

Adaptive radiation versus intraspecific differentiation: morphological variation in Caribbean *Anolis* lizards

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Abstract

Lizards in the genus *Anolis* have experienced adaptive radiation in the Greater Antilles, producing a suite of species morphologically adapted to use different parts of the environment. In the Lesser Antilles, adaptive radiation has not occurred, but on some islands, interpopulational variation is high and represents adaptation to different habitats. We compared the extent of morphological differentiation among Greater Antillean habitat specialists with that exhibited among populations of two species, *Anolis marmoratus* and *A. oculatus*, from the Lesser Antillean islands of Guadeloupe and Dominica. Although extensive, intraspecific divergence in the Lesser Antilles is substantially less in magnitude than the differences among habitat specialists in the Greater Antilles. All populations of *A. marmoratus* are most similar to Greater Antillean trunk-crown habitat specialists, but populations of *A. oculatus* differ in their affinities: some are similar to trunk-crown anoles, but others are more similar to trunk-ground habitat specialists.

Introduction

Lizards in the genus *Anolis* have radiated extensively on islands in the Greater Antilles (i.e. Cuba, Hispaniola, Jamaica and Puerto Rico): on each island, species have diversified independently, producing a suite of species morphologically adapted to different parts of the habitat (Williams, 1983; Losos, in press, and references therein). Remarkably, although divergence has occurred for the most part independently on these islands (Losos *et al.*, 1998), the same set of habitat specialists, termed 'ecomorphs' (Williams, 1972, 1983), has evolved on each island (with several exceptions). Recent studies have indicated that the morphological features that distinguish the different ecomorph types, such as limb length and lamella number, represent adaptations to the use of different habitats (reviewed in Larson & Losos, 1996).

By contrast, on smaller Caribbean islands, anoles have failed to speciate, much less radiate (Losos & Schluter, 2000). On oceanic Caribbean islands (i.e. islands that have never been connected to a larger landmass), the maximum number of anole species is two (Rand, 1969), and on most, and perhaps all, two-species islands, the two species resulted from multiple colonization events rather than divergence *in situ* (Schneider *et al.*, 2001; Creer *et al.*, 2001). Why speciation has not occurred on islands less than 3000 km² is a perplexing question, particularly given that anoles have occupied some of these islands for millions of years (Roughgarden, 1995).

This is not to say, however, that evolution has not occurred on these smaller islands. Quite the contrary, anole taxa on many of these islands are endemic species, greatly divergent from their relatives elsewhere. Moreover, on the high islands of the Lesser Antilles, extensive geographical differentiation has occurred, so much so that 12 subspecies were described for Guadeloupe and nearby islets, six for Martinique, and four for Dominica (Lazell, 1972). In a series of detailed studies on Guadeloupe and Dominica, Malhotra & Thorpe (1991a, b, 1994,

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1997) have demonstrated that this intraspecific variation correlates with geographical differences in habitat and is under the power of natural selection (reviewed in Thorpe & Malhotra, 1998; Thorpe, in press).

Given that adaptive evolution has led to a set of habitat specialists in the Greater Antilles and to geographically distinctive populations on some Lesser Antillean islands, one might wonder whether the extent of differentiation evident among Lesser Antillean populations is comparable in magnitude with the differences exhibited by different habitat specialists in the Greater Antilles. Or, to put it another way: Are populations within a species in the Lesser Antilles so distinctive that they represent different ecomorphs?

In this study, we addressed three related questions:

1 Is the extent of morphological variation among populations of *Anolis oculatus* from Dominica and *A. marmoratus* from Guadeloupe comparable in magnitude with the morphological differences among different ecomorph classes on the Greater Antilles?

2 Do populations of the Lesser Antillean species correspond to any of the ecomorph classes and does variation exist among populations in which ecomorph they most resemble (we note in passing that a previous study (Losos & de Queiroz, 1997) indicated that all but one Lesser Antillean species from a one-species island were clearly identifiable as trunk-crown ecomorphs; however, *A. oculatus* was not included in this study and only one population of *A. marmoratus* was examined).

3 Do the two Lesser Antillean species differ in extent of interpopulational variation?

Methods

We included 29 species of Greater Antillean species representing each ecomorph type from each island on which it is present (Appendix 1; Jamaica lacks grass-bush and trunk anoles and Puerto Rico lacks trunk anoles).

One to two individuals were measured per species. For the Lesser Antillean species, we sampled populations from throughout the island (Fig. 1); 14 populations of *A. marmoratus* and 14 populations of *A. oculatus* were chosen from collections in the National Museum of Natural History, Smithsonian Institution and the Museum of Vertebrate Zoology, University of California, to maximize interpopulational morphological variation based on Malhotra & Thorpe (1991a, 1994, 1997). Mean number of individuals per locality were: *A. marmoratus*, 2.8; *A. oculatus*, 4.2 (Range: 1–6 specimens per locality). All measurements were taken on adult males.

Using a ruler, we measured the following traits to the nearest 0.5 mm: snout-vent length (SVL) from the tip of the snout to the anterior end of the cloaca; tail length from the anterior end of the cloaca to the tip of the tail, excepting individuals with broken, missing, or regrown tails; and length of digit IV of the hindfoot and digit III of the forefoot (referred to as metatarsal and metacarpal to correspond with the underlying bones). In addition, lizards were radiographed and the length of the following traits measured on the radiographs using a video imaging system: femur, tibia, and the longest tarsal bone. Unfortunately, specimens were too contorted to permit accurate measurement of the humerus, radius and ulna. The number of subdigital lamellae under the third and fourth phalanges of pedal digit IV was counted using an ocular micrometer. Except when breaks or fractures occurred or when the radiograph image was poor, all measurements were taken on the right side of the specimen. Each variable was measured twice; an additional measurement (occasionally two additional measurements) was taken when the two original measurements were not within 5% of each other. Measurements were then averaged.

To examine the extent of morphological variation, we first removed the effect of body size for Greater Antillean ecomorph species by regressing species values for each variable against SVL to calculate residuals (all variables

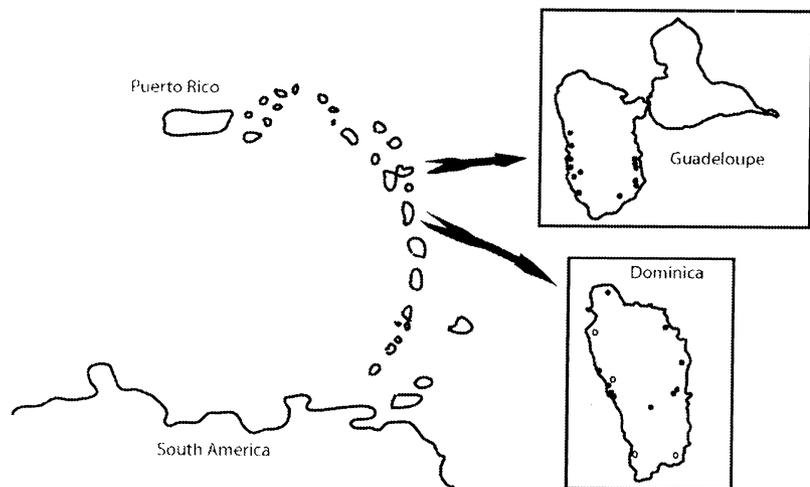


Fig. 1 Map of Guadeloupe and Dominica showing population localities. On Dominica, open circles are populations classified as trunk-crown anoles and closed circles are populations classified as trunk-ground anoles. On Guadeloupe, all populations were classified as trunk-crown anoles.

ln-transformed in these and all subsequent analyses). Using regression equations generated from the Greater Antillean species, we then calculated residual values for each population of the two Lesser Antillean species; for each population, mean values were used.

To classify the Lesser Antillean populations to ecomorph type, we conducted a discriminant function analysis (DFA). Two DFAs were conducted. The first used all variables. For this analysis, many populations had to be excluded because all individuals of those populations had broken or regenerated tails. The second DFA used all variables except tail length, which permitted the inclusion of all populations. In each DFA, Greater Antillean species were used to designate the six ecomorph classes. Lesser Antillean populations were then classified *a posteriori* to ecomorph class. The DFAs were conducted on non-size-adjusted data.

Results

Figure 2 presents the mean values for each ecomorph class and each population of the two Lesser Antillean species. For *A. marmoratus*, all population means fall within or near the range of values exhibited by trunk-crown anoles, with the exception of the number of lamellae of several populations. Conversely, *A. oculatus* populations fall within the range of values exhibited by trunk-ground anoles for most variables; with the exception of number of lamellae, *A. oculatus* populations also display many affinities to trunk-crown anoles. By contrast, populations of these two species differ substantially in one or more variables from the other ecomorph classes: twig anoles diverge in many variables, trunk anoles are smaller and have relatively shorter tails, grass-bush anoles are smaller and have relatively longer tails, and crown-giants are substantially larger and have relatively shorter metacarpals. An additional variable that distinguishes the ecomorphs is mass (Beuttell & Losos, 1999). We did not have field data on mass for the Lesser Antillean specimens and mass measurements from preserved specimens are inaccurate. Nonetheless, it is clear that these are relatively heavy anoles, more similar to trunk-ground and some trunk-crown anoles than to the relatively lighter twig, grass-bush, and, to a lesser extent, crown-giant anoles.

The DFA was highly significant, regardless of whether analyses included ($\lambda = 0.0004$, $F = 7.28$, d.f. = 40, 59, $P < 0.0001$) or excluded (Wilks' $\lambda = 0.002$, $F = 7.35$, d.f. = 35, 73, $P < 0.0001$) tail length. In the analysis including tail length, all ecomorph species were assigned to correct ecomorph class with a probability >0.95 . All five populations of *A. marmoratus* were classified as trunk-crown anoles with probabilities >0.95 . Two of the populations of *A. oculatus* also were classified as trunk-crown anoles and the other nine as trunk-ground anoles; only two of the trunk-ground and one of the trunk-crown classifications, however, had a probability

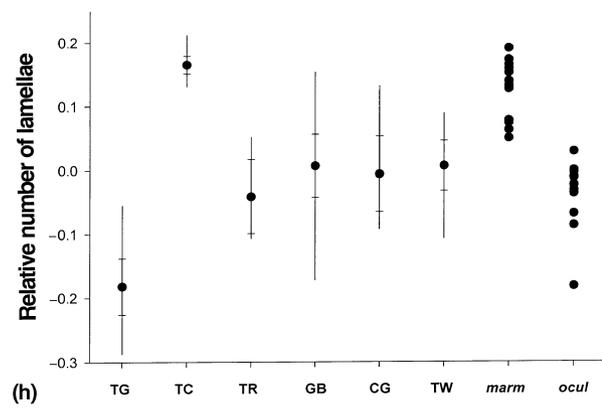
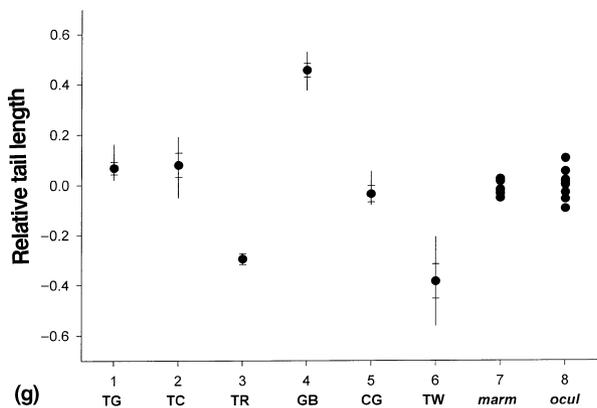
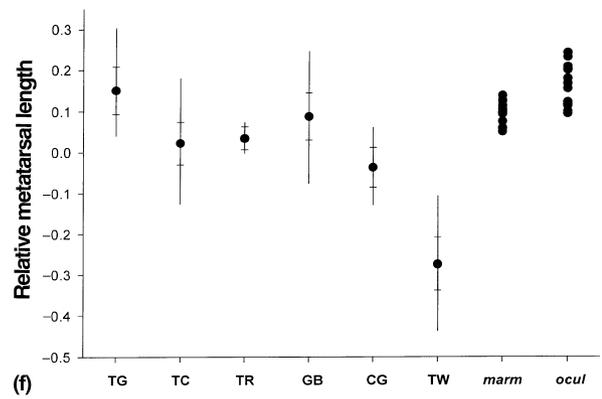
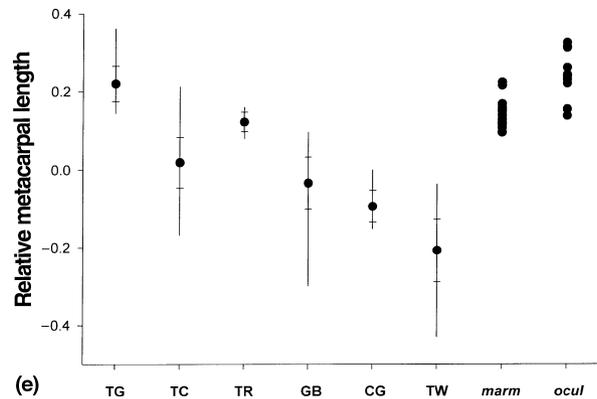
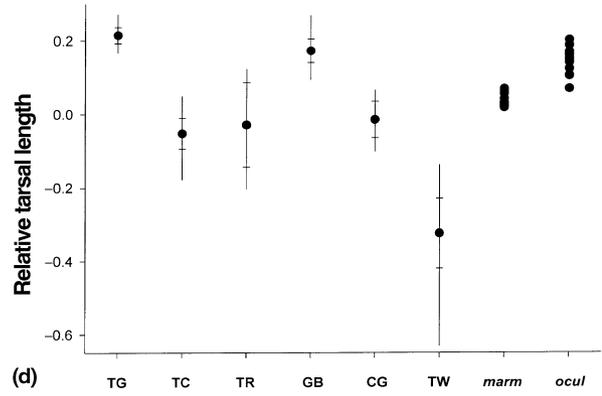
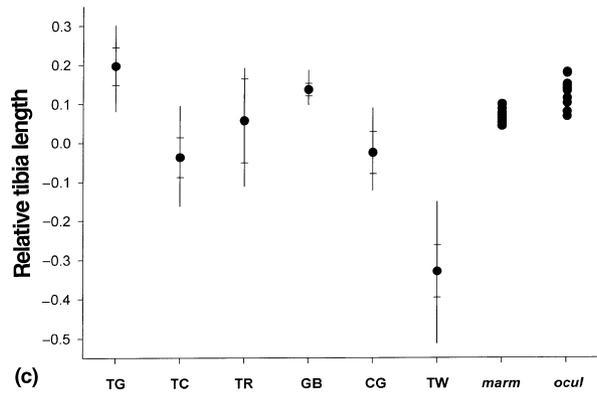
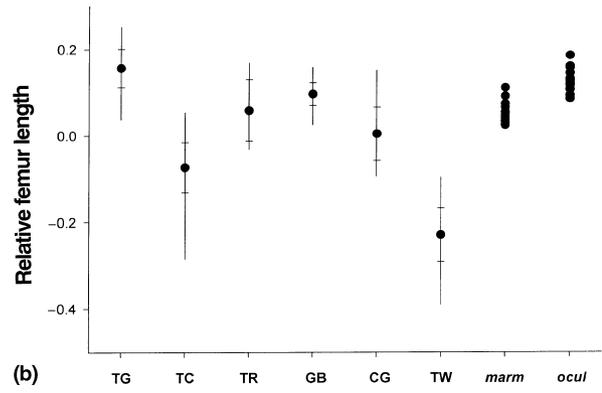
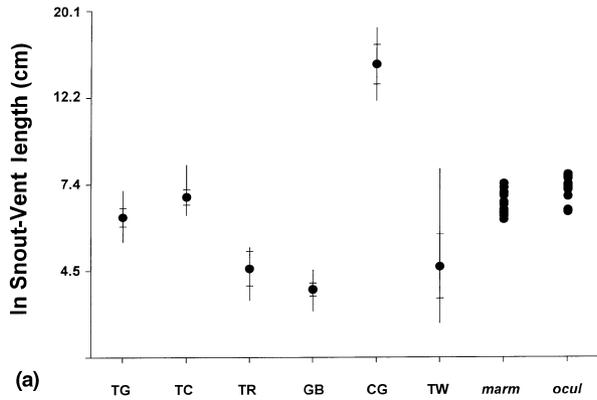
>0.95 . In the analysis excluding tail length, one ecomorph species was misclassified (the grass-bush species *A. pulchellus*, classified as a trunk anole), and all but three of the others were classified correctly with a probability >0.95 . All 14 *A. marmoratus* populations were classified as trunk-crown anoles, 13 with probability >0.95 ; four of the *A. oculatus* populations, including the two from the previous analysis, were classified as trunk-crown anoles; all nine populations classified in the previous analysis as trunk-ground anoles were again so classified; and one population was exactly tied, with equal probability of classification for trunk-ground and trunk-crown. Only one *A. oculatus* population, classified as a trunk-ground anole, had a classification probability >0.95 .

Discussion

Our results confirm the existence of substantial inter-populational variation in *A. marmoratus* and *A. oculatus*. Although geographical variation for some of the same characters has been reported for some Greater Antillean species (e.g. Lister, 1976a, b; Losos *et al.*, 1994), quantitative comparisons presently are not possible. Nonetheless, we suspect that the amount of variation exhibited by *A. marmoratus* and *A. oculatus* is rivalled by few Greater Antillean taxa; certainly, no one – including the only two quantitative examinations of interpopulational variation in ecomorph classification within Greater Antillean species (Losos *et al.*, 1994; Losos & de Queiroz, 1997) – has suggested that populations of a Greater Antillean species are so different that they belong to different ecomorph classes, as is true for *A. oculatus*.

Nonetheless, our results also make clear that interpopulational variation in these Lesser Antillean species is considerably less than the variation exhibited among sympatric ecomorphs in the Greater Antilles. Despite their great variation, all populations of *A. marmoratus* and *A. oculatus* are most similar to either trunk-ground or trunk-crown anoles; none of the populations display the more extreme morphologies characteristic of other ecomorphs such as twig or grass-bush anoles. This is perhaps not surprising, because in localities in the Greater Antilles at which only one species is present, that species is almost invariably a trunk-ground or trunk-crown ecomorph (Losos & de Queiroz, 1997). These two ecomorphs are

Fig. 2 Morphological variables for the Greater Antillean ecomorphs (TG = Trunk-ground; TC = Trunk-crown; TR = trunk; GB = Grass-bush; CG = Crown-giant; TW = twig) and Lesser Antillean populations. For the ecomorphs, circles are the mean value of all species within that ecomorph. Error bars represent one standard error and the vertical bars indicate the range of values exhibited. For the Lesser Antillean species, each symbol is the mean value for one population. (a) Body size, as indicated by snout-vent length; (b–h) variables relative to body size. Each variable is the residual of a regression against SVL. See text for details.



the most generalized in their morphology and habitat use and may be the best adapted type for a one-species community (i.e. they may represent the highest 'adaptive peak' in such a situation). By contrast, the other ecomorph classes are more specialized in their morphology and habitat use. Twig anoles, for example, are divergent in morphology and use narrow-diameter vegetation that is only rarely used by other ecomorphs; similarly, grass-bush anoles have extraordinarily long tails and are usually found in vegetation not used by other ecomorphs.

The evolution of the other ecomorphs, thus, seems tied to adaptive radiation; as anoles diversified on the Greater Antilles, they evolved a variety of species specialized to use different habitats and thus capable of coexisting in sympatry (Williams, 1972, 1983; Losos, 1994). The absence of most of these ecomorphs in the Lesser Antilles, then, results from lack of adaptive radiation on these islands. Why anoles have not radiated on such large and vegetationally and topographically complex islands as Dominica and Guadeloupe, where they have been present for millions of years, is an interesting question for which no good answer currently exists (Losos & Schluter, 2000).

Our results also indicate that interpopulational variation in *A. oculatus* is greater than in *A. marmoratus*. One possible explanation is that the range of environments occupied by *A. oculatus* on Dominica is greater than that occupied by *A. marmoratus* on Guadeloupe. An alternative possibility is that the relationship between morphology and habitat use is different in the two species such that, over a similar range of habitat use, populations of *A. oculatus* diverge to a greater extent morphologically. Critical to evaluating these possibilities is better knowledge of the habitat use and behaviour of these species. Literature reports suggest that *A. oculatus* uses a wide range of habitats and can often be found on the ground, although it usually is found on vertical surfaces (Lazell, 1962; Malhotra & Thorpe, 1997). Little information is available, however, on interpopulational differences in habitat use in either species (e.g. Bullock *et al.*, 1993).

In a similar vein, it would be interesting to compare the habitat use and behaviour of populations of these two species with that of the Greater Antillean ecomorphs. Previous studies indicate that most Lesser Antillean species on one-species islands, including *A. marmoratus*, are ecologically similar to trunk-crown anoles (Lazell, 1972; Losos & de Queiroz, 1997). Consequently, it is not surprising that these species are morphologically similar to trunk-crown anoles. If, in fact, the relationship between morphology and ecology for these species is the same as that for Greater Antillean ecomorphs (Losos & de Queiroz, 1997), then one would predict that great variation would exist in the habitat use and behaviour of *A. oculatus* and that many populations would show a considerable extent of activity near the ground, like trunk-ground anoles. Indeed, *A. oculatus* does use the

ground relatively frequently (Lazell, 1962; Malhotra & Thorpe, 1997), and apparently much more than does *A. marmoratus*.

In this study, we have focused on morphometric differences in body size and limb and tail proportions and overall size, the features that distinguish the ecomorphs. Populations of *A. oculatus* and *A. marmoratus* also differ greatly in scalation, tail height and colour pattern, which appear to be adaptive responses to environmental variation in vegetation type and climate (Malhotra & Thorpe, 1991a, 1997). Such variation also occurs within species and among closely related species in the Greater Antilles (e.g. Underwood & Williams, 1959; Lazell, 1983). Whether the variation in these characteristics within the Lesser Antillean species is also unusually great is an interesting question requiring further investigation.

In summary, the extent of geographical variation in *A. marmoratus* and *A. oculatus* is exceptional. A full understanding of why these species exhibit so much variation requires much more detailed information on the natural history of these species. Studies on habitat use, behaviour, natural selection and gene flow would be particularly valuable.

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Appendix 1

Species Included. Islands: C = Cuba; H = Hispaniola; J = Jamaica; PR = Puerto Rico

Trunk-Ground:

A. gundlachi (PR), *A. lineatopus* (J), *A. longitibialis* (H), *A. mestrei* (C), *A. sagrei* (C)

Trunk-Crown:

A. allisoni (C), *A. chlorocyanus* (H), *A. coelestinus* (H), *A. evermanni* (PR), *A. grahami* (J), *A. porcatius* (C)

Trunk:

A. brevirostris (H), *A. loysiana* (C)

Grass-Bush:

A. alutaceus (C), *A. olssoni* (H), *A. poncensis* (PR), *A. pulchellus* (PR), *A. semilineatus* (H), *A. vanidicus* (C)

Crown-Giant:

A. cuvieri (PR), *A. equestris* (C), *A. garmani* (J), *A. luteogularis* (C)

Twig:

A. angusticeps (C), *A. darlingtoni* (H), *A. guazuma* (C), *A. occultus* (PR), *A. valencienni* (J)