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A Critical Comparison of the Taxon-Cycle and Character-Displacement Models for Size Evolution of *Anolis* Lizards in the Lesser Antilles

JONATHAN B. LOSOS

FEW convincing examples of character displacement exist (reviews in Grant, 1972; Simberloff, 1983; Schoener, 1988a). One of the most frequently cited cases (Simberloff, 1983) concerns Caribbean *Anolis* lizards. Studies on the anoles of the northern Lesser Antilles have revealed an interesting pattern: on most islands with only one species, that species is of intermediate size, but two-species islands usually contain both a large and a small species (Schoener, 1970; Table 1). The evolution of large and small size has often been interpreted as an example of character displacement (e.g., Schoener, 1988b; Williams 1972; Losos, 1990). Roughgarden and associates (e.g., Roughgarden et al., 1987; Roughgarden and Pacala, 1989; Rummel and Roughgarden 1985a) have proposed an alternative hypothesis; they argue that a taxon cycle is operating in the northern Lesser Antilles in which a larger species invades an island occupied by an intermediate-sized species, and both evolve smaller size until the former species is intermediate in size and the latter species is extinct (Fig. 1). Roughgarden and Pacala (1989) reviewed the pertinent data and concluded that the available evidence overwhelmingly favors the taxon-cycle model. Here I argue that much of this evidence is either inconclusive, incorrect, or more consistent with the character-displacement model.

MODELS

Both models posit that intermediate size is optimal for solitary species (i.e., a species on a one-species island). This premise has recently been supported by a physiological model based on foraging energetics and incorporating data on lizard metabolism, locomotion, digestion, and

visual acuity (Naganuma and Roughgarden, 1990).

The character-displacement model predicts that, when an intermediate-sized species colonizes an island already occupied by another intermediate-sized species, the two species may evolve in opposite directions (larger and smaller) until competition is decreased enough for stable coexistence (i.e., character displacement; Fig. 1). In many cases, however, competitive exclusion will result in the extinction of one species before enough time has elapsed for size evolution to occur; the relative likelihood of displacement vs extinction has been modeled extensively (e.g., Slatkin, 1980; Taper and Case, 1985; Abrams, 1986). If a large or small species invaded an island occupied by an intermediate-sized species, then competition would ensue. The time to competitive exclusion relative to the rapidity with which displacement occurred would determine whether extinction or coexistence would result. Further, the scarcity of two-species islands containing an intermediate and a large or small species suggests either that invasion is infrequent or that displacement occurs quickly in these circumstances.

The taxon-cycle hypothesis suggests that asymmetric competition favors larger species, which therefore can invade islands occupied by intermediate-sized species. When this happens, the larger species evolves toward the optimal solitary size whereas the smaller species evolves even smaller to diminish competitive effects; eventually the larger species reaches intermediate size, the smaller species becomes extinct, and the stage is set for another round in the cycle (Fig. 1).

The source of the large colonists in the taxon-cycle hypothesis is theorized to be the large montane populations that occur on Dominica

TABLE 1. *Anolis* SIZE ON 1- AND 2-SPECIES ISLANDS IN THE LESSER ANTILLES. Data from Schoener (1970).

Island	Species	Size*
Anguilla	<i>gingivinus</i>	18.8
St. Barthelemy	<i>gingivinus</i>	19.7
Saba	<i>sabanus</i>	18.3
Redonda	<i>nubilus</i>	21.1
Montserrat	<i>lividus</i>	18.7
Guadeloupe	<i>marmoratus</i>	18.9
La Desirade	<i>marmoratus</i>	19.9
Marie Galante	<i>ferreus</i>	28.4
Iles de Saintes (1)	<i>terraealtae</i>	21.3
Iles de Saintes (2)	<i>terraealtae</i>	21.5
Dominica	<i>oculatus</i>	22.3
St. Maarten	<i>gingivinus</i>	19.6
	<i>pogus</i>	13.5
St. Eustatius	<i>bimaculatus</i>	23.6
	<i>schwartzi</i>	14.3
St. Christopher	<i>bimaculatus</i>	27.9
	<i>schwartzi</i>	14.2
Nevis	<i>bimaculatus</i>	27.1
	<i>schwartzi</i>	14.2
Barbuda	<i>leachi</i>	28.6
	<i>wattsi</i>	14.5
Antigua	<i>leachi</i>	28.8
	<i>wattsi</i>	14.9

* Mean jaw length of males.

(Lazell, 1972) and are postulated to occur on other high elevation islands (Roughgarden and Pacala, 1989). Roughgarden and Fuentes (1977) discovered a correlation between insect abundance and lizard size among populations of two species of *Anolis* and attributed the large size of montane *A. oculatus* on Dominica to the increased insect abundance at high elevations [the model of Naganuma and Roughgarden (1990) did not address what the optimal size for these populations would be].

Figure 1 contrasts the models. Stage (c) is identical in both models and corresponds to the situation on all two-species islands except St. Maarten, which corresponds to (d) in the taxon cycle scenario and is not predicted by the character-displacement model. No examples of (b) in the taxon-cycle model exists. *Anolis ferreus* on Marie Galante might be an appropriate example of (a) in the taxon-cycle model (though it is a little too small), but Roughgarden and Pacala (1989) discount this possibility for other reasons. No other suitable example of (a) exists.

The two models, thus, differ importantly in two respects: the chronology of size evolution (whether large size evolves in a species allopatric

or sympatric to a second species) and whether the coexistence of a large and small species is an evolutionarily stable equilibrium or just one stage in an endless cycle. The taxon cycle envisions the size of species on Lesser Antillean islands as representing several stages in the cycle, whereas the character-displacement model sees the large and small species sympatric on five islands as the end-result of character displacement (see Fig. 1). Roughgarden and Pacala (1989) reviewed data on competition, introductions, present-day distribution, and fossils of Lesser Antillean *Anolis* and concluded that the data "support [the taxon-cycle] hypothesis, and falsify the alternative hypothesis of faunal build-up through invasion followed by character displacement." (p. 430) My purpose in this analysis is to reevaluate these data and their interpretation, provide additional relevant data on these points, and provide several other lines of evidence pertinent to the taxon cycle-character displacement controversy.

EVIDENCE

Competition on two-species islands.—A basic tenet of the taxon-cycle model is that asymmetric competition favors larger species (i.e., the larger species has a greater effect on the smaller species than vice versa). By contrast, the outcome of character displacement should be two species (large and small) coexisting with relatively weak competition in an evolutionarily stable equilibrium. Both models predict that the competition should exist between species that are too close in size (e.g., an intermediate and a small species).

These hypotheses are pertinent to experiments on competition between the anoles on St. Eustatius and St. Maarten (Pacala and Roughgarden, 1982, 1985; Rummel and Roughgarden, 1985b). Both hypotheses predict the observed substantial competition on St. Maarten between the intermediate-sized *A. gingivinus* and the small *A. pogus* (Roughgarden et al., 1984; Pacala and Roughgarden, 1985) but differ in their predictions concerning St. Eustatius. The experiments on St. Eustatius demonstrated that the presence of the smaller *A. schwartzi* had no measurable effect on the larger *A. bimaculatus* (Pacala and Roughgarden, 1985). The presence of *A. bimaculatus* did not affect the growth, egg production, or food intake of *A. schwartzi*; *A. schwartzi* was, however, active at different times and in hotter microclimates in the presence of *A. bimaculatus* (Rummel and Roughgarden,

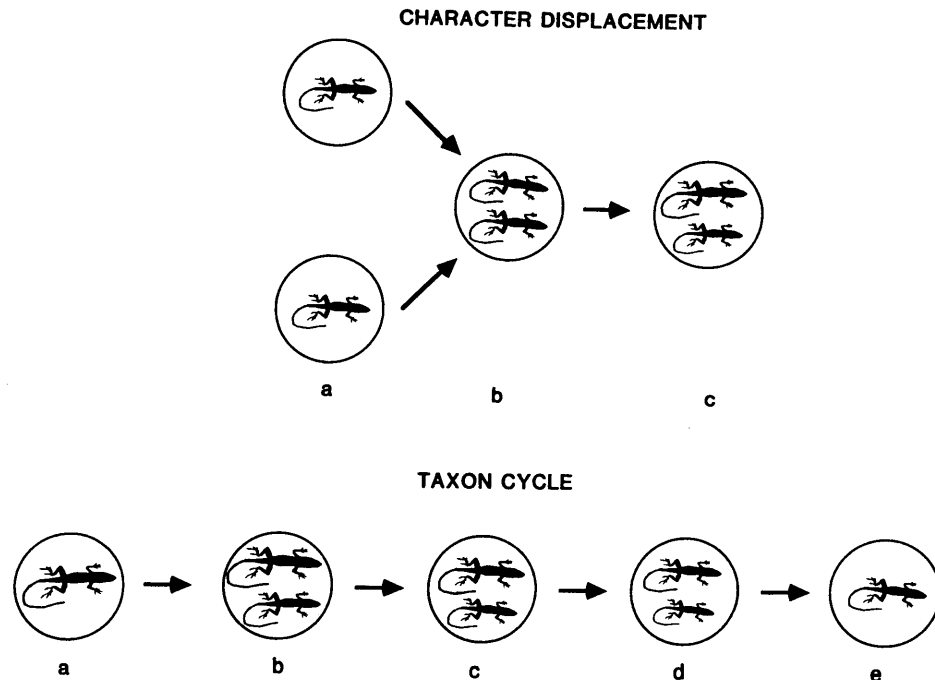


Fig. 1. The character-displacement (top) and taxon-cycle (bottom) models. In the taxon-cycle model, a species evolves to large size on a one-species island (a), colonizes an island occupied by an intermediate-sized species (b), both evolve to smaller size (c), the larger species approaches intermediate size as the smaller species becomes very small (d), and the larger species attains intermediate size as the small species perishes (e). In the character-displacement model, one-species islands are occupied by intermediate-sized species (a); when a species colonizes an island already occupied by another intermediate-size species (b), it usually becomes extinct; but occasionally both species evolve in size, resulting in a large and a small species (c).

1985b). Rummel and Roughgarden (1985b) interpreted this shift in perch position and activity time as evidence that competition is asymmetric, favoring *A. bimaculatus* over *A. schwartzi*, which, according to the taxon-cycle model, would force *A. schwartzi* to evolve smaller body size to minimize competition with *A. bimaculatus* (Roughgarden et al., 1984; Roughgarden and Pacala, 1989). But the fact that *A. bimaculatus* does not affect *A. schwartzi*'s food capture, growth, or reproductive rates indicates that the competitive effect of *A. bimaculatus* on *A. schwartzi* is negligible, as predicted by the character-displacement model. It does not seem likely that *A. schwartzi* would evolve smaller size to minimize these seemingly inconsequential effects.

Furthermore, the difference in size between the two species on St. Eustatius is considerably less than on the other four islands that contain a large and a small species in the northern Lesser Antilles [based on the data of Schoener (1970), see Table 1; Roughgarden (1979), however, found that the difference on one of these four islands, Antigua, is only slightly greater than the difference in size on St. Eustatius]. Because

degree of competition is a function of how similar in size two species are, competitive effects leading to size evolution are thus even less likely in these putative earlier stages of the taxon cycle.

Accidental and experimental introductions.—A number of cases of introduction of anoles have been reported. Roughgarden and Pacala (1989) summarize the literature on introductions to Bermuda, the Dominican Republic, the Bahamas, St. Lucia, and cays near St. Maarten, and claim that (1) species can invade and expand their range on islands only when the resident species is smaller than the invader; and (2) when the invading species and the resident are similar in size, the invader can only establish local "enclaves" within the range of the resident. They conclude from (2) that two similar-sized species cannot become widely established on the same island; consequently, they claim character displacement is not possible. The success of larger species (1) is taken as indicative of asymmetric competition, in accord with the taxon-cycle hypothesis. I will demonstrate that these claims are not correct.

Introduction of larger or smaller species.—Bermuda, originally free of *Anolis*, has been the site of several introductions (Wingate, 1965). The intermediate-sized *A. grahami* was introduced from Jamaica in 1905 and rapidly expanded throughout the island. The large-sized *A. leachi* was introduced around 1940 and has expanded its range over much of the central portion of the island. However, the success of *A. leachi* may not be generalizable to interactions among Lesser Antillean taxa. Greater Antillean anoles, such as *A. grahami*, are more ecologically specialized and occur in more complex faunas [as many as 10 sympatric species in some communities (Williams, 1983)]. For example, up to four Greater Antillean species co-occur on some islands in the Bahamas (Schoener, 1969; Williams, 1969, 1983), whereas in the Lesser Antilles, no island contains more than two of the less-specialized Lesser Antillean species. In Jamaica, *A. grahami* co-occurs widely with a large species (*A. garmani*); consequently, it would not have been expected to exclude *A. leachi* on Bermuda. Similarly, the outcome of other introductions involving Greater Antillean taxa (see below) may be more a function of microhabitat and microclimatic specialization than of size differences.

Roughgarden and Pacala (1989) report two instances of an introduced small species failing to persist in the presence of an intermediate-sized species [*A. wattsi* on St. Lucia (Williams, 1977) and *A. pogus* onto a small cay off St. Maarten (Roughgarden et al., 1984)] but fail to note a number of cases in which a smaller species successfully colonized in the presence of a larger species. In Florida, originally occupied only by the intermediate-sized *A. carolinensis*, the smaller *A. distichus* and *A. sagrei* have successfully colonized and are now widespread (Wilson and Porras, 1983). *Anolis sagrei* has also recently invaded and is expanding its range rapidly on both Grand Cayman Island (Minton and Minton, 1984; G. C. Mayer, pers. comm.) and Jamaica (Williams, 1969; G. C. Mayer, pers. comm.), despite the presence of similar-sized and larger species.

Introduced species of the same size as resident species.—The third, and last, species introduced to Bermuda, the intermediate-sized species *A. extremus* from Barbados, appeared sometime around 1945. Contrary to previous claims (Roughgarden et al., 1984; Pacala and Roughgarden, 1985; Roughgarden and Pacala, 1989),

Wingate (1965) reported *A. extremus* is also expanding its range in sympatry with *A. grahami*, which indicates that a species can expand on an island with species of the same size.

Two species (*A. cristatellus* and *A. porcatius*) have been introduced to Hispaniola, where species of similar size and ecology occur. Both have been established for over 20 years, but Roughgarden and Pacala (1989) emphasized their lack of range expansion. *Anolis porcatius*, in fact, has increased its range (Haneline, 1977; Powell et al., 1990). The failure of *A. cristatellus* to expand its range from the city of La Romana, Dominican Republic, more probably results from the lack of appropriate habitat (the city is surrounded by arid scrub), rather than competition from native anoles (Williams, 1977; Fitch et al., 1989).

In any case, the ability of introduced populations simply to persist in the face of competition from native species of similar size is sufficient for character displacement to occur. Even if the populations were parapatric, the selective pressure for size divergence would be present. In particular, the introduced population would likely be small; a relatively large proportion of individuals would occur on the population's border and face strong competitive pressures from the other species surrounding it. Widespread sympatry might only result after size divergence had occurred, though the spread of *A. extremus* in Bermuda indicates that this need not always be the case. Rather than indicating that character displacement is impossible (Roughgarden and Pacala, 1989), the establishment and survival of these populations in Hispaniola, as well as the spread of *A. extremus* in Bermuda, fulfills the first stage of a character-displacement scenario.

Roughgarden and Pacala (1989) also commented on introductions to Bahamian islands already occupied by an *Anolis* species, citing Schoener and Schoener (1983). That paper did not report such introductions, but the experiments were subsequently performed in 1984. Not enough time has passed, however, to adequately assess the outcome of these introductions (T. Schoener, pers. comm.).

Size change documented by fossil data.—Roughgarden and Pacala (1989) suggest that, if the character-displacement hypothesis is correct, then fossil evidence should document evolutionary increases, as well as decreases, in size, whereas the taxon-cycle hypothesis predicts that only decreases in size would be observed. They

argue that subfossil data from Anguilla, Antigua, and Barbuda reveal only decreases in size. These claims, however, are not supported by their data or the literature.

Before the *Anolis* fossil data can be considered, however, it must be placed in the context of patterns observed in all recent lizard fossil data. Pregill (1986) has documented a worldwide trend for reduction in size of insular lizards occurring in the late Pleistocene and, primarily, the Holocene. A hypothesis peculiar to size reduction in Lesser Antillean *Anolis* thus seems too narrowly focused. Whether human habitat destruction is the causative agent for this universal decrease in size is disputed (Pregill, 1986; Roughgarden and Pacala, 1989). Roughgarden and Pacala's (1989) ad hoc alternative suggestion that processes similar to the proposed taxon cycle are affecting insular lizards of all kinds worldwide is without theoretical or empirical foundation.

Anguilla.—Both *A. gingivinus* and *A. pogus* historically occurred on Anguilla, but *A. pogus* has not been collected there since 1922 (Lazell, 1972). Roughgarden and Pacala (1989) reported on the excavation of a subfossil cave site. Based on the recovery of anole dentaries, they presented data on the distribution of lizard sizes at 15 strata, ranging in age from >8000 years b.p. to recent. The results are summarized in Table 2. Roughgarden and Pacala (1989) interpret these results as indicating that *A. gingivinus* arrived on Anguilla approximately 3000–4000 years b.p. (stratum 8). After the extinction of *A. pogus* (stratum 1), *A. gingivinus* decreased in size, in accordance with the taxon-cycle hypothesis.

There are several difficulties with this interpretation. Roughgarden and Pacala could not assign the fossil remains to particular species, which makes the interpretations of events problematic. For example, it is not possible to determine whether *A. gingivinus* arrived at a larger size, as Roughgarden and Pacala assert, or arrived at the same size as *A. pogus* and subsequently evolved to a larger size on Anguilla (the rapid decrease in size of *A. gingivinus* in the last stratum indicates that such rapid size change could evolve in situ). Even if they are correct about *A. gingivinus* arriving at a larger size 3000–4000 years ago, other details do not fit the taxon-cycle hypothesis. If *A. pogus* were the only species present prior to 3000–4000 years ago, it was inexplicably only slightly larger than it is

TABLE 2. DENTARY SIZE OF FOSSIL *Anolis* ON ANGUILLA. Data from Roughgarden and Pacala (1989, table 1).

Stratum	Mean \pm SE	n
1	8.55 \pm 0.23	22
2	9.10 \pm 0.12	63
3	9.03 \pm 0.16	42
4	9.18 \pm 0.09	92
5	8.96 \pm 0.09	96
6	8.90 \pm 0.15	43
7	8.69 \pm 0.23	23
8	8.53 \pm 0.20	7
9	7.83 \pm 0.53	6
10	7.85 \pm 0.34	12
11	7.78 \pm 0.51	5
12	8.28 \pm 0.78	4
13	8.33 \pm 0.23	3
14	7.1	1
15	8.75 \pm 0.85	2

currently on St. Maarten (Roughgarden and Pacala, 1989; Table 2), well below the solitary size typical of one-species islands. Similarly, at its largest, *A. gingivinus* was not substantially larger than its present intermediate size (Roughgarden and Pacala, 1989; Table 2). Thus, this situation cannot be viewed as an intermediate stage in a size reduction cycle beginning with a species the size of *A. bimaculatus*. Furthermore, the fossil record does not document a gradual decline in *A. gingivinus*, as predicted by the taxon cycle hypothesis. Rather, *A. gingivinus* actually increases slightly in size from stratum 8 to stratum 2 [although t-tests between successive strata are all nonsignificant, the overall trend is toward an increase in mean size over time (Kendall's test of rank concordance, $\text{Tau} = 0.81$, two-tailed, $P < 0.05$)], before decreasing in size in stratum 1. Roughgarden and Pacala (1989) present an ad hoc scenario to account for this situation.

An alternative explanation, akin to the failed invasion theory of Williams (1969), is consistent with the character-displacement model. The species first came together 3000–4000 years ago (which species was the colonist and which the resident is irrelevant). *Anolis gingivinus* increased slightly in size, but *A. pogus* became extinct before the species could evolve a great enough size difference to allow coexistence. Subsequently, *A. gingivinus* evolved back to the solitary size.

A more conservative approach would remain agnostic on the cause of the size increase 3000–

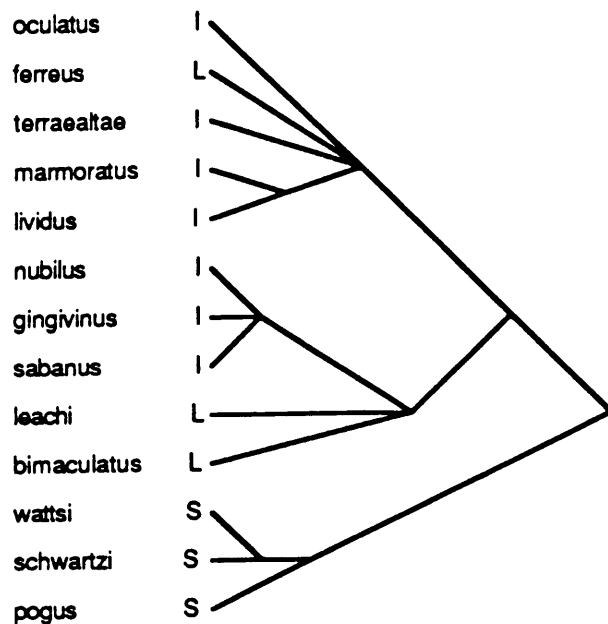


Fig. 2. Phylogeny of northern Lesser Antillean *Anolis* (from Roughgarden et al., 1987). S = Small size; I = Intermediate size; L = Large size.

4000 years (possible alternatives include natural or humanmade habitat alterations and changes in the foraging behavior of the kestrels which caught the lizards and left their remains in the cave). The coincident extinction of *A. pogus* and size decrease in *A. gingivinus*, not separable in the fossil record, might have resulted from human habitat modification or other factors.

Antigua.—On Antigua, the fossil record indicates that the large species (*A. leachi*) has decreased substantially in size but the small species (*A. wattsi*) has not changed in size since the late Pleistocene [Pregill, 1986; contrary to Pregill et al. (1988), *A. wattsi* fossils can be distinguished from similar-sized *A. leachi* (G. K. Pregill, pers. comm.)]. This is inconsistent with both models. Pregill (1986) suggests human habitat alteration as the cause for the size reduction in *A. leachi*.

Barbuda.—Fossil data from Barbuda is also inconsistent with the taxon cycle model. Etheridge (1964) reported three species of *Anolis* from cave deposits. The largest species was *A. leachi*, which, Etheridge reported, was larger than it is now on Barbuda. Neither of the other two taxa could definitely be associated with the small species, *A. wattsi*, currently found on Barbuda, but the smaller of the two was approximately the size of *A. wattsi* on Barbuda now. Lazell (1972) subsequently demonstrated that the large fossils were male *A. leachi* and that the intermediate-

sized ones were female *A. leachi*, which means the small fossils probably are *A. wattsi*. He further demonstrated that the *A. leachi* on Barbuda now are the same size as the large fossils. Consequently, neither the large *A. leachi* nor the small *A. wattsi* has evolved in body size, in agreement with the prediction of the character-displacement model that a stable equilibrium has been established.

Size change in recently introduced populations.—Data also exist on contemporary change in size in *A. leachi* since it was introduced from Antigua to Bermuda around 1940 (see above). Pregill (1986) compared the size of *A. leachi* on Antigua and Bermuda and found that the lizards on Bermuda have increased in size. This finding is in disagreement with the taxon-cycle model but is what the character-displacement model would predict when a large species is introduced to an island already occupied by an intermediate-sized species.

Phylogenetic inference of the cause of size change.—The taxon-cycle model predicts that large size evolves on certain one-species islands (i.e., mountainous islands; see above), and that after a large and an intermediate-sized species come into sympatry, both evolve to smaller size. The character-displacement model predicts that the evolution of large and small size occurs subsequent to sympatry. Parsimony techniques (Farris, 1970; Huey and Bennett, 1987) can be used to reconstruct the evolution of body size in Lesser Antillean *Anolis*. A reconstruction of ancestral character states, based on a phylogeny of northern Lesser Antillean *Anolis* (Roughgarden et al., 1987; Fig. 2), suggests that the common ancestor of *A. bimaculatus* and *A. leachi* evolved to large size and the ancestor of the *wattsi* group (*A. wattsi*, *A. pogus*, and *A. schwartzi*) evolved to small size when the two became sympatric (Losos, 1990), which supports the character-displacement model.

Anoles of St. Maarten.—Roughgarden and Pacala (1989) consider the occurrence of an intermediate-sized (*A. gingivinus*) and a small (*A. pogus*) species on St. Maarten to be fundamentally incompatible with the character-displacement model. The coexistence of two such species is a predicted stage of the taxon-cycle model but could only coexist transitorily (prior to extinction of the small species or evolution of increased difference in size) in the character-displacement model. Because both populations are

morphologically and biochemically differentiated from other nearby taxa, Roughgarden and Pacala (1989) contend that they must have been on St. Maarten too long for the character-displacement scenario. However, no necessary relationship exists between morphological differentiation and time of divergence. Data from a wide variety of organisms refutes the existence of such a "morphological clock," including examples from *Anolis* (e.g., Williams, 1975; Webster, 1975; Case and Williams, 1987). The molecular clock is also disputed (e.g., Gillespie, 1986; Vawter and Brown, 1986). Even if the molecular clock is correct, the genetic data do not preclude the possibility that *A. pogus* recently colonized St. Maarten from a well-differentiated population on another island which subsequently went extinct (J. L. Patton, pers. comm.). Anguilla is one obvious possible source.

If *A. pogus* and *A. gingivinus* have actually cooccupied St. Maarten for a long time, then why *A. pogus* has not yet perished may be a problem for the character-displacement model. In fact, *A. gingivinus* excludes *A. pogus* from much of the island, as predicted by both models. Introduction of *A. pogus* to offshore cays suggests that populations cannot long survive with *A. gingivinus* in the xeric habitat characteristic of low elevations (Roughgarden et al., 1984). *Anolis pogus* has a restricted and central range in the cooler and wetter higher elevations of St. Maarten, where it is better adapted physiologically, but drought or climatic change could cause its extinction (Roughgarden et al. 1984). This scenario perfectly fits the taxon-cycle model; whether the extinction of *A. pogus*, if and when it occurs, took too long to be compatible with the character-displacement model, is debatable.

Roughgarden and Pacala (1989) also point out that only the *wattsi* group demonstrates geographic variation worthy of subspecific designation within an island bank north of Guadeloupe, which, they contend, indicates that they occupied these islands prior to the *bimaculatus* group, as predicted by the taxon-cycle model. Subspecific designation is based on morphological differences, which are not necessarily related to time of differentiation (see above). In any case, the character-displacement model makes no prediction about which group colonized the islands first.

Difficulties with the taxon-cycle model.—The source of an ancestor larger than *A. bimaculatus* is a difficulty of the taxon-cycle model. Roughgar-

den and Pacala (1989) identified Guadeloupe as the source of large colonists. In particular, they suggested that the montane subspecies, *A. marmoratus alliaceus*, might be the ancestral taxon because it is similar in some respects to *A. bimaculatus* and because montane *A. oculatus* on Dominica reach relatively large sizes (Lazell, 1972). However, *A. oculatus montanus* attains sizes considerably less than *A. bimaculatus* (Lazell, 1972; Roughgarden and Fuentes, 1977), and *A. marmoratus alliaceus* is smaller still (Lazell, 1972; C. J. Schneider, pers. comm.). Further, the phylogeny of the anoles of the northern Lesser Antilles, which must be considered tentative and in need of further work (Roughgarden, pers. comm.), does not indicate a close relationship between *A. bimaculatus* and *A. marmoratus*. In addition, most *Anolis* colonists are intermediate in size or smaller (Schoener, 1969; Williams, 1969). A large species adapted to the cool montane climate would seem an unlikely colonist (Williams, 1969).

The taxon-cycle model also has difficulty explaining patterns produced over millions of years of colonization. Dominica and Guadeloupe, the putative sources of large colonizing species, are very old islands (Roughgarden et al., 1987) and presumably have been sending out potential colonists for millions of years. If this is true, then one would expect that the taxon cycle has been in operation long enough to go through several cycles (one cycle should occur very rapidly, perhaps less than 5000 years, if one believes the interpretation of the evidence from Anguilla). Species that colonize as large species would evolve to intermediate size. When that island is next colonized (perhaps by propagules from the same source population as the preceding colonist), the originally large species would evolve to small size. Consequently, small species should have as some of their closest relatives intermediate and large, as well as small, species. This does not appear to be the case. All small species (*A. wattsi*, *A. pogus*, and *A. schwartzi*) are more closely related to each other than to any other species (Gorman and Kim, 1976; Roughgarden et al., 1987; Fig. 2). The large species (*A. bimaculatus* and *A. leachi*) may also be sister taxa (Roughgarden et al., 1987). A more likely explanation for this pattern is that small and large size each only evolved once as a result of character displacement, and only members of these two lineages subsequently were able to jointly colonize an island and coexist (Losos, 1990).

It is also unlikely that the taxon cycle should

only occur on islands occupied by the *wattsi* series. If one assumes that members of this series were of intermediate size before the islands were invaded by large species, then there would have been 16 islands in the northern Lesser Antilles occupied by a single intermediate-sized species [seven islands with *wattsi* group populations (including *Anguilla*, where it is now extinct), and the nine other islands currently occupied by an intermediate-sized species]. It is unlikely ($P < 0.002$) that, of these 16 islands, the only ones colonized by large lizards should be those seven occupied by the *wattsi* group. Even if colonization occurred at times of lower sea level, when the present islands were distributed on eight island banks, it is still improbable that large species would land only on the three banks occupied by members of the *wattsi* group ($P = 0.05$, even if Dominica and Guadeloupe are excluded as potential islands for colonization). Again, a hypothesis of character displacement and subsequent essentially simultaneous colonization of other islands by large and small species is more likely (Losos, 1990).

CONCLUSIONS

The data reviewed by Roughgarden and Pacala (1989) neither falsify the character-displacement model nor strongly support the taxon-cycle model: (1) the insignificant competition between the large and small species on St. Eustatius is in accord with the character-displacement model and is too weak to cause the small species to evolve even smaller, as predicted by the taxon-cycle model; (2) the data do not support Roughgarden and Pacala's contention that only larger species can successfully invade an island occupied by another species; (3) the historical record of size change indicates two cases consistent with character displacement but not with the taxon cycle (the stability of size among the large and small species on Barbuda and the recent increase in size of *A. leachi* on Bermuda), one case (Antigua) which is inconsistent with both models, and one case (*Anguilla*) which is ambiguous; (4) the occurrence of an intermediate and a small species on St. Maarten is predicted by the taxon-cycle model [in fact, it was the inspiration for the model (Roughgarden et al., 1983)] but should only occur transiently in the character-displacement model. Whether the data indicate that *A. gingivinus* and *A. pogus* have been sympatric on St. Maarten too long to be consistent with the character-displacement

model is debatable. In addition, several other difficulties exist with the taxon-cycle hypothesis: (1) phylogenetic reconstruction of size evolution indicates that large size evolved in the *bimaculatus* group evolved subsequent to the attainment of sympatry with the *wattsi* group, which is consistent with the character-displacement model but not with the taxon-cycle model; (2) montane *A. ocellatus* and *A. marmoratus* are too small to have been the source of the large invading colonists that initiated the cycle and are unlikely candidates for colonists; (3) the likelihood that large colonists would land only on islands occupied by members of the *wattsi* group is small.

Neither hypothesis has been falsified; indeed, given the diversity in species and islands in the Lesser Antilles, both processes could be operating in different areas. Nonetheless, at this point, the weight of the data more strongly support the character-displacement model.

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- MUSEUM OF VERTEBRATE ZOOLOGY, UNIVERSITY OF CALIFORNIA, BERKELEY, CALIFORNIA 94720. PRESENT ADDRESS: CENTER FOR POPULATION BIOLOGY, 2320 STORER HALL, UNIVERSITY OF CALIFORNIA, DAVIS, CALIFORNIA 95616. Accepted 27 Oct. 1991.

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Comments on the Paper by Losos: Character Displacement versus Taxon Loop

JONATHAN ROUGHGARDEN

I thank J. Losos for contributing a thoughtful and professional critique of my conclusions concerning the role of competition in the assembly and coevolution of Lesser Antillean *Anolis* guilds. In this comment I wish to acknowledge some of the empirical points Losos raises and to detail where I believe Losos is mistaken. My conclusion continues to be that theory and data actually falsify the character-displacement hypothesis for the northern Lesser Antilles and weakly support the taxon-cycle hypothesis. Incidentally, I have never claimed, as Losos writes, that evidence "overwhelmingly favors the taxon-cycle model." What seems overwhelming is the evidence against character displacement, while the taxon-cycle hypothesis, although still afloat, is taking on water and listing to starboard. The following sections parallel those of Losos, and should be read correspondingly.

MODELS

It seems to me that not two, but one overall model, is being discussed, with character displacement and the taxon cycle being two of several scenarios possible with the same model. For this overall model, both Losos and I accept major premises in common, premises that had been strongly disputed during the debates about competition during the 1980s. We accept that there is an optimal body size—the so-called solitary size, that competition occurs, that competition exerts ecological and evolutionary effects on anoles, and that the strength of competition depends on the difference in body size. Specifically, both of us agree that West

Indian anole species highly dissimilar in body size do not compete, whereas two West Indian anole species of the same, or nearly same, body size do. However, for a given difference in body size, I further assume that the competition is asymmetrical, with the larger lizard having a greater effect on the smaller lizard than the reverse. Finally, both of us are comfortable with the idea of a steady state in population dynamics and coevolution, although my analysis emphasizes that a steady state is not a necessary result of coevolution. To avoid repetitious qualification, it is worth stating that only anoles of the West Indies, and in my work only those of the northeastern Caribbean, are being referred to. Any relevance to other groups is best assessed by those most familiar with such groups. Given these assumptions, models using the textbook Lotka-Volterra competition equations have been developed that predict ecological scenarios in which invasions occur, followed by coevolutionary readjustments.

To begin, suppose the competition is symmetric (which I believe is unrealistic). If the resident is assumed to have the solitary size, then two scenarios for invasion are the most likely: invasion by a species much smaller than the resident and by a species much larger than the resident. These are mathematically symmetrical alternatives. Invaders with any other sizes require a longer time for establishment, and an invader very similar to the resident should take an infinite time to establish.

This result is a fundamental challenge for the character-displacement scenario. The initial condition for character displacement, in which