (dwarfism in each case) has occurred by chance. With the geologically independent populations, the probability of four events of dwarfism remains small, although only marginally significant. This consistent direction of body size evolution is not predicted under genetic drift.

Selection Intensity and Evolutionary Rates

Empirical comparisons

Interpreting evolutionary rates.—For the reasons outlined above, it seems reasonable to compare the present evolutionary rates and selection differentials to theoretical models and other known empirical cases. The values that we report for body size in *Bradypus* are averages over the roughly 9000-year existence of Isla Escudo (or over the various intervals of existence of the islands). The pattern of smaller sloths with increasing island ages suggests a uniform selection regime, but given the coarse resolution afforded by this study, other scenarios could produce the same pattern. For example, weak or no selection on size in most intervals, but occasional

extreme selection for small size, such as in episodes of aberrant weather, could produce an overall pattern of smaller sloths over time that could not be distinguished from the observed one (see fig. 2 of Hendry and Kinnison 1999). Nevertheless, uniform directional selection pressure for small body size remains the most parsimonious explanation for the observed pattern of dwarfism in the sloths of Bocas del Toro.

Two important factors should be considered in comparisons of evolutionary rates: (1) the interval over which the estimates were measured; and (2) the confidence in the estimate. Several review articles have shown that estimates of evolutionary rate tend to decrease with the interval over which they are measured (Gingerich 1983, 1993, 2001; Kinnison and Hendry 2001). This phenomenon may be due to: (1) exponential assumptions in the calculation of the darwin; (2) mathematical artifacts of plotting a rate versus the time interval over which it was measured; and/or (3) undetected interspersed periods of stasis that dilute estimates measured over longer time intervals (Hendry and Kinnison 1999; see also Schluter 2000, pp. 61–62). Rates in haldanes are not subject to the first problem, and it is thus desirable to separate the effects of intervening periods of stasis from artifactual ones when comparing rates in haldanes. Toward this end, Gingerich (1993, 1994, 2001) proposed log rate versus log interval (LRI) analyses. LRI regressions establish a scaling factor that holds potential for allowing valid comparisons of rates measured over differing time scales. Although the debate regarding evolutionary rates is not yet fully resolved, it currently appears prudent to compare only rates measured over similar time intervals or to take into account a scaling factor in making comparisons of rates measured over differing intervals. Even then, rates in darwins may be difficult to interpret.

Second, the error associated with estimates of evolutionary rates may often be high, but the precision of the estimates can seldom be evaluated because confidence intervals are generally not reported (Hendry and Kinnison 1999). Here, we present confidence intervals for our estimate of evolutionary rate in haldanes (based on the slope of the regression line through all geologically independent populations). Although the precision of that estimate is fairly high (and the rate is certainly greater than zero), all of our estimates are based on a generation time of 6 years for *Bradypus* in the wild. As previously mentioned (see Materials and Methods) *Bradypus* reach sexual maturity at approximately 3 years of age, and birth frequency is about 12 months, but data regarding longevity and survivorship are lacking (Taube et al. 2001). A change in estimated generation time of only one year (e.g., to 5 years), would decrease the resulting evolutionary rate to nearly the lower limit of the confidence interval (to -0.00356 haldanes). However, even with extremely low survivorship and longevity, the plausible generation time should be no lower than 4 years, which yields a rate of -0.00285 haldanes; similarly, a generation time of 8 years would correspond to -0.00570 haldanes. Thus, given the uncertainty regarding generation time, a reasonable range for evolutionary rate (including consideration of the confidence interval of the slope), varies less than a half degree of magnitude (from -0.00191 to -0.00664 haldanes). Furthermore, the precision of the estimates of island age is not known but

should be investigated (C. O. Handley, Jr. and M. Varn, unpubl. ms.). With these caveats, we proceed to compare with recent reviews.

Comparisons.—Unfortunately, few studies measuring evolutionary rates over similar intervals of time are available. Although examples of fossil vertebrates (measured over millions of years) ranged from zero to 26.2 darwins in Gingerich's (1983) review of evolutionary rates, most were low (geometric mean = 0.08 darwins). The evolutionary rate of over 16 darwins in *Bradypus* also greatly surpasses average rates reported for body size in Cenozoic horses, which did not exceed 0.28 darwins (also measured over millions of years; MacFadden 1986). In contrast, the present rates in darwins lie within the range of the few studies for other post-Pleistocene mammals considered by Gingerich (1983; rates in haldanes not available). Gingerich (1983) plotted \log_e rate (in darwins) versus \log_e measurement interval (in years) for the studies he considered, yielding a roughly linear pattern and revealing an apparent scaling factor for such studies. The Bocas del Toro sloths would fall nicely into that relationship. Thus, when measured in darwins, they represent a typical value for the interval of measurement.

In contrast, several recent reviews of evolutionary rates from studies reported in the literature consider only micro-evolutionary time scales. Interestingly, comparisons of the Bocas del Toro sloths with rates calculated in haldanes differ from comparisons with rates in darwins. For example, Hendry and Kinnison (1999) surveyed rates measured over 1–125 years (1–140 generations). Despite being measured over a much longer time interval, the absolute value (0.00434 haldanes) of the evolutionary rate of sloths in Bocas del Toro lies near the center of the cluster of magnitudes they report in haldanes. In contrast, all but a few of those studies showed a rate in darwins faster than that of the sloths. Reconstructed rates for the sloths of Bocas del Toro are also similar to the median of absolute values of rates reported in haldanes (0.00580) in a subsequent, larger review of studies measured over 300 generations or less (Kinnison and Hendry 2001). In contrast, when measured in darwins, the rate of evolution of sloths (16.18–17.02 darwins) pales in comparison with their median of 1151.3 darwins. Likewise, rates measured over about 50 years for insular populations of rodents showed estimates in haldanes similar to the sloths of Bocas del Toro but much larger ones in darwins (Pergams and Ashley 2001). These differences derive partially from the relatively long generation time of sloths (taken into account in calculating haldanes but not darwins), but also highlight the difficulty of interpreting rates measured in darwins (Gingerich 1993; Hendry and Kinnison 1999; see above). Extending the regression line of evolutionary rate (in \log_{10} haldanes) on \log_{10} generations from Kinnison and Hendry (2001)—potentially correcting for the interval over which the rates were measured—the case of *Bradypus* in Bocas del Toro would lie above the regression line, but no farther above it than many of the points used to make the line. Thus, after taking into account a scaling factor, the present rates appear typical, or perhaps even strong, when measured in haldanes.

Our reconstructed selection intensity (i), of -0.0062 to -0.0217 (from reduced-major-axis regression) standard deviations for body size in the Bocas del Toro sloths is weak

compared with some strong selection intensities that have been measured in the field in short-term studies. For example, the selection intensity on corporal measurements of one of the Galápagos finches, *Geospiza fortis*, ranged 0.21–0.30 during an intense drought, but was less or even opposite in trend direction in other years (Grant 1986; Futuyma 1998). Selection intensities of one or two standard deviations per generation in quantitative traits under natural conditions are not uncommon (Endler 1986, pp. 208–211), but such strong directional selection is seldom maintained for many generations (Hendry and Kinnison 1999).

Clearly, scaling of evolutionary rates remains a controversial area of much current research. Perhaps the most salient feature of the present analyses regards the consistency of the pattern. Because the time series of sloths of Bocas del Toro provides an example of linear decrease in body size with increasing island age, they likely represent a system whose estimates of evolutionary rates and selection intensity are not diluted by intervening periods of stasis. Similar rates in haldanes have been reported over short time intervals (<100 years; Pergams and Ashley 2001). What is noteworthy is that such rates are evidently sustained in the sloths of Bocas del Toro. We detected no slowing of evolutionary rates in the four geologically independent populations of dwarf sloths (regression of \log_e haldanes on \log_e island age following Gingerich 1993, 2001; $P = 0.692$, $R^2 = 9.5\%$). Thus, this example may represent continuity between micro- and macroevolutionary processes, as the differentiation in body size has been an integral part of the speciation process in the oldest insular population (see Anderson and Handley 2001). The archipelago of Bocas del Toro clearly constitutes an outstanding system for similar studies of other taxa, as well as complementary work examining genetic differentiation among the various populations.

It is noteworthy that sustained strong selection would likely lead to population extinction, especially in small populations (Bürger and Lynch 1995). If compared with selection intensities and evolutionary rates in haldanes measured over very short time frames, selection on the sloths of Bocas del Toro was not especially strong (but note complications of comparing across intervals of measurement). The empirical rates here, at least as measured over thousands of years between samples, lie well below what are considered maximal sustainable rates (Bürger and Lynch 1995; Hendry and Kinnison 1999).

Finally, the dependence of body size in sloths on time (years since isolation) highlights the fact that when more than one case of dwarfism or gigantism is present in the same taxon, the largest absolute divergence (rather than the average divergence) best reflects the evolutionary potential of that taxon for change in body size. Unfortunately, such an estimate may suffer from higher error because of smaller sample sizes. However, when possible, we suggest that synthetic treatments of the evolution of body size on islands (e.g., Lawlor 1982; Brown et al. 1993) should use maximal divergence in body size for each taxon in further analyses.

Comparisons with theory

Models from population genetics describing the evolution of quantitative characters predict a morphological shift under

changing environmental conditions such as those experienced by the sloths of Bocas del Toro (Lande 1980, 1986; change in the "individual fitness function" of Kirkpatrick 1982). Furthermore, environmental change that fosters a change in selection pressures can promote a morphological shift of several standard deviations in a small, isolated population within "a few thousand generations" (Lande 1980, p. 476). The shift of seven standard deviations in body size in the *Bradypus* of Isla Escudo probably occurred in approximately 1500 generations, falling within the predictions of theory.

However, the linearity of the response does not fulfill theoretical expectations. If a particular smaller body size is optimal on islands, then selection should be strongest immediately after island formation, when the population is farthest from the new adaptive peak. Body size would then asymptotically approach the equilibrium (optimal body size) over time, as selection intensity decreased. This is clearly not the case in the *Bradypus* from Bocas del Toro, where sloths from the youngest islands (Isla Popa and Isla Cristóbal) are not significantly different in body size from mainland samples. Skulls of sloths from those islands do appear slightly more gracile than those of mainland individuals, however (Anderson and Handley 2001). One possible explanation is that the basis for changes in optimal body size lies with the disappearance of other species in the community, which does not occur immediately upon island formation. Alternatively, the adaptive peak for optimal body size might shift as a function of the population's average body size (presumably by some frequency-dependent mechanism; see Bürger and Lynch 1995). Because of these discrepancies, future work is necessary to reconcile the present results with theory or perhaps develop theoretical models regarding conditions under which morphological divergence would be linear for thousands of generations in new selective environments.

Possible Selective Forces

Changes in diet, resource limitation, and absence of mainland predators may all have contributed to selection for smaller size. Many small sloths on the islands, and all from Isla Escudo, were collected in mangroves, a habitat that *Bradypus* usually does not inhabit on the mainland. Thus, some sloths on the outer islands, and certainly those on Isla Escudo, probably eat primarily *R. mangle* leaves, which are coarse and leathery (Everett 1981). Mainland sloths eat the leaves of many terra firma forest trees, especially those of *Cecropia*, a short-lived successional tree with tender leaves protected by ants rather than by chemicals or lignin (Carroll 1979; Everett 1981). Therefore, a poorer food source may have interacted with evolutionary processes in these sloths.

Based on what is known of folivore biology, however, one would not necessarily predict smaller body size given a poorer food source. Principles of energetics and allometry of body proportions (Grand 1978; McNab 1978) demonstrate that in primates, for example, the largest species must acquire protein from leaves because they cannot gather enough insects (which are high in protein) and fruits are too low in protein (Hladik 1978). Furthermore, the relatively large storage capacity of herbivore intestines is related to their need to retain large volumes of plant matter for long periods of time, to

accommodate the fermentation process (Parra 1978). Smaller herbivores, in fact, "are faced with a paradox, that is as their size is decreased their energy requirements per unit weight are increased and their fermentation contents per unit weight are decreased" (Parra 1978, p. 208).

Even though an energetically poorer food source might favor larger body size, a smaller sloth's absolutely lower energy requirements could allow survival and successful reproduction with less total resources (Roth 1992). Large mammals are often resource limited on islands, favoring smaller size (Heaney 1978; Lomolino 1985; Roth 1992). Conversely, larger size may be advantageous for greater digestive efficiency and in antipredator defense on the mainland (see also discussion in Alder and Levins 1994). Several species of felids that prey on *Bradypus* are present on the mainland but have not been observed on the outer islands of Bocas del Toro and are assumed to have been extirpated subsequent to isolation (Handley 1993, unpubl. data). Additional studies are clearly called for, investigating possible relationships between optimal body size and metabolism, diet, and community composition.

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