Evolution, 44(3), 1990, pp. 558–569

A PHYLOGENETIC ANALYSIS OF CHARACTER DISPLACEMENT IN CARIBBEAN *ANOLIS* LIZARDS

JONATHAN B. LOSOS
Museum of Vertebrate Zoology and Department of Integrative Biology, University of California, Berkeley, CA 94720

Abstract.—Twenty-seven islands in the Lesser Antilles contain either one or two species of *Anolis* lizards. On nine of the ten two-species islands, the species differ substantially in size; 16 of the 17 one-species islands harbor an intermediate-sized species. Two processes could produce such a pattern: size adjustment (or character displacement), in which similar-sized species evolve in different directions in sympatry; and size assortment, in which only different-sized species can successfully colonize the same island together. Previous analyses implicitly have assumed that size is evolutionarily plastic and determined solely by recent ecological conditions, and consequently have tested the hypothesis that character displacement has occurred on each of the ten two-species islands. Other studies have focused only on size assortment.

By analyzing such patterns in a phylogenetic context, I explicitly consider historical effects and can distinguish between size adjustment and size assortment. Using a minimum evolution algorithm, I assess evidence for size adjustment by partitioning changes in size along branches of the phylogenetic tree. Size evolution appears rare (a minimum of 4–7 instances of substantial size evolution). In the northern (but not the southern) Lesser Antilles, size change was significantly greater when a descendant taxon occurred on a two-species island and its hypothetical ancestor occurred on a one-species island, thus supporting the size adjustment hypothesis, though size adjustment might have occurred only once. The relative rarity of size evolution suggests that size assortment might be responsible for non-random patterns. In both the northern and southern Lesser Antilles, a null model of no size assortment is convincingly rejected. Closely related taxa, however, are usually similar in size, and hybridization between species has been reported. Consequently, similar-sized species might not coexist because they interbreed and coalesce into one gene pool. A null model that only allows species from different "clades" to co-occur is rejected for the northern Lesser Antilles, but is ambiguous with regard to the southern Lesser Antilles. Thus, competitive exclusion is probably responsible for the pattern of size assortment in the northern Lesser Antilles; both competitive exclusion and interbreeding of closely related species of similar size might be responsible for the patterns evident in the southern Lesser Antilles.

Received November 16, 1988. Accepted December 20, 1989.

The role of interspecific interactions in structuring communities has been debated for more than half a century. Recent discussion has focused on the appropriate method to judge observed patterns of body sizes and geographic distributions relative to random expectations. Numerous authors have proposed formulae for constructing "null models" (sensu Harvey et al., 1983) with which to compare observed patterns. Others have argued, however, that it is impossible to construct biologically realistic null models that do not inadvertantly incorporate the results of the processes for which they are supposed to serve as null hypotheses (e.g., Grant and Abbott, 1980; Diamond and Gilpin, 1982; Case and Sidell, 1983; Colwell and Winkler, 1984; Schoener, 1984). Often lost amidst this debate (but see Colwell and Winkler, 1984) has been the simple fact that species and populations do not appear de novo, shaped only by current ecological conditions; rather, they have a history of evolution (Lauder, 1981; Felsenstein, 1985; Huey and Bennett, 1987). This paper uses the much discussed case of the *Anolis* lizards of the Lesser Antilles to show that the importance of interspecific interactions often can be analyzed most appropriately by examining them in historical context.

Schoener (1970) found that the size of lizard species on 27 Lesser Antillean islands varied in a remarkably consistent way with the number of species on an island (Fig. 1). Ten of these islands have two species, whereas 17 have only one species. On nine of the two-species islands, one species is large and the other small. Specifically, the species differ in size by a factor of 1.5 or more (on the 10th island, St. Maarten, the difference is 1.45). In contrast, on 16 of the 17 one-species islands, species are intermediate in size (defined as 15.0 mm < jaw length <

21.5 mm; the exception is *ferreus* on Marie Galante).

Two fundamentally different processes could produce such a pattern of size dissimilarity among sympatric species (Case, 1983; Case and Sidell, 1983; Case et al., 1983; Grant and Abbott, 1980; Grant, 1986): (1) size adjustment (or character displacement): species of similar size colonize an island and evolve in opposite directions in situ to minimize resource competition; (2) size assortment: competitive exclusion or other processes prevent similar-sized species from colonizing the same island; only species that are already dissimilar in size can successfully colonize and coexist. Schoener (1969*a*, 1988) and Williams (1969, 1972) have suggested that character displacement has occurred frequently in Lesser Antillean *Anolis*, but also have considered size assortment to be important in generating observed patterns; others (e.g., Simberloff, 1983; Simberloff and Boecklen, 1981) have implicated only size adjustment as a cause of these patterns of size distribution.

In this paper, I utilize a phylogenetic approach to investigate whether size adjustment and/or size assortment are responsible for producing non-random patterns in the Lesser Antilles. I first determine when size evolution most likely occurred in the diversification of Lesser Antillean *Anolis*; I use this information to test whether size adjustment was responsible for this evolution. I then ask whether differential colonizing success (i.e., size assortment) of different-sized species has occurred.

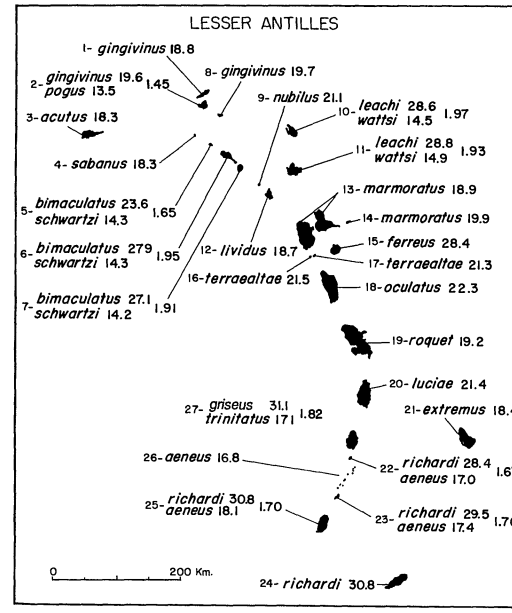

FIG. 1. Distribution and sizes of *Anolis* in the Lesser Antilles (modified from Schoener 1970). Species and mean jaw lengths for males are noted for each island. For two-species islands, the ratio between the larger and the smaller species is given. Islands are: 1. Anguilla; 2. St. Maarten; 3. St. Croix; 4. Saba; 5. St. Eustatius; 6. St. Christopher; 7. Nevis; 8. St. Barthelemy; 9. Redonda; 10. Barbuda; 11. Antigua; 12. Montserrat; 13. Guadeloupe; 14. La Desirade; 15. Marie Galante; 16–17. Iles des Saintes; 18. Dominica; 19. Martinique; 20. St. Lucia; 21. Barbados; 22. Bequia; 23. Carriacou; 24. Tobago; 25. Grenada; 26. the Grenadines; 27. St. Vincent. I do not include two non-Lesser Antillean island groups in Schoener (1970), St. Croix and the Cayman Islands. Including them does not alter the results of the analysis presented here.

Size Adjustment

Null models have been developed to test this and other purported examples of size adjustment (e.g., Simberloff and Boecklen, 1981; Simberloff, 1983), but these models do not incorporate historical information. Implicitly, they assume that each population has evolved to its current size on the island it occupies. As a result, these methods risk overestimating the frequency of size adjustment and prevent separate evaluation of the effects of historical and ecological processes potentially capable of generating patterns of size dissimilarity.

Phylogenetic analysis of the patterns of body size and of island distribution circumvents these difficulties and permits a statistical assessment of both size adjustment and size assortment. Figure 2 displays how a pattern of size dissimilarity, with a large and a small species on two-species islands and intermediate species on one-species islands, could be produced by size adjustment and/or size assortment. Figure 2a demonstrates size assortment. For some unspecified reason, ancestral species evolve size differences while on one-species islands, and then only taxa dissimilar in size (i.e., large and small) can successfully co-occur. Figure 2b illustrates size adjustment. When two taxa colonize the same island, they evolve differences in size that allow coexistence. Figure 2c demonstrates both processes. Size adjustment occurs when two similar-sized

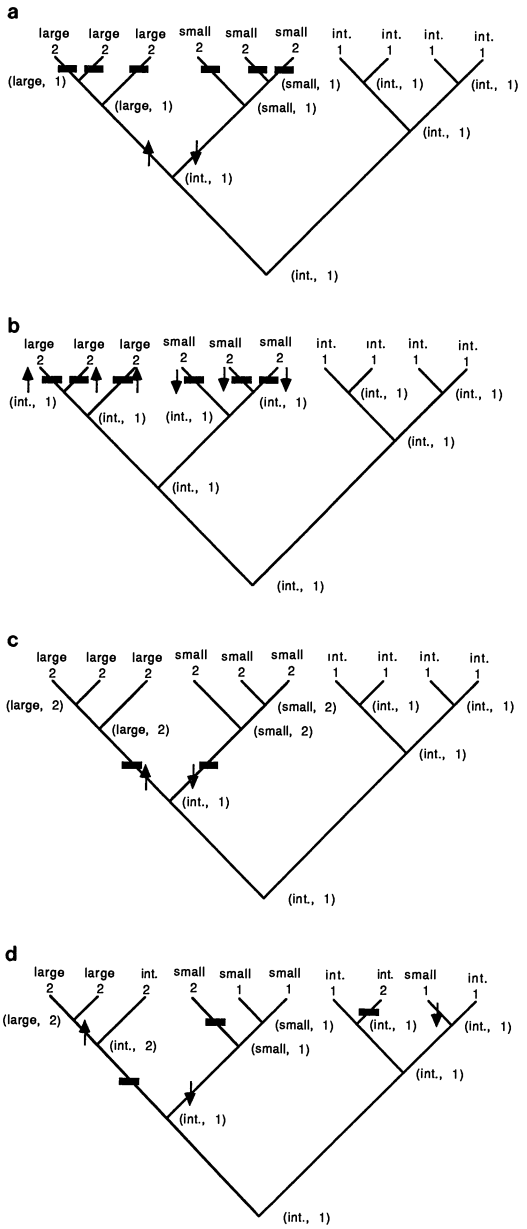

FIG. 2. Phylogenetic illustration of the capability of size assortment and character displacement to generate patterns of size dissimilarity. Figure 2a illustrates size assortment; Figure 2b size adjustment; Figure 2c both size assortment and size adjustment; Figure 2d neither. See text for discussion. Arrows represent evolutionary increase or decrease in body size. Black rectangles indicate that descendant taxa occur on two-species islands, whereas ancestral taxa occur on one-species islands. Numbers refer to the number of species on the island occupied by that taxon. Except in 2d, two-species islands contain a large and a small species.

species first co-occur; subsequent successful colonization of additional islands by descendants of both forms constitutes size assortment. Figure 2d illustrates a chaotic pattern resulting from neither character displacement nor size assortment.

Interpretation of the ecological context of evolutionary change requires a well-corroborated phylogenetic hypothesis (Felsenstein, 1985; Donoghue, 1989). The *Anolis* of the northern and southern Lesser Antilles are derived from different stocks; Figure 3 presents a phylogeny for each. Despite several unresolved polychotomies, I will demonstrate that the phylogenetic resolution is sufficient to indicate that size adjustment has not been widespread.

A minimum evolution algorithm (Huey and Bennett, 1987) can be used to test the hypothesis that size change occurred simultaneously with the transition from one-species to two-species islands, or vice versa. The algorithm assigns values to hypothetical ancestral taxa so as to partition character change along the branches of the phylogeny to minimize the sum of the evolutionary changes (i.e., the difference between each descendant and its ancestor) squared. An alternative approach (Farris, 1970; Larson, 1984; Sessions and Larson, 1987), which minimizes the sum of the absolute amount of evolutionary changes, was not used because the algorithm finds numerous equally parsimonious solutions (Swofford and Maddison, 1987).

Whether an ancestral form occurred alone or in sympatry can also be determined, based on whether descendant species occur on one- or two-species islands. *Anolis* distribution in the Lesser Antilles results primarily from colonization and fragmentation of island banks caused by the post-glacial increase in sea level (Williams, 1969). Thus, the ancestor of any pair of sister taxa probably occurred on one of the islands that its descendants occupy (In this sense, the ancestor may be essentially identical with a descendant. For example, if a species colonized one island, and from there a second island, then the common ancestor of the taxa on the two islands would be the population that had colonized the first island before it colonized the second). For example, because *A. wattsi* occurs on Barbuda and Antigua,

and both islands contain another species, then the ancestor of these two populations of *wattsi* probably occurred in sympatry with another species on either Barbuda, Antigua, or the island bank containing both. For cases in which sister taxa differ, I considered the nearest outgroup to determine whether the ancestral form probably occupied a one- or two-species island. In the case of the *wattsi* and *bimaculatus* groups, which co-occur on six islands, this reasoning predicts that colonization of an island (e.g., Antigua) by both groups was essentially simultaneous.

Thus, for each species in the phylogeny, both extant and hypothetical ancestral, one can infer how much each species changed in size from its most immediate ancestor, and whether it occurred on an island with a different number of species than its ancestor. The prediction of the size adjustment hypothesis, that changes in size are associated with a move to an island with a different number of species, can then be tested. Statistical results must be received cautiously, however, because the size value assigned to each hypothetical ancestor depends on values assigned to its hypothetical ancestor and descendants (Felsenstein, 1988, Huey, 1987). Further, these results depend on the reconstruction of character evolution based on parsimony.

Results of such an analysis depend on how unresolved polychotomies in Roughgarden's, et al. (1987) phylogeny are resolved. One example dealing with anoles of the northern Lesser Antilles is presented in Figure 4. In this phylogeny, *Anolis bimaculatus* and *leachi* were assumed to be sister taxa because Lazell (1972), in the last taxonomic revision of the group, considered them conspecific. In all other cases, I resolved polychotomies by assuming that geographically proximate species or populations were more closely related than either was to taxa on more distant islands. The original species colonizing the northern Lesser Antilles (the outgroup in Figure 4) was assumed to occur on a one-species island.

Given these assumptions, character displacement is demonstrable in the northern Lesser Antilles; size adjustment is greater when descendants occur on two-species islands and their ancestors occurred on one-species islands (Mann-Whitney U-test, $P <$ 0.056, see Table 1; the three taxa that occupied two-species islands and had immediate ancestors that occupied one-species islands are indicated by boxes in Fig. 4).

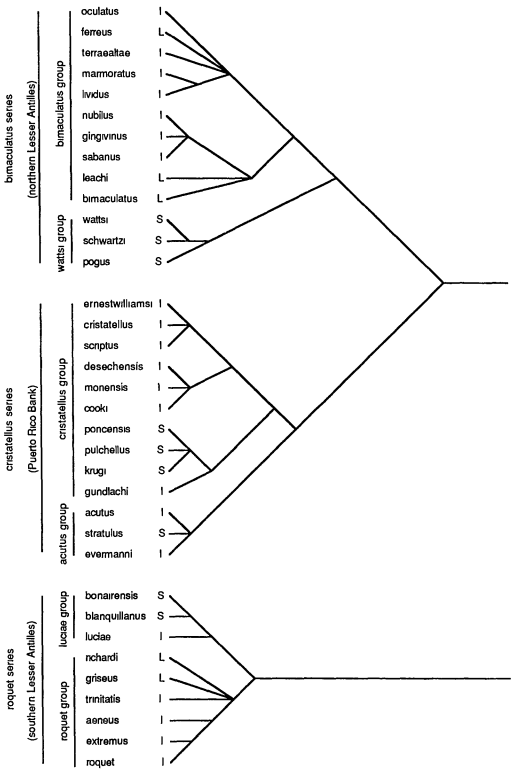

FIG. 3. Phylogeny of *Anolis* in the eastern Caribbean based on immunological, electrophoretic, karyological, and morphological (primarily scale characters; body size is not used in constructing the phylogeny) studies by Gorman and others (modified from Roughgarden, et al. 1987). The *roquet* series is most closely related to South American anoles and only distantly related to the *cristatellus* and *bimaculatus* series. Recent controversy over *Anolis* systematics (Guyer and Savage, 1986; Cannatella and de Queiroz, 1989) does not affect this arrangement. Size: L = large (jaw length > 21.5 mm); I = intermediate (21.5 > jaw length > 15.0); S = small (jaw length < 15.0).

Figure 4 also reveals that substantial changes in body size have been uncommon in the northern Lesser Antilles. The evolution of small size occurred only once, in the ancestor of the *wattsi* group; large size only evolved twice, in *ferreus* and in the *bimaculatus-leachi* group (large size evolved three times if *bimaculatus* and *leachi* are not sister taxa). Intermediate size, ancestral to the entire clade (which accords with Schoe-

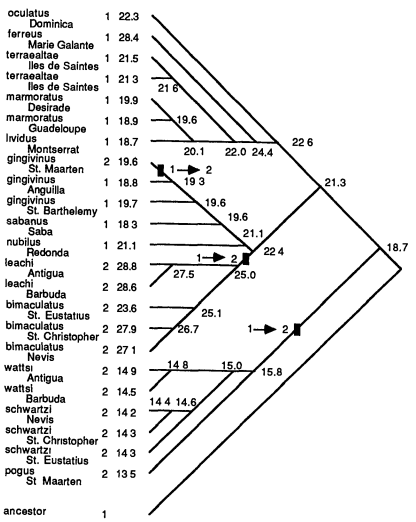

FIG. 4. One possible resolution of the phylogeny for the *bimaculatus* series. Numbers across the top row are, for each taxon, jaw length (in mm) and number of species on the island it occupies. Sizes of ancestral forms, calculated using the minimum evolution algorithm described in the text, are noted next to the node for each ancestral form. Boxes represent the evolutionary transition from one-species to two-species islands.

ner's (1969*a*) prediction that *Anolis* colonists are usually approximately this size), never re-evolved from large or small taxa.

Results for the southern Lesser Antilles are clear-cut: size adjustment cannot be demonstrated regardless of how the polychotomies are resolved, even if *richardi* on Tobago (which was probably recently introduced by man [Gorman et al., 1978]) is excluded (Table 1). In several cases, substantial size change accompanies change in island-species number, but in several other cases it does not. As with the northern Lesser Antilles, substantial size evolution was uncommon (one–three instances, depending on resolution of polychotomies).

Size Assortment

Given that size evolution has been rare, size assortment might account for non-random distributional patterns of Lesser Antillean *Anolis*. The scarcity of intermediate-sized species on two-species islands suggests that only large and small species can successfully colonize islands occupied by the other (Williams, 1969). Further, if size evolution is uncommon, then the scarcity of large or small species on one-species islands indicates either that only intermediate-sized species can colonize vacant islands, or that intermediate-sized species normally triumph over large or small species when they occur sympatrically. The latter suggestion accords with suggestions that intermediate-sized anoles are the optimal size given prey size distributions on these islands (Schoener, 1969*b*; Roughgarden, 1974; Roughgarden and Fuentes, 1977).

Hypotheses of size assortment can be tested using standard null model procedures (e.g., Strong et al., 1979; Grant and Abbott, 1980; Hendrickson, 1981; Simberloff and Connor, 1981; Case, 1983; Case and Sidell, 1983; Colwell and Winkler, 1984; Schoener 1984, 1988). Unlike previous null model tests of size assortment, my analysis does not risk confounding size assortment and size adjustment. Size adjustment, though responsible for most size differences among northern Lesser Antillean species, appears to have occurred only once, and in the relatively distant past. Consequently, to the extent that non-random patterns exist, size assortment must be the cause.

Although size assortment is primarily an ecological process, a phylogenetic perspective can be enlightening. When islands have been colonized from the mainland, which mainland species might reasonably be included as potential colonists is often unclear (e.g., Strong et al., 1979; Grant and Abbott, 1980; Schoener 1984, 1988). For Lesser Antillean *Anolis* (and also the much debated example of the Galapagos finches [Grant, 1986]), Figure 3 indicates that there is no pool of mainland colonists that have populated the islands (contra Schoener, 1988). The *roquet* and *bimaculatus* species groups are each monophyletic; thus, the islands are inhabited by species descended from a single colonization event, with all subsequent speciation and colonization occurring within the archipelago.

Using the species occurring within an island group to generate the null pool can lead to incorporation of competitive effects into the null model if some species have become extinct on all islands (Grant and Abbott,

1980; Colwell and Winkler, 1984; Schoener, 1988), which would make the detection of competitive processes more difficult. Nonetheless, I use this approach for Lesser Antillean *Anolis,* because no better alternative exists. Only knowledge of all species that had ever occurred in the archipelago would allow this difficulty to be circumvented.

In constructing the null distribution predicted under random expectations, whether to draw species from the pool of potential colonists in proportion to their occurrence is debated. Doing so might also lead to incorporation of competitive effects into the null model (Grant and Abbott, 1980; Diamond and Gilpin, 1982; Colwell and Winkler, 1984); not doing so might attribute rarity of particular species or species combinations to competition, when other factors, such as limited dispersal ability or restrictive habitat requirements, might be responsible (Connor and Simberloff, 1979, 1983). I employ both approaches below.

In the northern Lesser Antilles, all six two-species islands have a size ratio greater than 1.45. A null model, which assumed that the distribution of potential colonists mirrors the size distribution of extant species was constructed by calculating the size ratio of every possible species pair. Ratios for species pairs were calculated by using each possible combination of the populations of each species, but these were given only fractional weight in the species pool (i.e., if a species had three populations, then each ratio involving one of these populations was given a weight of one third). There are 78 species pairs in the northern Lesser Antilles; the probability that a randomly drawn pair would have a size ratio greater than 1.45 is 0.34 (Table 2). The probability that all six such pairs would have a ratio of 1.45 or greater is $0.34^6 = 0.0014$. Similarly, I evaluate the probability that species on one-species islands will be of intermediate size (18.3 mm < jaw length < 22.3 mm; to be conservative, I define intermediate size more narrowly than above). The probability that a randomly chosen species falls between these points is 0.46, and the probability that 10 of 11 occupants of single species islands should be of intermediate size is $\binom{11}{10}(0.46^{10})(0.54^1) = 0.003$. These are independent tests of the hypothesis of size assortment. The probability of achieving two such results, by Fisher's test for combining probabilities (Sokal and Rohlf, 1981), is $P < 0.0005$ (Table 2).

TABLE 1. Size change associated with shifts from one-species to two-species islands, and vice versa.

	Taxon occupies an island with a different number of species than the island occupied by most immediate ancestor	Taxon occupies an island with the same number of species as the island occupied by most immediate ancestor
Northern Lesser Antilles		
Number of populations*	3**	41
$\bar{x} \pm$ SE	1.9 ± 1.0	0.9 ± 0.1
(range)+	(0.3 to 3.0)	(0 to 4.0)
	$t_s = 1.61$, $P < 0.056$++	
Southern Lesser Antilles+++		
Number of populations*	5	19
$\bar{x} \pm$ SE	1.4 ± 1.2	0.8 ± 0.2
(range)+	(−0.5 to 4.3)	(0.1 to 3.4)
	$U_s = 57$, $P < 0.50$++++	

* Includes present and hypothetical ancestral species and populations.
** These are the taxa in the phylogeny in Figure 4 directly above the closed boxes.
+ Calculated by subtracting the size of a taxon's immediate ancestor from that taxon's own size. Absolute value of size change is reported for taxa on islands with the same number of species as their ancestors. Taxa whose ancestors occurred on one-species island and that occurred on an island with a smaller taxon were expected to evolve to larger size, and vice versa. Taxa that evolved in the opposite direction to that predicted were assigned negative values.
++ Mann-Whitney U-test, one-tailed, normal approximation for samples >20. Given the low power of a statistical test (particularly a nonparametric one) with a sample size of three (Sokal and Rohlf, 1981), I treat this result as significant.
+++ Using a phylogeny in which *trinitatis* is the sister group to the *roquet-extremus-aeneus* clade, *richardi* and *griseus* are sister taxa, *richardi* on Tobago is included, and the relationships of populations within a species reflect geographic proximity. Alternative resolutions of the unresolved polychotomies in Figure 1 do not alter qualitatively the results.
++++ Mann-Whitney U-test, one-tailed.

To account for species-specific differences in frequency of occurrence, the same calculations can be made, using as the null pool size ratios from all combinations of populations weighted equally, with the exception that size ratios from two conspecific populations are excluded, because the absence of such combinations would be expected to be caused by interbreeding. Using this pool, the null hypothesis of random placement of populations on islands is convincingly rejected (Table 2). Similarly, using either method of generating the null pool, the null hypothesis can be rejected for *Anolis* on the southern Lesser Antilles (Table 2). Using a similar null model, Schoener (1988) came to identical conclusions.

TABLE 2. Tests for size assortment.

Probability that species on two-species islands are so dissimilar in size*	Probability that so many taxa on one-species islands are intermediate in size**	Combined probability
Northern Lesser Antilles Species		
1. $P < 0.0014$	$P < 0.0028$	$P < 0.0005$
2. $P < 0.0002$	$P < 0.0039$	$P < 0.0001$
Southern Lesser Antilles Species		
1. $P < 0.0013$	$P < 0.57$	$P < 0.01$
2. $P < 0.008$	$P < 0.23$	$P < 0.025$
Northern Lesser Antilles Clades		
1. $P < 0.0035$	$P < 0.0029$	$P < 0.0001$
2. $P < 0.005$	$P < 0.0029$	$P < 0.0001$
Southern Lesser Antilles Clades (phylogeny #1)		
1. $P < 0.100$	$P < 0.553$	$P < 0.30$
2. $P < 0.028$	$P < 0.23$	$P < 0.05$
Southern Lesser Antilles Clades (phylogeny #2)		
1. $P < 0.221$	$P < 0.574$	$P < 0.40$
2. $P < 0.068$	$P < 0.23$	$P < 0.10$

1 = not weighting by frequency of occurrence of species.
2 = weighting by frequency of occurrence.
* The hypotheses are: for the NLA, what is the probability that all six two-species islands should have a size ratio > 1.45? For the SLA, what is the probability that all four two-species islands should have a size ratio > 1.67?
** The hypotheses are: what is the probability that 10 of 11 (NLA) or 3 or 4 (SLA) species on one-species islands should be of intermediate size?

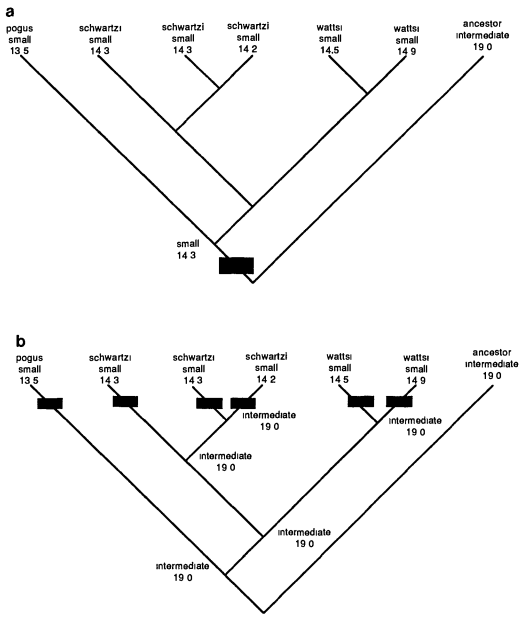

FIG. 5. Size evolution in the *Anolis wattsi* series. All members are small; the outgroup is of intermediate size. This phylogeny only provides evidence for one evolution of size change (a). If one suggests that small size has arisen on each island currently occupied by members of the series, phylogeny (b), which requires a minimum of six evolutionary changes in body size, is appropriate. Boxes represent evolution of small size.

Competitive Exclusion or Interbreeding as the Cause of Size Assortment

The phylogenetic perspective provides an important and overlooked insight into the cause of size assortment. On two-species islands, one striking regularity emerges: no island contains two relatively closely related species, with one possible exception (*trinitatis* and *griseus* may be sister taxa [Yang et al., 1974, but see Baverstock et al., 1979]). This may be caused by the apparent rarity of size change in these lizards; most closely related species are of the same size and may competitively exclude each other. However, delimiting the reproductive species boundary for allopatric populations is notoriously difficult, and interspecific hybridization is known for these lizards (Gorman and Yang, 1975); Gorman and Kim (1976) postulated occasional hybridization with invading colonists as one possible explanation for the low genetic distances among solitary members of the *bimaculatus* series. Consequently, this pattern of close relatives never co-occurring on an island might result from a lack of reproductive isolation of currently recognized species. When a species colonizes an island occupied by a closely related species of similar size, interbreeding might occur, which would prevent establishment and coexistence of similar sized species (Williams, 1969).

If this were the case, treating each species as an independent entity in the analyses above would be incorrect, and the appropriate null model would consider only those size ratios possible between members of different "clades" (defined below). Accordingly, I have recalculated the null models using the methods above. In the northern Lesser Antilles, I assume there are four distinct clades: the *wattsi* series, *bimaculatus-leachi, sabanus-gingivinus-nubilis,* and the remaining five species. In the southern Lesser Antilles, I consider three clades: *luciae, richardi-griseus,* and the remaining four species. Alternatively, I also consider the possibility that *trinitatis* is the sister taxon to *richardi-griseus* and part of their clade.

For the northern Lesser Antilles, the combined probability of generating as extreme

a pattern of size dissimilarity on two-species islands and intermediate size on one-species islands is $P < 0.0005$ regardless of whether one weights by frequency of occurrence. For the southern Lesser Antilles, if *trinitatis* is not the sister taxon to *richardi-griseus,* the combined probabilities are $P < 0.05$ if the likelihood of drawing each species is weighted by frequency of occurrence, and $P < 0.30$ if species occurrences are unweighted. If *trinitatis* is part of the *richardi-griseus* clade, the probabilities are $P < 0.10$ and $P < 0.40$, respectively. Thus, whether size dissimilarity of sympatric anoles in the southern Lesser Antilles is caused by competitive exclusion or possible reproductive compatibility of similar-sized species is unclear. However, this approach greatly reduces sample size and hence is a very conservative test.

Discussion

Size Distribution Patterns and Phylogeny

The major point of this exercise is to illustrate the desirability of a phylogenetic approach in examining the results of historical ecological processes such as those resulting from interspecific interactions. Previous workers have suggested that *Anolis* in the Lesser Antilles show great evolutionary plasticity in size and that size adjustment is a major factor determining the current size of species on islands. Elaborate analyses of this proposition have assumed that each population on each island is a completely independent entity (Simberloff and Boecklen, 1981; Simberloff, 1983), which is unjustified (Felsenstein, 1985).

By contrast, my findings support the hypothesis that size adjustment has occurred, but indicate that it has occurred infrequently—perhaps only once. Nevertheless, the distribution of *Anolis* body size on islands is highly non-random; competition very likely has been a major force determining the distribution of these lizards, but it acts primarily by allowing only species of dissimilar size to colonize an island and coexist. My analysis raises the possibility that the dissimilarity in size of sympatric species in the southern Lesser Antilles might result not from competitive exclusion, but from interbreeding of similar-sized and closely related species, which consequently cannot coexist. More detailed knowledge of the phylogeny and species boundaries in this group is needed.

Size Evolution and Parsimony

Size evolution could be more frequent than indicated by minimum evolution approaches. In many species, considerable additive genetic variation exists for body size (Falconer, 1981), which is generally a relatively labile character evolutionarily. In *Anolis,* in particular, body size appears to evolve readily in response to selective forces (Schoener, 1969*a*, 1969*b*; Lister, 1976; Roughgarden and Fuentes, 1977).

My analysis neither assumes that size is an evolutionarily conservative character, nor disproves the hypothesis that size adjustment has occurred on each of the ten two-species islands. It does, however, consider only those evolutionary changes for which evidence exists. For example, because the ancestral size is intermediate, small size has evolved at least once in the *wattsi* group (Figs. 3, 4), as depicted in Figure 5a. No evidence suggests that small size has evolved multiple times, as an hypothesis of widespread size adjustment would require (Fig. 5b). If, in fact, the latter depiction were correct, my analysis would be conservative by underestimating the extent of size adjustment.

Data from other sources (e.g., fossil data from each island) could provide additional evidence. However, without any other source of information, as in any reconstruction of historical events, one can base deductions only on the evidence at hand. To draw other conclusions (which implicitly is done when phylogenetic information is ignored), amounts to pure speculation. In this case, no evidence suggests widespread evolution of body size in Lesser Antillean *Anolis.*

Intraspecific Size Variation

Subsequent to Schoener's (1970) discussion, Lazell (1972) reported that substantial variation in size exists among *marmoratus, oculatus,* and *roquet.* I have not included intra-island variation in this analysis, because it is readily interpretable without recourse to explanations involving interspecific interactions. All three species occur on relatively large islands with considerable

geographic variation in climate; populations of larger lizards are always found in more mesic habitats. On Dominica, Roughgarden and Fuentes (1977) have shown that insect abundance varies inversely with aridity, and that lizard size, in turn, is correlated with insect abundance.

Vicariant Events as an Explanation for Size Assortment

Vicariant events also may be responsible for patterns of species distributions. Possibly as recently as 7,000 years ago, lower sea levels during the last glacial period resulted in the emergence of several island banks (e.g., the St. Kitts bank, comprising St. Christopher, St. Eustasius, and Nevis [Williamson, 1981]). Consequently, the presence of particular species or species pairs on several islands in the same bank might not indicate independent colonization of these islands. On the other hand, islands on the same bank do not necessarily have the same anole fauna (e.g., both the St. Maarten and Grenada banks). Thus, although recent island connections may explain similarities in fauna, the dynamics determining species composition have been operating on each island since the banks were fragmented by rising seas. In any case, analyzing the data using banks rather than islands does not qualitatively alter the results.

The distribution of the *wattsi* and *bimaculatus* groups also could suggest a vicariant interpretation. An area cladogram (Rosen, 1978) superimposing the phylogeny of these groups upon their geographic distribution (cf. Fig. 4) implies that size assortment occurred on only one island, with the present distribution resulting from the fragmentation of this island into six islands. Genetic distances within these groups, however, indicate that they have diverged much too recently for this scenario to be plausible (Gorman and Kim, 1976). Furthermore, there is no question that *Anolis* can and have colonized Caribbean islands by overwater dispersal (Williams, 1969; Schoener, 1975; Schoener and Schoener, 1983).

Character Displacement or Taxon Cycle as the Cause of Size Adjustment

Roughgarden and colleagues (Roughgarden and Pacala, 1989; Roughgarden et al., 1983, 1984, 1987) have suggested, based on their work in the northern Lesser Antilles, that character displacement is unlikely because similar-sized species could not coexist long enough for character displacement to occur without one becoming extinct. Rather, they argued that a taxon cycle occurs in which: (1) A one-species island is invaded by a large species from a one- or two-species island. Larger species are competitively superior (Pacala and Roughgarden, 1985; Rummel and Roughgarden, 1985*a*); hence, (2) The large species evolves toward the optimal solitary size, (3) causing the smaller species to evolve to a smaller size and eventually perish (Roughgarden et al., 1987). In support of this theory, studies have shown that within the northern Lesser Antilles: competition is most intense between *gingivinus* and *wattsi* on St. Maarten, which are in size the most similar sympatric species pair; *wattsi* on St. Maarten is smaller than on any other island; and *wattsi* has become extinct in historic times on Anguilla, where *gingivinus* is even smaller (Pacala and Roughgarden, 1982; Roughgarden et al., 1983; Rummel and Roughgarden, 1985*b*). In addition, Roughgarden and Pacala, (1989), have cited fossil data (Etheridge, 1964; Steadman et al., 1984; Roughgarden and Pacala, 1989; also see Pregill, 1986) that indicate that large species have decreased in size on several two-species islands over the last several thousand years. Pregill (1986; Pregill et al., 1988), however, argued that, contrary to the predictions of this hypothesis, only *leachi,* and not *wattsi,* has decreased in size on Antigua; he interpreted recent changes in size as phenotypic and/or genotypic responses to human habitat degradation.

Roughgarden's scenario is plausible, but it faces several difficulties when considered phylogenetically. If the cycle has occurred several times, then solitary species should not all be most closely related to each other; some should have as their closest relatives the larger species on two-species islands, others should have the smaller species on two-species islands as their nearest relatives. The observations that all of the small species form one clade, all of the large species on two-species islands are closely related and may be sister taxa, and all solitary island species are members of two monophyletic groups suggest that, if a taxon cycle is

operating, it has not gone through more than one loop (Roughgarden and Pacala, 1989). If, in fact, the cycle is in the first loop, it still seems improbable that the islands (or island banks) upon which large colonizing species have landed should be only those occupied by members of the *wattsi* group.

Furthermore, the hypothesis does not adequately explain why large size originally evolved in *bimaculatus* and *leachi*. The taxon-cycle hypothesis predicts that large size originally evolved on a single-species island, not coincident with the move from a one-species to a two-species island, as I have argued. Roughgarden et al. (1987) and Roughgarden and Pacala (1989) have suggested that *bimaculatus* and *leachi* are descended from large colonists from Guadeloupe. Phylogenetic analysis, however, lends no support to this position; *bimaculatus-leachi* and *marmoratus* are not closely related (Roughgarden et al., 1987). In addition, the largest *marmoratus* are substantially smaller than the largest *bimaculatus* and *leachi* (Lazell, 1972). Consequently, even if *marmoratus* were the ancestor of *bimaculatus-leachi,* the increase of size in the descendant species (*bimaculatus-leachi*), contrary to the taxon-cycle hypothesis, would require explanation.

My analysis indicates that large size in the *bimaculatus-leachi* lineage evolved simultaneously with the achievement of sympatry with the *wattsi* group. The conservative conclusion, given the evidence at hand, is that most size differences between co-occurring species in the northern Lesser Antilles stem from a few, relatively old phylogenetic events probably caused by character displacement. Subsequently, differential assortment of species of different sizes, perhaps coupled with the fragmentation of island banks caused by rising ocean levels, have produced the current distributional pattern—one dominated by size assortment.

The advent of rigorous statistical testing as a means of examining claims of unusual patterns of species distributions and co-occurrences has been a valuable advance. However, these patterns reflect an historical legacy as well as the results of ongoing ecological processes. By ignoring history, null models implicitly assume that adaptation to current conditions occurs so rapidly that the vestiges of history are quickly erased. In many cases this is not correct (Gould and Lewontin, 1979). I have outlined a methodology that, by incorporating historical information, permits an evaluation of both the ecological (size assortment) and evolutionary (size adjustment) processes potentially responsible for generating patterns of species distributions.

Acknowledgments

I thank K. de Queiroz, T. Garland, G. C. Gorman, H. W. Greene, E. Grosholz, J. Groth, R. B. Huey, E. C. Losos, G. C. Mayer, A. Meyer, J. Roughgarden, D. Schluter, C. J. Schneider, and D. B. Wake for helpful comments on previous versions of this paper. Thanks to K. Klitz for drawing Figure 1, and to D. Cannatella and K. de Queiroz for assistance on the other figures.

Literature Cited

Baverstock, P. R., S. R. Cole, B. J. Richardson, and C. H. S. Watts. 1979. Electrophoresis and cladistics. Syst. Zool. 28:214–219.

Cannatella, D. C., and K. de Queiroz. 1989. Phylogenetic systematics of the anoles: Is a new taxonomy warranted? Syst. Zool. 38:57–69.

Case, T. J. 1983. Sympatry and size similarity in *Cnemidophorus,* pp. 297–325. *In* R. B. Huey, E. R. Pianka, and T. W. Schoener (eds.), Lizard Ecology: Studies of a Model Organism. Harvard Univ. Press, Cambridge.

Case, T. J., J. Faaborg, and R. Sidell. 1983. The role of body size in the assembly of West Indian bird communities. Evolution 37:1062–1074.

Case, T. J., and R. Sidell. 1983. Pattern and chance in the structure of model and natural communities. Evolution 37:832–849.

Colwell, R. K., and D. W. Winkler. 1984. A null model for null models in biogeography, pp. 344–359. *In* D. R. Strong, Jr., D. Simberloff, L. G. Abele, and A. B. Thistle (eds.), Ecological Communities: Conceptual Issues and the Evidence. Princeton Univ. Press, Princeton, NJ.

Connor, E. H., and D. Simberloff. 1979. The assembly of species communities: Chance or competition? Ecology 60:1132–1140.

———. 1983. Interspecific competition and species co-occurrence patterns on islands: Null models and the evaluation of evidence. Oikos 41:455–465.

Diamond, J. M., and M. E. Gilpin. 1982. Examination of the "null" model of Connor and Simberloff for species co-occurrences on islands. Oecologia 52:64–74.

Donoghue, M. J. 1989. Phylogenies and the analysis of evolutionary sequences, with examples from seed plants. Evolution 43:1137–1156.

Etheridge, R. 1964. Late Pleistocene lizards from Barbuda, British West Indies. Bull. Fla. State Mus. 9:43–75.

FALCONER, D. S. 1981. Introduction to Quantitative Genetics. 2nd ed. Longman, London, U.K.

FARRIS, J. S. 1970. Methods for computing Wagner trees. Syst. Zool. 19:83–92.

FELSENSTEIN, J. 1985. Phylogenies and the comparative method. Amer. Natur. 125:1–15.

———. 1988. Phylogenies and quantitative characters. Ann. Rev. Ecol. Syst. 19:445–471.

GORMAN, G. C., AND Y. J. KIM. 1976. *Anolis* lizards of the Eastern Caribbean: A case study in evolution. II. Genetic relationships and genetic variation of the *bimaculatus* group. Syst. Zool. 25:62–77.

GORMAN, G. C., Y. J. KIM, AND S. Y. YANG. 1978. The genetics of colonization: Loss of variability among introduced populations of *Anolis* lizards (Reptilia, Lacertilia, Iguanidae). J. Herpet. 12:47–51.

GORMAN, G. C., AND S. Y. YANG. 1975. A low level of backcrossing between the hybridizing *Anolis* lizards of Trinidad. Herpetologica 31:196–198.

GOULD, S. J., AND R. C. LEWONTIN. 1979. The spandrels of San Marco and the Panglossian paradigm: A critique of the adaptationist programme. Proc. R. Soc. Lond. B. 205:581–598.

GRANT, P. R. 1986. Ecology and Evolution of Darwin's Finches. Princeton Univ. Press, Princeton, NJ.

GRANT, P. R., AND I. ABBOTT. 1980. Interspecific competition, island biogeography and null hypotheses. Evolution 34:332–341.

GUYER, C., AND J. M. SAVAGE. 1986. Cladistic relationships among anoles (Sauria: Iguanidae). Syst. Zool. 35:509–531.

HARVEY, P. H., R. K. COLWELL, J. W. SILVERTOWN, AND R. M. MAY. 1983. Null models in ecology. Ann. Rev. Ecol. Syst. 14:189–211.

HENDRICKSON, J. A., JR. 1981. Community-wide character displacement reexamined. Evolution 35: 794–809.

HUEY, R. B. 1987. Phylogeny, history, and the comparative method, pp. 76–98. *In* M. E. Feder, A. F. Bennett, W. Burggren, and R. B. Huey (eds.), New Directions in Ecological Physiology. Cambridge University Press, Cambridge.

HUEY, R. B., AND A. F. BENNETT. 1987. Phylogenetic studies of coadaptation: Preferred temperatures versus optimal performance temperatures of lizards. Evolution 41:1098–1115.

LARSON, A. 1984. Neontological inferences of evolutionary pattern and process in the salamander family Plethodontidae. Evol. Biol. 17:119–217.

LAUDER, G. V. 1981. Form and function: Structural analysis in evolutionary morphology. Paleobiology 7:430–442.

LAZELL, J. D., JR. 1972. The anoles (Sauria: Iguanidae) of the Lesser Antilles. Bull. Mus. Comp. Zool. 143:1–115.

LISTER, B. C. 1976. The nature of niche expansion in West Indian *Anolis* lizards II: Evolutionary components. Evolution 30:677–692.

PACALA, S. W., AND J. ROUGHGARDEN. 1982. Resource partitioning and interspecific competition in two two-species insular *Anolis* lizard communities. Science 217:444–446.

———. 1985. Population experiments with the *Anolis* lizards of St. Maarten and St. Eustatius. Ecology 66:129–141.

PREGILL, G. K. 1986. Body size of insular lizards: A pattern of Holocene dwarfism. Evolution 40:997–1008.

PREGILL, G. K., D. W. STEADMAN, AND S. L. OLSON. 1988. Late Holocene fossil vertebrates from Burma Quarry, Antigua, W.I. Smith. Cont. Zool. 463: 1–28.

ROSEN, D. E. 1978. Vicariant patterns and historical explanation in biogeography. Syst. Zool. 27:159–188.

ROUGHGARDEN, J. D. 1974. Niche width: Biogeographic patterns among *Anolis* lizard populations. Amer. Natur. 108:429–442.

ROUGHGARDEN, J. D., AND E. R. FUENTES. 1977. The environmental determinants of size in solitary populations of West Indian *Anolis* lizards. Oikos 29: 44–51.

ROUGHGARDEN, J. D., S. D. GAINES, AND S. W. PACALA. 1987. Supply side ecology: The role of physical transport processes, pp. 491–518. *In* P. Giller and J. Gee (eds.), Organization of Communities: Past and Present. Blackwell Scientific, London, U.K.

ROUGHGARDEN, J. D., D. HECKEL, AND E. R. FUENTES. 1983. Coevolutionary theory and the island biogeography of *Anolis*, pp. 371–410. *In* R. B. Huey, E. R. Pianka, and T. W. Schoener (eds.), Lizard Ecology: Studies on a Model Organism. Harvard Univ. Press, Cambridge.

ROUGHGARDEN, J. D., AND S. PACALA. 1989. Taxon cycle among *Anolis* lizard populations: Review of evidence, pp. 403–432. *In* D. Otte and J. A. Endler (eds.), Speciation and Adaptation. Acad. Nat. Sci., Philadelphia, PA.

ROUGHGARDEN, J. D., S. PACALA, AND J. D. RUMMEL. 1984. Strong present-day competition between the *Anolis* lizard populations of St. Maarten (Neth. Antilles), pp. 203–220. *In* B. Shorrocks, (ed.), Evolutionary Ecology. Blackwell, London, U.K.

RUMMEL, J. D., AND J. D. ROUGHGARDEN. 1985*a*. Effects of reduced perch-height separation on competition between two *Anolis* lizards. Ecology 66: 430–444.

———. 1985*b*. A theory of faunal buildup for competition communities. Evolution 39:1009–1033.

SCHOENER, T. W. 1969*a*. Size patterns in West Indian *Anolis* lizards: I. Size and species diversity. Syst. Zool. 18:386–401.

———. 1969*b*. Models of optimal size for solitary predators. Amer. Natur. 103:277–313.

———. 1970. Size patterns in West Indian *Anolis* lizards. II. Correlations with the sizes of particular sympatric species—displacement and convergence. Amer. Natur. 104:155–174.

———. 1975. Presence and absence of habitat shift in some widespread lizard species. Ecol. Monogr. 45:233–258.

———. 1984. Size differences among sympatric, bird-eating hawks: A worldwide survey, pp. 254–281. *In* D. R. Strong, Jr., D. Simberloff, L. G. Abele, and A. B. Thistle (eds.), Ecological Communities: Conceptual Issues and the Evidence. Princeton Univ. Press, Princeton, NJ.

———. 1988. Testing for nonrandomness in sizes

and habitats of West Indian lizards: Choice of species pool affects conclusions from null models. Evol. Ecol. 2:1–26.

SCHOENER, T. W., AND A. SCHOENER. 1983. Distribution of vertebrates on some very small islands. I. Occurrence sequences of individual species. J. Anim. Ecol. 52:209–235.

SESSIONS, S. K., AND A. LARSON. 1987. Developmental correlates of genome size in plethodontid salamanders and their implications for genome evolution. Evolution 41:1239–1251.

SIMBERLOFF, D. S. 1983. Sizes of coexisting species, pp. 404–430. *In* D. J. Futuyma and M. Slatkin (eds.), Coevolution. Sinauer, Sunderland, MA.

SIMBERLOFF, D. S., AND W. BOECKLEN. 1981. Santa Rosalia reconsidered: Size ratios and competition. Evolution 35:1206–1228.

SIMBERLOFF, D. S., AND E. F. CONNOR. 1981. Missing species combinations. Amer. Natur. 118:215–239.

SOKAL, R. R., AND J. ROHLF. 1981. Biometry, 2nd ed. Freeman, San Francisco, CA.

STEADMAN, D. W., G. K. PREGILL, AND S. L. OLSON. 1984. Fossil vertebrates from Antigua, Lesser Antilles: Evidence for late Holocene human-caused extinctions in the West Indies. Proc. Nat. Acad. Sci. U.S.A. 81:4448–4451.

STRONG, D. R., JR., L. A. SZYSKA, AND D. S. SIMBERLOFF. 1979. Test of community-wide character displacement against null hypotheses. Evolution 33:897–913.

SWOFFORD, D. L., AND W. P. MADDISON. 1987. Reconstructing ancestral character states under Wagner parsimony. Math. Biosci. 87:199–229.

WILLIAMS, E. E. 1969. The ecology of colonization as seen in the zoogeography of anoline lizards on small islands. Quart. Rev. Biol. 44:345–389.

———. 1972. The origin of faunas: Evolution of lizard congeners in a complex island fauna—a trial analysis. Evol. Biol. 6:47–89.

WILLIAMSON, M. 1981. Island Populations. Oxford Univ. Press, Oxford, U.K.

YANG, S. Y., M. SOULÉ, AND G. C. GORMAN. 1974. *Anolis* lizards of the eastern Caribbean: A case study in evolution. I. Genetic relationships, phylogeny, and colonization sequence of the *roquet* group. Syst. Zool. 23:387–399.

Corresponding Editor: R. B. Huey