Body Size Evolution in Snakes: Evidence from Island Populations

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The current literature reports divergent conclusions on the patterns of body size change in island snakes. I reviewed body size data in the published literature and tested the effects of island biogeographic variables on such changes. I found that none of the physiographic variables (island area, island age, distance to mainland, and latitude) was important in determining changes in size of island snakes. Additionally, a current hypothesis of phylogenetic history had no effect on changes in body size. Rather, the proportional change in body size of island snakes was bimodal, consistent with a diet alteration hypothesis that suggests that snake body size is principally influenced by prey size and that island snakes encounter prey that are larger or smaller in size compared with those on the mainland. Also, snakes that became small on islands did so to a relatively greater degree than those that became large. Ontogenetic changes in foraging strategies appeared to explain this pattern. The distribution of gigantic and dwarf snake populations on islands differed significantly between the families Viperidae and Colubridae. The foraging style of colubrids, specifically nest-robbing behavior, may predispose these species to become larger on islands. Numerous colubrid (and one elapid) species attain their largest sizes on islands that also support nesting seabirds, whereas dwarfed populations consume mainly squamates.

BODY size is a conspicuous trait that is strongly associated with the life history of an organism (Tinkle, 1962; Ankney and Mac-Innes, 1978; Charnov, 1993). Because of this, ecologists have long been interested in the effects of size on such life-history variables as age at first reproduction, reproductive output, and survival (Blueweiss et al., 1978; Stearns, 1983; Shine, 1994). Less emphasis has been directed toward investigating the determinants of body size (but see Willemsen and Hailey, 1999). In reptiles and other vertebrates, geographic variation in body size is well documented (Lindsey, 1966; Gould and Johnston, 1972; Parker and Plummer, 1987) and suggests that regional environmental differences may cause phenotypically plastic changes and/or select for local genetic adaptation.

Island populations have provided a model for comparative research in ecology and evolution (Gorman, 1968; Gotelli and Graves, 1990; Losos, 1995) because of different, and sometimes predictable, body sizes compared with mainland relatives (Mertens, 1934; Carlquist, 1965). In fact, distinct patterns of change in body size for a variety of taxa have spurred development of hypotheses that explain trends of insular gigantism and dwarfism across broad taxonomic groups (e.g., Foster, 1964; Case, 1978; Lomolino, 1985).

Case (1978) inventoried body size data for snakes and found a tendency for dwarfism on islands. He proposed that changes in food availability on islands could explain these decreases in size. However, more recent studies describe populations with larger body size on islands than mainlands (Schwaner and Sarre, 1988; Forsman, 1991b; Mori, 1994). In fact, some authors now claim insular gigantism as the rule for snakes (e.g., Rodriguez and Drummond, 2000).

Regardless of the direction of size change on islands, island biogeography theory can assist in understanding the influences on such changes by predicting the relative magnitude of change. The theory predicts an increase in species diversity as island area increases and/or distance from mainland decreases (MacArthur and Wilson, 1967). Hence, the number of interspecific competitors should increase with island area and decrease with distance from mainland. Additionally, island biogeography theory states that colonization (or resistance to extinction) is affected by the degree of isolation of an island (measured as the distance from a source). Body size is thought to be an important variable in predicting the ability of an organism to disperse to, and compete within, islands (Schoener, 1970; Roughgarden, 1995). For example, in *Anolis*, single-species islands support species of an optimum, moderate size (Roughgarden, 1995). Subsequent colonists are predicted to be of a larger average size and the resident is predicted to decrease in size to minimize competition with the large species as it evolves toward the optimum size (taxon cycle; Roughgarden and Pacala, 1989). Alternatively, both the resident and colonist may undergo simultaneous shifts in body size, one becoming larger and the other smaller to reduce interspecific competition (character displacement model; Losos, 1992). Further, as island

area increases and more complex communities are established, a greater number of size classes (i.e., ecomorphs; Williams, 1983) are possible (e.g., see Rodriguez-Robles and Greene, 1996). Competition and colonization ability may influence the relative magnitude of body size changes of other squamates on islands, like snakes. If so, then, all else being equal, I expected a positive relationship between island area and changes in snake body size, and a negative relationship between island distance (from mainland) and changes in snake body size.

A relationship between body size and latitude has been noted for many organismal groups (Mayr, 1956). Previous work on snakes (Lindsey, 1966; Ashton, 2001) suggests that members of this group are smaller at higher latitudes (i.e., the opposite of Bergmann's rule). Thus, I predicted latitude to have a negative relationship with the relative magnitude of snake body size changes.

Island age may also modify body size distribution within a species' range. For example, if one assumes that colonization rates of islands have not changed through evolutionary time, populations on older islands will have had a greater chance to diverge from the source population, on average, compared with those on younger islands. For island communities isolated in situ (e.g., land-bridge islands), island age, as measured by sea level rise, should be a direct measure of time since isolation. Populations evolving in isolation for a longer time will have more of an opportunity to diverge in body size from the source population (Soule, 1966). If changes in body size are influenced by the amount of time a population has been in isolation, a positive relationship is expected between island age and changes in snake body size.

Alternatively, the selective response to local prey availability could explain the difference in body size of snake populations on islands relative to the mainland (Barnett and Schwaner, 1985; Forsman, 1991b; Madsen and Shine, 1993; Rodriguez-Robles and Greene, 1996). Charnov's (1976) optimal diet model suggests that the most profitable prey-type should be the one most often consumed. Because island environments typically have reduced prey diversity relative to the mainland, altered prey communities are expected on islands. The consensus of previous authors is that prey consumed most often by adult snakes on islands differ in size compared with prey consumed by the same species on the mainland (Case, 1978; Schwaner, 1985). Decreased average prey size on some islands is associated with increased abundance of squamates and decreased abundance of birds and mammals (Case, 1978; Hasegawa and Morigu-

chi, 1989). Other islands may exhibit increased average prey size because of increased availability of seabird chicks (Schwaner and Sarre, 1988; Kohno and Ota, 1991; Mori, 1994). If prey size is the primary factor determining snake size on islands, and if islands conform to one of two types mentioned above, then the proportional change in body size of snakes on islands should form a bimodal distribution. I term this the ''diet alteration hypothesis.''

In this review, I examine the influence of island area, island age, distance to mainland and latitude on changes in body size in island snake populations. I examine these variables first using unadjusted data and then adjust the data to account for the effects of a current hypothesis of phylogenetic relationships. Finally, I use patterns in the magnitude of dwarfism and gigantism to assess the role of the diet alteration hypothesis in explaining changes in body size of island snakes.

Materials and Methods

I reviewed data describing body sizes of 76 mainland and island populations of 30 species of snakes representing the Boidae, Colubridae, Elapidae, and Viperidae (Appendix 1). For each of these populations, I determined island age, area, distance to mainland, and latitude. When values for these variables were not readily available in the literature, I estimated them from methods described below.

I used body length as an estimate of body size in all analyses. Although some authors argue that body mass is the best indicator of body size (e.g., Hedges, 1985), length is correlated with body mass (Kaufman and Gibbons, 1975; Guyer and Donnelly, 1990) and is less sensitive than mass to short-term changes in body condition, prey consumption, and reproductive status (Seigel and Ford, 1987). Body length can be reported as a mean or maximum and may include all or part of the body (e.g., total length or snout–vent length, SVL). Because the most consistently reported measure was maximum SVL (37 of 76 populations), I used this variable to estimate body size. I encountered three other measures of length among the remaining 39 populations surveyed: mean SVL of the five largest adults ($n = 6$), mean SVL of the 10 largest adults ($n = 12$), and mean SVL for all adults ($n = 21$). I assumed the first two to be functionally identical to maximum SVL. For studies reporting mean SVL for all adults, I estimated maximum SVL from an equation generated from a subset of data for which both maximum and mean SVL measures were reported (17 species from La Sel-

va, Costa Rica [C. Guyer and M. A. Donnelly pers. comm.] and six populations from the literature). A regression of maximum SVL on mean SVL from these data resulted in a linear relationship (max SVL = 1.2 × mean SVL + 5.0) in which mean SVL explained 94% of the variation in maximum SVL. From this regression line I predicted maximum SVL for the 21 populations for which only mean SVL was known.

Island area (km²) was estimated by overlaying a translucent mat containing a 1 × 1-mm grid system on a chart (see Appendix 2 for the list of charts used). The number of 1 × 1 mm blocks contained within an island was counted; those blocks bisected by the island outline were estimated to the closest half block. Block area was determined using the scale on the map and, when multiplied by the total number of blocks within the outline, gave an estimate of island area. I used a divider to measure distance in kilometers from the mainland to the island. Latitude was measured at the geometric center of each island.

Island age was estimated for land-bridge islands (those islands once connected to the mainland and isolated by sea-level rises) from minimum ocean depths between the mainland and the island (Defense Mapping Agency [DMA] hydrographic charts compared with the rate of post-Wisconsin eustatic sea level rise; Rawlinson, 1974; Wilcox, 1978; Devoy, 1987). Milliman and Emery (1968) have established general features of these sea level changes. From the curve generated by these authors (sea level as a function of time), I estimated island age from minimum ocean depths. This technique ignores geologic processes such as crustal uplift and coastal erosion that may influence date of island isolation (Gastil et al., 1983), but this assumption is reasonable for two reasons. First, coastal erosion is not likely to influence isolation significantly within the time scale of sea level isolations estimated in this study (< 10,500 yr). Second, of the 14 islands with ages estimated with the sea level curve, the majority (86%) occur in regions with either stable tectonics (Jennings, 1971) or with rates of crustal movement that are not likely to affect island isolation within this time frame (Jacobs et al., 1959; Strahler, 1998).

Deep-water (oceanic or volcanic) islands presented additional difficulties in my ability to estimate age of origin. Ages of most islands of the Caribbean and Gulf of California were estimated from potassium/argon dates of base rock (e.g., Gastil et al., 1983; Lonsdale, 1989; Lewis and Draper, 1990). Other methods included employment of Milliman and Emery's (1968)

curve (see above) and published geologic data (Kaye, 1959; Schoenherr et al., 1999).

Several islands were quite small (< 3 km²) and located adjacent to a larger island (10 of the 76 populations). The source of propagules for these satellite islands is typically an adjacent larger island (Soule, 1966; MacArthur and Wilson, 1967). Indeed, phylogenetic information confirms this for some of these satellite populations (e.g., Kohno and Ota, 1991). Further, two of the adjacent larger "source" islands were greater than 67,000 km² in size. Therefore, populations on these satellite islands were considered to originate from "mainland" populations on the nearest larger island.

I used path analysis to test the influence of island biogeographic variables on body size changes in snake populations. This technique requires an a priori model to test the effect of predictor (independent) variables on one or more criterion (dependent) variables. Path analysis is similar to multiple regression in that both techniques attempt to determine the effect of one independent variable on a dependent variable, while all influences of other independent variables are held statistically invariant (Sokal and Rohlf, 1995). Path analysis differs from multiple regression in requiring the use of standardized partial regression coefficients (i.e., path coefficients). Therefore, path analysis is favored over multiple regression when the independent variables are measured on different metrics (Sokal and Rohlf, 1995), as is the case with the current study. My path model estimated the effect of five predictor variables (island area, island age, distance to mainland and latitude) on percent change in body size on islands. This analysis was performed on all 30 species of snakes. For those species in which data from multiple island localities were available, I calculated mean values for all predictor variables for that species because these localities were relatively close to one another.

I employed network autocorrelation to identify and remove the influence of phylogenetic history on body size in snakes (Cheverud et al., 1985). Unlike the commonly used independent contrasts method (Felsenstein, 1985), which uses paired comparisons, network autocorrelation compares branching sequences (represented by a taxon-taxon matrix) with trait variation (Miles and Dunham, 1992). Also, this technique is superior to the independent contrasts method when tree resolution is not complete or branch lengths are unavailable (Gittleman and Luh, 1992), both of which were true of the tree used in this study. Finally, network autocorrelation provides adjustments to trait values that are
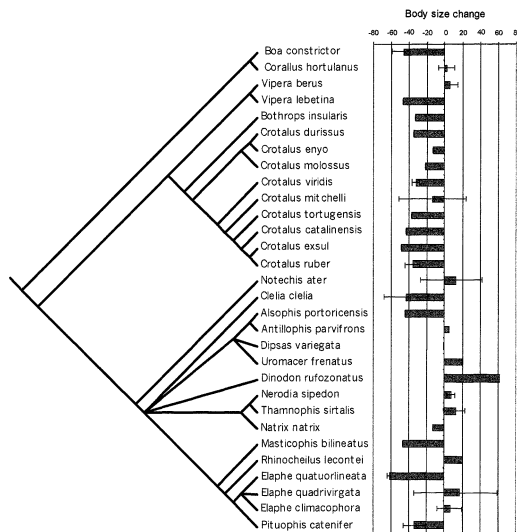
Fig. 1. Phylogenetic hypothesis of the relationships among snake taxa used in this study. The branching pattern is based on published molecular phylogenies (Lawson, 1987; Kluge, 1991; Densmore et al., 1992; De Queiroz and Lawson, 1994; Nilson et al., 1994; Heise et al., 1995; Lopez and Maxson, 1995; Keogh, 1998; Crother, 1999; Parkinson, 1999; Rodriguez-Robles and DeJesus-Escobar, 1999; Parkinson et al., 2000; Murphy et al., in press). The graph indicates mean percent size change for each species: y-axis = mean percent change in maximum size on island compared with maximum size of mainland population. For species with multiple island populations, the range in percent size change (about the mean) is indicated with T-lines.

appropriate for use in multiple regression or path analyses.

I used recent phylogenies based on molecular data to produce a phylogenetic tree representing the current hypothetical branching sequence of the taxa in this study (Fig. 1). This tree was used to generate a pairwise connectivity matrix for the 30 species of snakes.

I calculated percent change in body size as [|log(island max SVL)—log(mainland max SVL)|/log(mainland max SVL)] × 100. I used the largest individual, irrespective of sex, for each species from island and mainland populations. Log-transformations were used to ensure independence of variances (Miles and Dunham, 1992). I then used residuals from the network autocorrelation analysis as "phylogeny-free" data and repeated the path analysis described above.

Path (and multiple regression) coefficients may be biased if predictor variables are significantly intercorrelated (collinearity, Petraitis et al., 1996). The association of the predictor variables to each other can be assessed using correlation coefficients and collinearity tests (variance inflation factors [VIFs] and condition indices; Shannon and Davenport, 2000). VIFs indicate whether standard errors of path coefficients are inflated because of effects of collinearity; high VIFs indicate potentially inflated confidence intervals for path coefficents. Condition indices determine whether path coefficients are inflated because of collinearity of the predictor variables; high condition indices suggest potential biases in the value of the path coefficients (Shannon and Davenport, 2000).

I tested each of the predictor variables for normality using a Shapiro-Wilk test. Based on these results, island area, distance to mainland, and island age were log-transformed. Transformation improved the distributions of island area and distance to mainland as evidenced by a lack of significance upon rerunning a Shapiro-Wilk test. Island age was still significantly non-normal after the transformation. This was likely because of the large variation in isolation times between land-bridge and deep-water (oceanic or volcanic) islands. I used transformed data for island age to maintain consistency.

To further investigate the effect of evolutionary history on body size changes in these island snake populations, I tested for taxonomic biases in the direction of body size changes between two families for which I had sufficient data: Colubridae and Viperidae. I used a Fisher's exact test to compare the distribution of insular gigantism and dwarfism within these two families (Zar, 1984).

To evaluate the distribution of the proportional change in body size of island snakes, I tested the observed distribution against a normal distribution using a Shapiro-Wilk test for normality (Zar, 1984). The null hypothesis for this test was a normal distribution because this distribution indicates that snake populations become small or large based on chance colonization by small or large propagules from the mainland source.

The Fisher's exact test was calculated using SAS (vers. 6, 4th ed. Vols. 1–2, Statistical Analysis Systems Institute, Inc., Cary, NC, 1990, unpubl.), whereas all other analyses were performed using SPSS (SPSS Inc., vers. 10.0, Chicago, 1999, unpubl.) statistical software, and included correlation, tests of normality, multiple regression, and collinearity diagnostics (condition indices and VIFs). For correlation matrices α was adjusted (Bonferroni method) to account for multiple tests, with α′ set at 0.003 and α set at 0.05 (Zar, 1984). For all other tests α was set at 0.05.
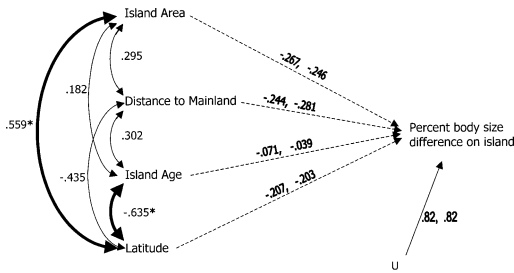
Fig. 2.   Path diagram generated from the analysis of 30 snake species and the predictor variables listed in Appendix 1. Correlations between predictor variables are to the left of these variables, path coefficients are to the right. Bolded double-headed arrows and * indicate significant correlations (with Bonferoni adjustment $P < 0.003$). Each direct path (depicted by one-headed arrows) has two values. The first value is the unadjusted path coefficient, and the second is the ''phylogeny-free'' path coefficient using network autocorrelation. Solid lines indicate positive paths; dotted lines indicated negative paths. U represents the path for unexplained variation.

RESULTS

Overall, the path analysis model explained a nonsignificant proportion of the variance in body size change ($R^2 = 0.18$, $F = 1.06$, df = 5, $P = 0.407$). The model did not show significant paths from any of the predictor variables, indicating that none of the proposed variables from island biogeographic theory explained a significant amount of variation in the absolute value of percent size change on islands (Fig. 2). The path coefficient for island area showed the largest beta weight ($\beta = -0.267$, $P = 0.25$). Significant correlations were documented between latitude and island area ($R = -0.559$, $P = 0.001$) and latitude and island age ($R = -0.635$, $P < 0.001$).

Collinearity of predictor variables did not influence path coefficients. All VIFs for the predictor variables were less than 10, the level that indicates significant collinearity among variables (Myers, 1990). Additionally, all condition indices, another measure of collinearity, were below values indicating significance (30; SAS, vers. 6, 4th ed. Vols. 1–2, Statistical Analysis Systems, Inc., Institute, Cary, NC, 1990). The largest condition index among all predictor variables was 29.0.

I used network autocorrelation to remove the effect of phylogeny on the dependent variable. Unadjusted (treating each species as an independent unit) and ''phylogeny-free'' (via network autocorrelation) path coefficients for all of the predictor variables were similar, indicating phylogenetic effects were insignificant (Fig. 2). This is corroborated by the fact that network
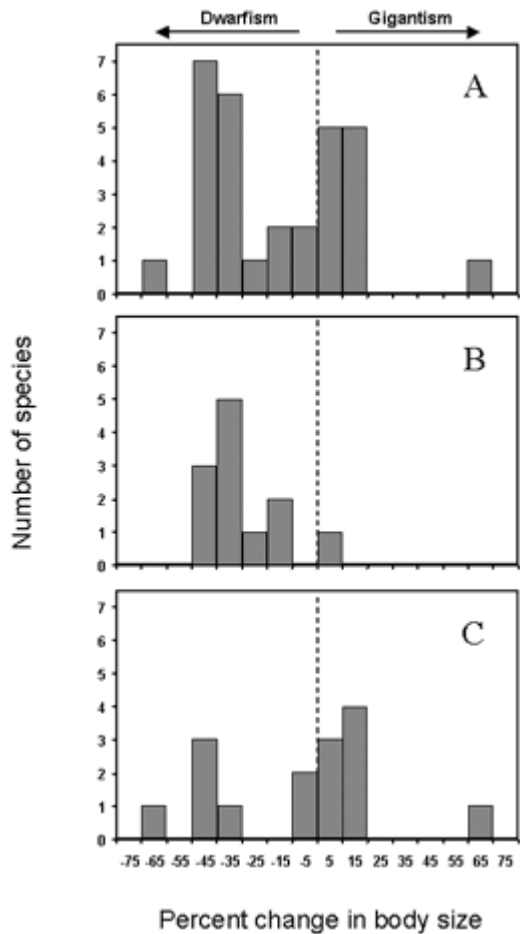

Fig. 3.   Frequency distribution of island body size changes of the 30 snake species used in the study. **A** = all species, **B** = Viperidae, **C** = Colubridae.

autocorrelation estimated that less than 5% of the size difference was explained by phylogeny ($\rho = -0.20$, $P > 0.25$, $R^2 = 0.046$).

The frequency distribution of the proportional change in body size of island snakes was significantly different from a normal distribution (Shapiro-Wilk statistic = 0.925, $P = 0.05$). Instead, this distribution was bimodal (Fig. 3A). Additionally, viperids typically decreased in SVL (11 species decreased, one increased) relative to mainland populations, whereas colubrids showed no consistent pattern (seven species decreased, eight increased; Fisher's exact $P = 0.014$, df = 1; Figs. 1, 3B–C, see Appendix 1 for population values).

DISCUSSION

Path analysis failed to show a strong influence of island area or distance to mainland on the

amount of body size change in island snake populations. Nearly identical path coefficients were found before and after controlling for the effects of evolutionary history on body size changes. The theory of island biogeography predicts an increase in species diversity with increasing area either directly because of an increase in target size or indirectly because of an increase in habitat heterogeneity (MacArthur and Wilson, 1967). Therefore, increases in area should increase the number of potential competitors and perhaps the effects of competition. Likewise, decreases in distance to mainland should increase the number of potential competitors. The fact that the path analysis did not show strong influences of island area or distance to mainland suggests that competition was not an important influence on these body size changes even when phylogenetic history is accounted for. This is in contrast to *Anolis* (Schoener, 1970; Williams, 1983), a genus in which competition has been shown to be important in determining patterns of body size and ultimately community structure. Additionally, because colonization ability should be affected by the degree of isolation of an island (MacArthur and Wilson, 1967), these results suggest that changes in body size are not associated with colonization ability. Hence, my results suggest that body size in island snakes does not appear to be shaped by competition or colonization ability. Confirmation of these ideas awaits experimental testing.

Extinction associated with vicariant events might also play a role in producing patterns of change in body size of island snakes. MacArthur and Wilson's (1967) original model predicts a negative relationship between extinction rate and area. If vicariance creates islands on which extinction rates are elevated relative to the mainland, I would expect, but did not find, a negative relationship between island area and changes in snake body size. Alternatively, extinction associated with human activities may be exacerbated on islands. For example, Pregill (1986) convincingly showed that human-induced extinction is primarily responsible for the pattern of Holocene dwarfism in some insular squamates. If these, and potentially other vertebrate prey (e.g., mammals: Lomolino, 1985), experience decreases in size on islands, dwarfism in carnivores, like snakes, may be favored, an idea consistent with my observations of greater numbers of dwarfed species and greater magnitude of dwarfism when it occurs. However, this explanation does not explain those populations that have increased in body size compared with their mainland source population unless human-induced extinctions occasionally result in increased average prey size. Humans also may play a direct role in affecting extinction probabilities of snake populations (e.g., Butterfield et al., 1997). Because this effect may be greatest for larger snake species, extinction caused directly by humans does not appear to explain the overall pattern of dwarfism and gigantism that I observed in insular snakes.

A hypothesis consistent with a bimodal distribution to body size change in island snakes is that insular prey are typically larger or smaller than those on the mainland and that prey availability exerts a strong selective pressure on snake body size (diet alteration hypothesis). Insular snakes that exhibit a smaller size (relative to the mainland) do so to a greater extent (mean = 34% smaller than on mainland) than those that exhibit a larger size (mean = 15% larger than on mainland). Snakes often have distinct ontogenetic shifts in prey throughout their lives, largely because they are gape-limited predators (Godley, 1980; Mushinsky et al., 1982). Many viperids, as well as other snakes, consume squamates as juveniles and rodents as adults (Saint Girons, 1980). The behavioral and morphological traits necessary to consume small prey items are, therefore, characteristic of many snakes. It may be easier for snakes to retain a small body size and consume small prey on islands than it is for snakes to evolve a large size and consume large prey on islands. Of the species used in this study, dwarfism on islands was most prevalent within viperids, whereas about half of boid and colubrid species fit this pattern. However, nearly all of the viperids (nine of 12) were within the genus *Crotalus*. More non-*Crotalus* viperids need to be examined to determine whether the trend of insular dwarfism is family or genus specific.

Most of the snakes that became larger on islands were colubrids (eight of 11) known to consume seabird chicks (Hasegawa and Moriguchi, 1989; Kohno and Ota, 1991; Mori, 1994) a prey rarely consumed by dwarfed island species. Therefore, nest-robbing may predispose this group to become large on some islands. Snake species that attained a smaller size on islands (e.g., rattlesnakes) rarely exhibit nest-robbing as a foraging behavior (Klauber, 1956). Further, the seasonality of large prey, such as seabird chicks, may have been a major selective pressure for a larger body size in the elapid *Notechis ater* because the largest snakes are better able to consume large, fast-growing chicks (Schwaner and Sarre, 1988). Finally, the absence (or scarcity) of intermediate-sized prey on some islands may select for large snakes capable of accumulating fat reserves and thereby, sur-

viving until seasonal prey become available (e.g., when seabirds return for nesting; Schwaner and Sarre, 1988; Hasegawa and Moriguchi, 1989; Mori, 1994).

Case's (1978) review reported a trend of dwarfism in island snakes, whereas more recent studies have documented island populations that attain large body sizes (e.g., Schwaner and Sarre, 1988, 1990; Kohno and Ota, 1991). This review indicates that dwarfism is the more common event but that both trends are exhibited by a significant number of snakes. Among the advanced snake families, dwarfism describes some groups (Viperidae) more than others (Colubridae). If published literature is representative of the overall pattern of body size change on islands, then there must be strong pressure to modify body size on islands. However, if species for which size does not change between islands and mainlands are underrepresented in published literature (a likely possibility), then additional data will be needed to understand how universal the pressures associated with body size change are for island snakes. Nevertheless, the existence of species capable of becoming larger on some islands and smaller on others (e.g., *Elaphe quadrivirgata*, *Notechis ater*, and *Crotalus mitchelli*) indicates that some insular size changes may be more parsimoniously explained by phenotypic plasticity rather than direct responses to selection (Madsen and Shine, 1993). Empirical tests designed to elucidate the proximate influences on snake body size (e.g., Bronikowski, 2000) should help to clarify these patterns.

ACKNOWLEDGMENTS

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APPENDIX 1. ISLAND BIOGEOGRAPHIC DATA COMPILED FOR THE 76 POPULATIONS (30 SPECIES) OF SNAKES USED IN THIS STUDY.

Source	Species	Island	Island type/△	% size difference	Area (km²)	DTM~ (km)	Age (K years)	Latitude
Boidae								
Schwartz and Henderson, 1991	*Boa constrictor*	Dominica	D	−40.00	750[b]	440[e]	2600[i]	15.25[n]
Zweifel, 1960		Maria Magdalena	D	−58.88	84[b]	104.6[b]	4500[i]	21.30[n]
Schwartz and Henderson, 1991		St. Lucia	D	−40.00	617[b]	305[e]	18400[i]	13.53[n]
Murphy, 1997	*Corallus hortulanus*	Trinidad	L	10.00	4769[b]	11[r]	6.5[j]	10.24[e]
Schwartz and Henderson, 1991		Grenada	D	>5.88	311[b]	160[b]	54000[i]	12.05[e]
Schwartz and Henderson, 1991		St. Vincent	D	−5.88	355$	267[a]	3500[i]	13.12[e]
Schwartz and Henderson, 1991		Grenadines	D	−5.88	34$	178[a]	38000[i]	12.39[e]
Colubridae								
Schwartz, 1966	*Alsophis portoricensis*	Mona	D	−44.75	52[a]	70[e]	5000*	18.05[n]
Henderson et al., 1988	*Antillophis parvifrons*	Ile de la Gonâve	D	5.09	406[g]	56[b]	38000[h]	18.48[e]
Schwartz and Henderson, 1991	*Clelia clelia*	Grenada	D	−20.00	311[b]	160[b]	54000[i]	12.05[e]
Murphy, 1997		Trinidad	L	−67.76	4769[b]	11[r]	6.5[j]	10.24[b]
Kohno and Ota, 1991	*Dinodon rufozonatus*	Nakanokamishima	D	60.98	0.35†	51†	6000[k]	24.11†
Peters, 1960	*Dipsas variegata*	Trinidad	L	−0.31	4769[b]	11[r]	6.5[j]	10.24[b]
Hasegawa and Moriguchi, 1989	*Elaphe climacophora*	Oh-shima	D	6.18	90.98†	27.2[e]	50[k]	34.44[e]
Hasegawa and Moriguchi, 1989		Kozo-shima	D	−6.64	18.37†	58.3[e]	50[k]	34.12[e]
Hasegawa and Moriguchi, 1989		Nii-jima	D	7.88	22.84†	44.3[e]	50[k]	34.23[e]
Mori, 1994		Kammuri-jima	L	19.07	0.23†	10.44[e]	20[k]	35.41†
Hasegawa and Moriguchi, 1989	*Elaphe quadrivirgata*	Oh-shima	D	−33.27	90.98†	27.2[e]	50[k]	34.44[e]
Hasegawa and Moriguchi, 1989		Kozo-shima	D	25.45	18.37†	58.3[e]	50[k]	34.12[e]
Hasegawa and Moriguchi, 1989		Tadanae-jima	D	59.31	0.1†	1.39[e]	50[k]	34.12[e]
Hasegawa and Moriguchi, 1989		Nii-jima	D	20.10	22.84†	44.3[e]	50[k]	34.23[e]
Hasegawa and Moriguchi, 1989		Mikura-jima	D	13.96	19.69†	100[e]	50[k]	33.55[e]
Clark, 1967	*Elaphe quatuorlineata*	Ios	D	−60.38	111[b]	147[e]	11.75[p]	36.42[b]
Clark, 1967		Paros	D	−64.23	200[b]	1117[e]	1.95[p]	37.03[e]
Lowe and Norris, 1955	*Masticophis bilineatus*	San Esteban	D	−47.06	43[c]	37[c]	1600[c]	28.42[e]
Madsen and Shine, 1993	*Natrix natrix*	Hallands Väderö	L	−13.82	2.6†	3†	5[z]	56.27†
King, 1989	*Nerodia sipedon*	Middle Bass	L	1.86	3[d]	9.5[d]	4[l]	41.41[e]
King, 1989		North Bass	L	3.22	2.8[d]	13.3[d]	4[l]	41.43[e]
King, 1989		Pelee	L	4.45	40.91[d]	13.5[d]	4[l]	41.47[e]
King, 1989		Kelly's	L	9.40	11.69[d]	5.1[d]	4[l]	41.36[e]
King, 1989		Johnsons	L	10.88	0.27[d]	1.1[d]	4[l]	41.30[e]

APPENDIX 1.   CONTINUED

Source	Species	Island	Island type/△	% size difference	Area (km²)	DTM~ (km)	Age (K years)	Latitude
King, 1989		Middle	L	10.88	0.21[d]	15.6[d]	4[l]	41.41[e]
Klauber, 1946; Klauber, 1949	*Pituophis catenifer*	South Coronado	L	−22.19	5.5[e]	14[e]	8.3[j]	32.23[q]
Klauber, 1946; Klauber, 1949		Santa Cruz	L	−46.68	96[f]	30[f]	23000[f]	34.00[f]
Grismer, 1990	*Rhinocheilus lecontei*	Cerralvo	D	19.81	160[c]	11[c]	5000[c]	24.10[e]
King, 1989	*Thamnophis sirtalis*	Middle Bass	L	−0.26	3[d]	9.5[d]	4[l]	41.41[e]
King, 1989		North Bass	L	0.24	2.8[d]	13.3[d]	4[l]	41.43[e]
King, 1989		Pelee	L	3.91	40.91[d]	13.5[d]	4[l]	41.47[e]
King, 1989		East Sister	L	18.12	0.26[d]	19.1[d]	4[l]	41.49[e]
King, 1989		West Sister	L	20.79	0.28[d]	13.4[d]	4[l]	41.44[e]
King, 1989		Kelly's	L	21.13	11.69[d]	5.1[d]	4[l]	41.36[e]
King, 1989		Middle	L	22.46	0.21[d]	15.6[d]	4[l]	41.41[e]
Henderson et al., 1988	*Uromacer frenatus*	Ile de la Gonâve	D	19.35	406[g]	56[b]	38000[h]	18.48[e]

Elapidae

Source	Species	Island	Island type/△	% size difference	Area (km²)	DTM~ (km)	Age (K years)	Latitude
Schwaner and Sarre, 1990	*Notechis ater*	Kangaroo	L	33.43	4350[a]	43.2[g]	10.25[m]	35.47†
Schwaner and Sarre, 1990		Reevesby	L	27.63	7.6[e]	15.2[e]	8[j]	34.32[e]
Schwaner and Sarre, 1990		Carnac	L	−22.71	1[e]	7.6[e]	6.3[j]	32.15†
Schwaner and Sarre, 1990		Tasmania	D	16.13	67800[a]	240[a]	12.75[m]	42.10†
Schwaner, 1985		East Franklin	L	22.59	1.5[e]	16.5[b]	10[m]	32.27[e]
Schwaner, 1985		West Franklin	L	21.48	1.5[e]	18.5[b]	10[m]	32.28[e]
Schwaner, 1985		Goat	L	16.20	2.4[e]	11[b]	10[m]	32.19[e]
Schwaner, 1985		Hopkins	L	18.89	1.78[e]	4.6[e]	7.8[j]	34.58[e]
Schwaner, 1985		KI476	L	1.85	0.5[e]	0.5†	6.1[j]	35.47[q]
Schwaner, 1985		Hareby	L	−5.28	0.89[e]	18[e]	8[j]	34.35[e]
Schwaner, 1985		Roxby	L	−27.31	1.14[e]	20.3[e]	8[j]	34.35[e]
Schwaner and Sarre, 1988		Chappell	L	41.67	3.25†	9.25[e]	10[m]	40.17†

Viperidae

Source	Species	Island	Island type/△	% size difference	Area (km²)	DTM~ (km)	Age (K years)	Latitude
Amaral, 1921	*Bothrops insularis*	Guiamada	L	−33.33	430†	33†	11[u]	24.30†
Cliff, 1954	*Crotalus catalinensis*	Santa Catalina	D	−44.03	43[e]	35[e]	20000[v]	25.38[e]
Brongersma, 1940	*Crotalus durissus*	Aruba	L	−34.57	193[a]	28.8[a]	68000[v]	12.24[q]
Klauber, 1956	*Crotalus enyo*	Cerralvo	D	−13.36	160[e]	11[e]	5000[e]	24.10[e]
Mertens, 1934	*Crotalus exsul*	Cedros	L	−48.63	347[g]	24[b]	9.1[w]	28.10[e]
Klauber, 1949	*Crotalus mitchelli*	El Muerto	L	−50.81	0.9[e]	4.8[e]	8.3[c]	30.05[e]
Klauber, 1956		Angel de la Guarda	D	22.71	895[c]	13[c]	1600[e]	29.45[b]
Klauber, 1949	*Crotalus molossus*	San Esteban	D	−21.88	43[c]	37[c]	1600[e]	28.42[e]
Radcliffe and Maslin, 1975	*Crotalus ruber*	San Lorenzo Sur	D	−42.78	35[c]	18[c]	1000[e]	28.37[e]
Klauber, 1956		Angel de la Guarda	D	−28.48	895[c]	13[c]	1600[b]	29.45[b]

APPENDIX 1. CONTINUED

Source	Species	Island	Island type△	% size difference	Area (km²)	DTM~ (km)	Age (K years)	Latitude
Klauber, 1956	*Crotalus tortugensis*	Tortuga	L	−37.21	6.3c	37c	10c	27.27e
K. G. Ashton, unpubl. data	*Crotalus viridis*	South Coronado	L	−35.45	5.5e	14e	8.3j	32.23e
K. G. Ashton, unpubl. data		Anaho	L	−28.50	3y	0.8y	10s	39.57y
K. G. Ashton, unpubl. data		Santa Catalina	D	−31.45	194f	32f	15000f	33.20e
Forsman, 1991b	*Vipera berus*	Kärringboskär	L	0.86		10s	8.9j	59.47e
Forsman, 1991b		Inre Hamnskär	L	9.48	1.43#	13.4s	8.9j	59.44e
Forsman, 1991b		Norrpada	L	0.00	0.84#	14.7s	10.5j	59.38e
Forsman, 1991b		Ängskär	L	6.90	1.26#	22.7s	10.5j	59.32e
Forsman, 1991b		In-Fredeln	L	13.79	0.5#	25.1s	10.5j	59.32e
Forsman, 1991b		Svenska Högarna	L	1.72	1#	39.6s	10.5j	59.26e
Mertens, 1934	*Vipera lebetina*	Cyclades	D	−46.67	2528a	94e	16p	36.50e

△ D = Deep water island, L = Land-bridge.
~ DTM = distance to mainland.
a Britannica Encyclopedia online.
b Seltzer, 1962.
c Gastil et al., 1983.
d King, 1987.
e Defense Mapping Agency or other chart (see Appendix 2 for list).
f Schoenherr et al., 1999.
g Huxley, 1962.
h Lewis and Draper, 1990.
i Maury et al., 1990.
j Estimated with Milliman and Emery (1968) curve (see Materials and Methods section for detail).
k T. Sato pers. comm., Geological Consulting Office, Geological Survey of Japan.
l King, 1986.
m Rawlinson, 1974.
n CIA World Fact Book online.
p Foufopoulos and Ives, 1999.
q Hutchinson, 1950.
r Murphy, 1997.
s Forsman, 1991a.
t Lonsdale, 1989.
u Vanzolini, 1973.
v Bellizzia and Dengo, 1990.
w Wilcox, 1978.
x United States Fish and Wildlife Report, unpubl. report (D. Withers pers. comm).
y Woodbury, 1966.
z Devoy, 1987.
† Data acquired from "Source" reference.
# Data acquired via personal communication with "Source" authors.
$ St. Vincent and Grenadines collectively cover an area of 389 km². 34 km² is an estimate for the Grenadines and is the area of St. Vincent group, the largest island group of the Grenadines.
* Kaye, 1959.

APPENDIX 2. CHARTS USED TO ESTIMATE ISLAND AREA, DISTANCE TO MAINLAND AND LATITUDE FOR SOME ISLANDS USED IN THIS STUDY.

Island	Chart number*
Ile de la Gonâve	DMA chart 26001
Dominica	DMA chart 25000
St. Lucia	DMA chart 25000
Grenada	DMA chart 25000
St. Vincent	DMA chart 25000
Grenadines	DMA chart 25000
Santa Catalina	TPC chart H-22C
Cerralvo	DMA chart 21008
Cedros	TPC chart H-22A
El Muerto	TPC chart H-22B
San Esteban	TPC chart H-22B
San Lorenzo Sur	TPC chart H-22B
Tortuga	TPC chart H-22C
South Coronado (in Pacific Ocean)	DMA chart 21003
Santa Catalina	DMA chart 18000
Oh-shima	DMA chart 97140
Kozo-shima	DMA chart 97140
Nii-jima	DMA chart 97140
Tadanae-jima	DMA chart 97140
Mikura-jima	DMA chart 97021
Paros	DMA chart 54320
San Esteban	TPC chart H-22B
Middle Bass	NOAA chart 14830
North Bass	NOAA chart 14830
Pelee	NOAA chart 14830
Kelly's	NOAA chart 14830
Johnsons	NOAA chart 14830
Middle	NOAA chart 14830
East Sister	NOAA chart 14830
West Sister	NOAA chart 14830
Reevesby	DMA chart 75130
Carnac	DMA chart 74555
East Franklin	ONC chart R-12
West Franklin	ONC chart R-12
Goat	ONC chart R-12
Hopkins	DMA chart 75130
KI476	DMA chart 75130
Hareby	DMA chart 75130
Roxby	DMA chart 75130
Chappell	DMA chart 75220
South Coronado (Gulf of Calif.)	TPC chart H-22C
Cerralvo	DMA chart 21008
Kärringboskär	DMA chart 41180
Inre Hamnskär	DMA chart 44180
Norrpada	DMA chart 44180
Ängskär	DMA chart 44180
In-Fredeln	DMA chart 44180
Sveska Högarna	DMA chart 44180
Cyclades	ONC chart G3

* DMA = Defense Mapping Agency, TPC = Tactical Pilotage Chart, NOAA = National Oceanic and Atmospheric Administration, ONC = Operational Navigation Chart.