3

FIVE ANOLE FAUNAS,
PART ONE
Greater Antillean Ecomorphs

In this and the next chapter, I break anole diversity into five groups, corresponding mostly to the anoles of different regions. "Fauna" is used loosely, as two of these faunas co-occur, and another fauna extends over the majority of the geographic distribution of these lizards. The rationale for this dissection is that these faunas exhibit different patterns of ecological and evolutionary diversity and consequently illuminate different phenomena. Moreover, the amount of study devoted to the faunas varies tremendously; as a result, much of this book will focus on the first of these faunas, the Greater Antillean ecomorphs, which are the subject of this chapter. The remaining four faunas will be discussed in Chapter 4.

GREATER ANTILLEAN ECOMORPHS

The ecomorph story was introduced in the prologue. Put simply: the same set of habitat specialists co-occur in communities throughout the Greater Antilles (Fig. 3.1). Williams (1972) coined the term "ecomorph" to refer to these habitat specialists (Fig. 3.2). A brief history of the study of *Anolis* ecological morphology is presented in Appendix 3.1 at the end of this chapter.

Williams' (1972, p. 72) definition of ecomorph: "species with the same structural habitat/niche, similar in morphology and behavior, but not necessarily close phyletically," has several components. In particular, the definition indicates that to constitute an ecomorph class, a set of species must share similarities in morphology, ecology, and

FIGURE 3.1

The West Indies. The Greater Antilles are the islands of Cuba, Hispaniola, Jamaica, and Puerto Rico and nearby smaller islands.

behavior, and these similarities must be independently derived.[39] In recent years, the term "ecomorph" has been widely applied to many types of organisms (see Appendix 3.1); however, most such designations are made only on the basis of similarity in morphology or ecology, and often without quantitative analysis. Williams' ecomorph concept is more elaborate than mere convergence; it is the idea that groups of species are recognizable as discrete and distinct entities that differ in coordinated aspects of their biology, encompassing behavior, ecology, and morphology.

Before getting into the gory statistical details concerning the existence and recognition of the anole ecomorph classes, I'll begin with a brief description of their key morphological, ecological, and behavioral attributes (summarized even more briefly in

39. Technically, distantly related taxa can share similarities as a result of retaining the ancestral condition, rather than from convergent evolution. However, because the ancestral anole could have been a member of only one ecomorph class (e.g., it couldn't have been both a grass-bush and a twig anole), the recognition of multiple different ecomorph classes—such as the six *Anolis* ecomorphs—implies that the similarity of species in most of the different ecomorph classes must have resulted from convergence.
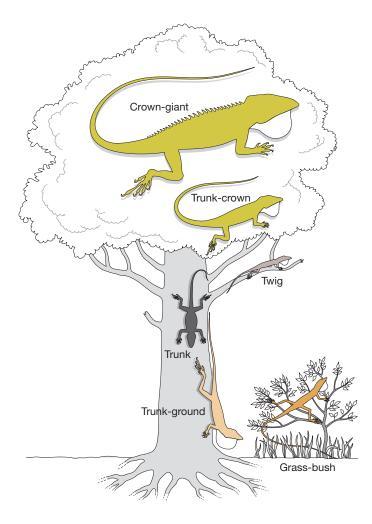
FIGURE 3.2
The ecomorphs.

Table 3.1 and illustrated for morphology in Fig. 3.3).[40] Ecomorph designations refer to the structural microhabitat[41] in which members of each ecomorph class are normally found.[42] The afterword at the end of the book provides a list of all West Indian species, including the ecomorph designations of Greater Antillean species.

40. In the table, the lower size range for crown-giants is not based on Schwartz and Hendersoni (1991) because the size they reported for *A. cuvieri:* is substantially underestimated (e.g., Losos et al., 1990).
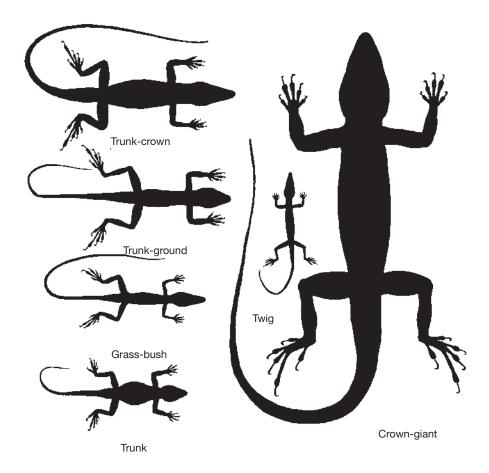
41. "Microhabitat" refers to the attributes of the subset of the habitat used by a species. "Structural microhabitat" refers to the characteristics of the structures—e.g., trunks, branches, leaves—in the parts of the habitat a species uses (Rand, 1964a).

42. Note that these designations refer to usual structural microhabitat use of a species and do not imply that ecomorph species are exclusively found in their designated location. Ernest Williams liked to tell the story of a now well known biologist who became concerned (more accurately: freaked out) when, on a field trip, a crown-giant anole was discovered on the ground. The occasional nonconformist anole notwithstanding, field studies always clearly indicate that species in the different ecomorph classes use different parts of the structural habitat (e.g., Rand, 1964a, 1967a; Schoener and Schoener, 1971a,b; Moermond, 1979a,b; Losos, 1990c).

TABLE 3.1 Ecomorph Characteristics

Ecomorph	Body size (maximum SVL, in mm)	Limb length	Number of lamellae on toepads	Tail length	Color	Structural microhabitat	Movement rate	Type of movement
Crown-giant	Large (130–191)	Short	Intermediate	Long	Usually green	High trunks and branches	Low	Walks and runs
Grass-bush	Small (33–51)	Long hindlimbs	Intermediate	Very Long	Brown, lateral stripe	Low, narrow supports	Low	Jumps and runs
Trunk	Small (40–58)	Intermediate, relatively even ratio of fore-limbs to hindlimbs	Intermediate	Short	Gray	Trunks	High	Runs
Trunk-crown	Small to intermediate (44–84)	Short	Many	Long	Green	Trunks, branches, leaves, eye level to high	High	Walks and runs
Trunk-ground	Intermediate (55–79)	Long hindlimbs	Intermediate	Long	Brown	Broad, low surfaces	Low	Runs and jumps
Twig	Small to intermediate (41–80)	Very short	Few	Short	Gray	Narrow supports	High	Walks

NOTE: Morphological data other than SVL are relative to body size (Beuttell and Losos, 1999). Movement data from Losos (1990c), Irschick and Losos (1996) and Losos (unpubl.).

Trunk-crown

Trunk-ground

Grass-bush

Trunk

Twig

Crown-giant

FIGURE 3.3

Silhouettes of common ecomorph species of Hispaniola: the large lizard is the crown-giant, *A. ricordii,* the small one next to it is the twig anole, *A. insolitus;* the remainder, in descending order of size are trunk-crown, *A. chlorocyanus;* trunk-ground, *A. cybotes;* grass-bush, *A. bahorucoensis;* and trunk, *A. distichus.* This image was drawn from photographs of museum specimens with some slight adjustments made to correct for preservation effects.

TRUNK-GROUND ANOLES

Trunk-ground anoles are medium-sized species typically observed within a meter and a half of the ground on broad surfaces: usually tree trunks, but also walls (rock or human-made), boulders or other such objects (Fig. 3.4).[43] Often, they perch head downward,

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43. A few species extensively use rocky surfaces as well as trees (e.g., *A. longitibialis, A. mestrei, A. imias, A. guafe*). These species are all closely related and morphometrically similar to more standard trunk-ground anoles. Because rock walls and tree trunks are similar in terms of the functional demands they make on lizards, I treat them all as trunk-ground anoles rather than subdividing the trunk-ground category. Some morphological differences do exist, however; for example, like rock-dwelling lizards in other genera (Revell et al., 2007b), rock-dwelling anoles have particularly long legs (Glor et al., 2003).

surveying the ground. From this position, they will rapidly descend, either by foot or air, to capture prey or interact with a conspecific. Males use these prominent perches both to advertise their presence by displaying frequently, as well as to spot prey, which they often capture by a quick dash to the ground.

Trunk-ground anoles are generally a dark color, ranging from light brown to darker brown or olive. They are stocky, muscular lizards with long hindlimbs and poorly developed toepads.[44] The tail is moderately long[45] and the dewlap is usually large. Trunk-ground anoles are the most visible and seemingly the most abundant anole at most localities.

TRUNK-CROWN ANOLES

Trunk-crown anoles are wide-ranging arboreal species. They are typically found from eye level to the top of the canopy and occur regularly on the full spectrum of surface diameters, from tree trunks to narrow twigs. In addition, they regularly occur on leaves and other vegetation. Trunk-crown anoles travel over moderately large three-dimensional areas. They move relatively frequently and use both sit-and-wait and actively searching foraging modes.

Almost all trunk-crown anoles are green, some quite beautifully so, and several species are to some extent blue (Fig. 3.5). All can change color to a dark shade of brown, and one species, *A. brunneus*, has lost its verdancy entirely and can only shift in color from a light grayish brown to almost black. Trunk-crown anoles have short legs and a slender body shape, with a long snout. The toepads are extremely well developed and the tail is usually, but not always, long.

Trunk-crown anoles are often very abundant and visible, occasionally rivaling sympatric trunk-ground anoles in these regards, particularly in more open habitats. In forests, the abundance of trunk-crown species is probably underestimated because they frequently are so high up that they can be hard to see from the ground. For example, in Puerto Rico the trunk-crown *A. stratulus* was thought to be relatively uncommon until the construction of a canopy walkway at the El Verde Field Station revealed that it is extraordinarily abundant in the treetops (Reagan, 1992).
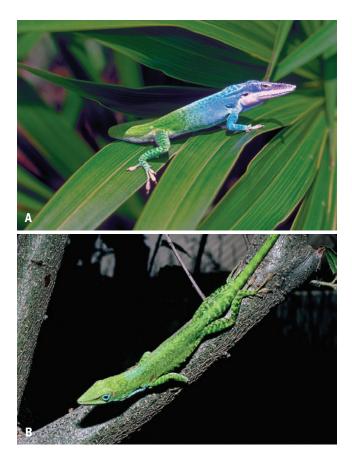
TRUNK ANOLES

Trunk anoles occur on broad tree trunks. They occur between, and overlap with, trunk-ground and trunk-crown anoles. However, unlike the former, they very rarely venture onto the ground, and unlike the latter, they do not often go out onto narrower branches or into the vegetation. Rather, they mostly stick to the trunk itself, moving up and down and round and round.

Trunk anoles only occur on the two largest Greater Antillean islands,[46] and the Hispaniolan species are more thoroughly studied, both because they are much more

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44. When referring to the size of morphological attributes, descriptions are implicitly expressed relative to overall body size unless otherwise indicated.
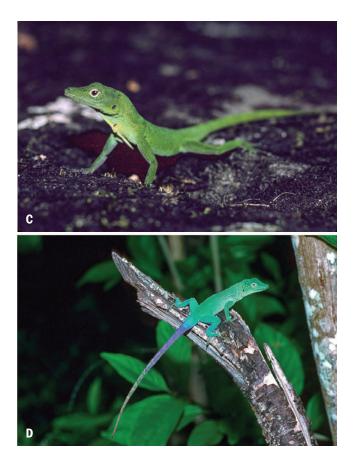45. Descriptions of tail length refer to unregenerated tails.
46. In addition, the Hispaniolan trunk anole *A. distichus* occurs naturally in the Bahamas and also in Florida, where some populations may be descended from natural colonists from the Bahamas, but most are the result of human introductions (Wilson and Porras, 1983; Meshaka et al., 2004).

accessible to American herpetologists and because they are much more abundant than the seemingly uncommon Cuban species (Rodríguez Schettino, 1999). Trunk anoles are fairly active, making many short movements;[47] the diet of Hispaniolan trunk anoles consists of ants to a greater extent than most anoles (little is known of diet of the Cuban trunk anole).

Trunk anoles are relatively small (Fig. 3.6). Their most obvious feature is a flattened body, with legs splayed more laterally than the legs of most anoles. Although their limbs are neither particularly long nor short compared to the limbs of other ecomorphs, trunk anoles have the longest forelimbs relative to the length of their hindlimbs, and also large forefoot toepads relative to the size of the pads on their hindfeet. These anoles have short tails and usually sport a grayish hue which blends in well on light-colored tree trunks.

47. The Hispaniolan species use an unusual form of locomotion consisting of short, spasmosdic hops in which an individual jerks forward a few centimeters, pauses briefly, and then jerks forward again, sometimes continuing for great distances (Mattingly and Jayne, 2004, 2005; Losos, unpubl.).

CROWN GIANTS

The most obvious feature of crown giants is their size. The largest anole species—the Cuban crown giant *A. luteogularis*—may reach a total length of well over one half a meter, perhaps not quite dinosaurian, but menacing enough in an anole world in which most species are 1/3 this long or shorter (and 1/20th in bulk).

Ecologically, these species do not differ much from trunk-crown anoles. They tend to be found high in trees, usually on trunks or branches, and they use narrower branches and leafy vegetation less than trunk-crown anoles. Probably as a result of their size, they have the most catholic diet among ecomorphs, adding fruits and verte-brates up to the size of small birds to the standard insect fare (Dalrymple, 1980; Meshaka et al., 2004). Similarly, their home ranges appear much larger than those of other ecomorph species (Losos et al., 1990). Although they cover a lot of ground, mov-ing from one tree to another by way of their interconnected canopies, they generally do not do so rapidly.

Morphologically, crown giants are in some respects super-sized trunk-crown anoles: they are generally green, but can change to a dark brown; their toepads are large, and

FIGURE 3.6
Trunk anoles. (a) *A. loysianus,* Cuba; (b) *A. distichus,* Hispaniola.
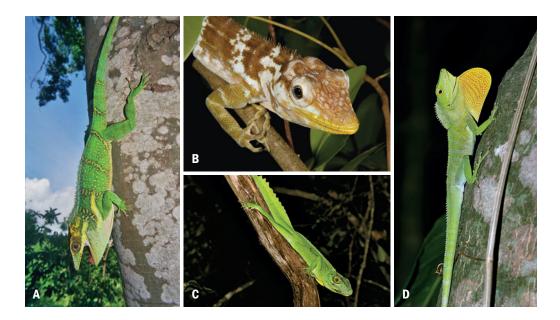
their limbs are moderately short (Fig. 3.7). In one respect, however, most crown giants differ substantially from trunk-crown anoles: the shape of the head. Most crown giants[48] have a massive, casqued head, a feature shared by some other large anoles. In addition, most crown-giants have a spiky crest running down their backs.

GRASS-BUSH ANOLES

Absent from Jamaica, grass-bush anoles are found on narrow vegetation near the ground, primarily grass stems and other low-lying vegetation, as well as on bushes and small tree trunks. They are agile lizards adept at moving through cluttered spaces. In some areas, particularly open grassy expanses, grass-bush anoles can occur at extremely high densities. Territories appear to be small and foraging conforms to the sit-and-wait mode. Grass-bush anoles often move by taking many short hops.

As would be expected given their structural microhabitat use, grass-bush anoles are always small. They are slender lizards with long hindlimbs, short forelimbs, and a long, narrow head. The toepads are poorly developed. Their most obvious feature, however, is their extremely long tail, which in some species can be four times the length of the body. Most grass-bush anoles are yellow and brown in color, with a light lateral stripe (Fig. 3.8).

48. *A. garmani* is the only exception.

Crown giants. (a) *A. Smallwoodi,* Cuba. Photo courtesy of Veronika Holanova; (b) *A. baleatus,* Hispaniola. Photo courtesy of Rick Stanley; (c) *A. cuvieri,* Puerto Rico; (d) *A. garmani,* Jamaica.

TWIG ANOLES

Twig anoles are the most extreme of the ecomorphs in just about every respect. Ecologically, they use narrow surfaces more frequently than most other anoles.[49] Behaviorally, they are active searchers, often moving steadily at low speed for extended periods. They search for prey by moving slowly on narrow surfaces, investigating holes, cracks, leaves and other places in which prey may be hidden (Fig. 3.9). Light grey with a mottled pattern, twig anoles rely on crypsis for predator avoidance. Upon spotting a potential threat, they move to the opposite side of a branch and slowly creep away. Only if directly threatened will they attempt to flee by running or jumping.

Morphologically, twig anoles are also extreme. They have very slender bodies with long pointed snouts and extremely short limbs and tails (Fig. 3.10). In many species, the tail seems to be weakly prehensile,[50] and they also have a tendency to have large scales on their heads.

49. Some grass-bush and trunk-crown anoles use narrow surfaces frequently, at least in some habitats (Mattingly and Jayne, 2004). Mattingly and Jayne (2004) painstakingly measured vegetation structure and pointed out that narrow surfaces actually predominate in terms of availability in the environment.
50. Though this capability is poorly documented in the literature.

Grass-bush anoles. (a) *A. vanidicus,* Cuba. Photo courtesy of Kevin de Queiroz; (b) *A. olssoni,*
Hispaniola; (c) *A. pulchellus,* Puerto Rico.

TESTING THE HYPOTHESIS OF THE EXISTENCE OF DISCRETE ECOMORPH CLASSES

It's one thing to assert the idea that ecomorphs exist and quite another to demonstrate it statistically. Although the idea of ecomorphs is now commonly applied in many different taxonomic groups,[51] quantitative morphological and ecological analysis supporting such a designation is still rare; such tests require investigating whether ecomorphs form

51. Prior to 1990, the term "ecomorph" was used primarily in reference to *Anolis* (see footnote 70 in the appendix at the end of this chapter for discussion of the history of the term); however, that has changed in recent years. A recent Google Scholar search found the term used in reference to ants, spiders, fish, bats, corals, and algae, and that was only on the first page of search results! Page two added crocodiles, badgers, rabbits, and pine trees.

FIGURE 3.9

Successful hunting by a twig anole. I will never forget observing this *A. valencienni* foraging in a concrete trash repository at the Discovery Bay Marine Laboratory in Jamaica. The lizard moved from one crack to the next, sticking its head in and apparently looking for concealed prey. Sure enough, it emerged from one crack with a large cockroach in its mouth.

discrete morphological clusters and whether these clusters also differ ecologically and behaviorally.
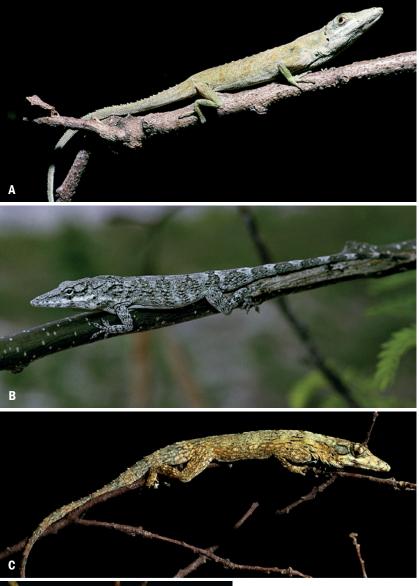
MORPHOLOGY

Two approaches have been taken to test the morphological component of the anole ecomorph hypothesis. First, a discriminant function analysis (DFA)[52] was performed on a data set comprised of morphological traits that are relevant to structural microhabitat use (see Chapter 13): radiological measurements of all limb elements plus external measurements of tail length, SVL, mass, and, for four toes, pad size and lamella number (Beuttell and Losos, 1999). Data were gathered from 32 species representing all six ecomorphs.[53] The DFA was highly significant (P less than 0.001), and all 32 species were classified a posteriori to the correct ecomorph class with probability of 1.0.

Because species are assigned to groups *a priori*, DFA is a good means of investigating whether previously established groups can be distinguished based on some combination of characters, but it is inappropriate as a means of asking whether those characters would produce those groupings if all variables were considered equally. In fact, DFA can
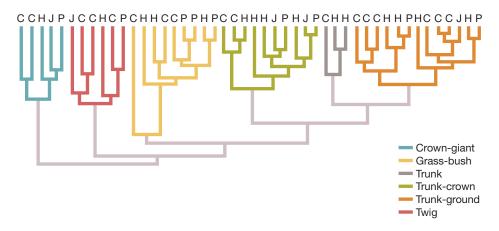
52. DFA constructs a series of linear equations that maximizes the separation of *a priori* defined groups by differential weighting of the variables.

53. Here and in the remainder of the analyses in this chapter, the data were collected only from males. The decision to focus data collection on males was made both on logistical grounds (male anoles are substantially easier to find, observe and capture than females) and because in some respects (e.g., body size [Butler et al., 2000]) differences among ecomorphs are greater for males than for females. Recent work, however, indicates that the same ecomorph categories apply to females as well as to males (Butler et al., 2007).

FIGURE 3.10

Twig anoles. (a) *A. insolitus,* Hispaniola;
(b) *A. angusticeps,* Cuba. Photo of *A. insolitus*
courtesy of Kevin de Queiroz; (c) *A. valenci-
enni,* Jamaica. Photo courtesy of Kevin de
Queiroz; (d) *A. occultus,* Puerto Rico. Photo
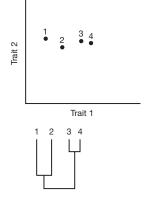courtesy of Alejandro Sanchez.

FIGURE 3.11

UPGMA phenogram indicating that species cluster by ecomorph in a multidimensional morphological space. Letters indicate island of origin (Cuba, Hispaniola, Jamaica, Puerto Rico). The study was based on external measurements from 46 species, including at least one representative from each ecomorph class on each island on which it occurs. Randomizing species identity across the phenogram revealed that such clustering is extremely unlikely to have occurred by chance (P ≪ 0.0001). Figure re-drawn from Losos et al. (1998) with permission.

find statistical support for particular groupings, even if most of the characters (at the extreme, all but one) do not differentiate the groups or even support very different groupings (Klecka, 1980). In other words, DFA confirms that the ecomorphs can be distinguished based on a set of morphological characters, but does not demonstrate that the characters would produce the observed ecomorph groupings in the absence of *a priori* categorization.

For this reason, the second approach for testing the ecomorph hypothesis asks whether ecomorph groupings are recovered when variables are weighted equally, thus avoiding effects of *a priori* categorization. One common means of visualizing the relative position of points in a multivariate space is to construct a similarity phenogram using the unweighted pair group method with arithmetic means (UPGMA).[54] Two different studies (Losos et al., 1998; Beuttell and Losos, 1999) have used UPGMA to summarize the position of anole species in morphometric space. Using different methods and sets of species that overlapped to a moderate extent, both studies revealed perfect clustering by ecomorph class (Fig. 3.11).

The UPGMA method has its own shortcomings, however, because it represents the position of species as a nested hierarchy of groups, which may distort the actual multi-dimensional position of the species (Sneath and Sokal, 1973; de Queiroz and Good,

54. UPGMA phenograms are constructed by joining the two points separated by the smallest Euclidean distance in a phenogram; these two points are replaced by their average, and again the two closest remaining points are joined, and so on, until all points have been connected into a single, bifurcating phenogram.

FIGURE 3.12

The problem with UPGMA phenograms. If species in a morpho-
logical space were distributed as in (a), a UPGMA analysis would
produce a phenogram like the one shown in (b), which would fail to
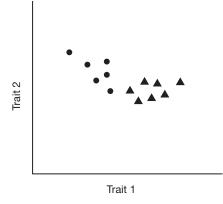indicate that species 2 and 3 occupy intermediate positions.

1997). To see why this is, consider a situation in which objects do not form discrete
clusters (Fig. 3.12). UPGMA will portray the intermediate points as clustering with
whichever of the other points is slightly closer. As a result, what may in reality be a con-
tinuum will be represented as a set of groups, with the implication that all members of
one group are equidistant from all members of other groups; in such a hierarchical ren-
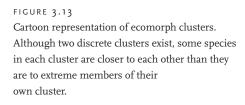dering, it is not possible to indicate that one object is intermediate between others.

For this reason, the results of UPGMA analysis are best thought of as a first pass, use-
ful for heuristic purposes, but requiring subsequent corroboration. To this end, we ex-
amined the actual Euclidean distances separating each pair of species in multivariate
space. In both studies, all species had as their nearest neighbor in morphological space
another member of the same ecomorph class (with one exception[55]). Moreover, all
species are closer to the centroid for their own ecomorph class than they are to the cen-
troid for any other ecomorph.[56]

Taken together, these analyses provide strong corroboration of the hypothesized exis-
tence of discrete ecomorph classes that occupy distinct regions of morphological space.
The nearest neighbor analysis reveals that ecomorph species are not uniformly distrib-
uted throughout morphological space; that is, all species are closest in morphological
space to a species that is a member of their own ecomorph class. Combined with the
perfect clustering revealed by the UPGMA analysis, this observation suggests that the
boundaries of the ecomorph classes correspond with gaps in the occupation of morpho-
logical space.

55. In the Beuttell and Losos (1999) study, the Hispaniolan trunk-crown *A. aliniger* and the Hispaniolan
twig *A. darlingtoni* were slightly closer to each other than each was to a member of its own ecomorph class. This
result is unexpected, because both species appear morphologically to be typical members of their ecomorph
classes and *A. aliniger* exhibits habitat use typical of trunk-crown anoles (Williams, 1965; Rand and Williams,
1969; Losos, unpubl.). Ecological data are not available for *A. darlingtoni*, which is from Haiti and has not been
collected frequently (Thomas and Hedges, 1991). Unlike most species in these analyses, our data for *A.
darlingtoni* came from a single specimen, which may have been a source of error.
56. The centroid is calculated as the mean position of all members of that ecomorph class in multivariate
space. This analysis was only conducted in the Beuttell and Losos (1999) study, which was a considerably more
in-depth morphometric analysis than Losos et al. (1998).

FIGURE 3.13
Cartoon representation of ecomorph clusters.
Although two discrete clusters exist, some species
in each cluster are closer to each other than they
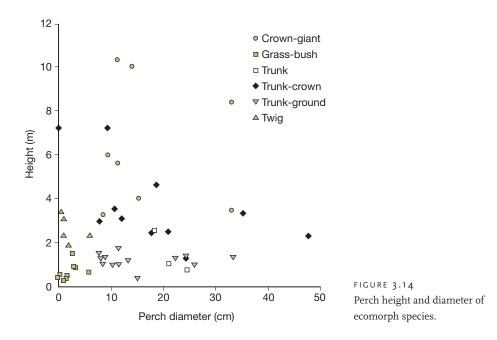are to extreme members of their
own cluster.

Nonetheless, the extent of ecomorph convergence should not be overstated. In particular, ecomorph classes are not so distinct that each species is more similar to all species in its own class than it is to any species from another class. Rather, in many cases a species is more similar in morphology to some members of another ecomorph class than it is to some members of its own class.[57] This occurs because extensive intra-ecomorph variation exists: e.g., trunk-ground anoles vary from being moderately to extremely long-legged; grass-bush anoles from having long tails to extraordinarily long tails; trunk-crown anoles from being rather small to moderately large. The result is that less extreme species may be more morphologically different from the more extreme members of their own class than they are from less extreme members of other ecomorph classes (Fig. 3.13).

ECOLOGY AND BEHAVIOR

Williams' (1972) formulation of the ecomorph categories referred to sets of species that are similar in ecology and behavior, as well as morphology. Because behavioral and ecological data are not as easy to collect as morphological data, many studies that discuss ecomorphs in other taxa include quantitative data for morphology, but not for ecology and behavior. This is not the case for anoles, however, as a result of the abundance of many species, and some hard work to find the scarcer ones. The discussion below is based on ecological data for 49 species and behavioral studies of 28 species (Losos, 1990c; Irschick and Losos, 1996; Johnson et al., 2008).

The two most frequently reported habitat variables are the height and diameter at which lizards are initially seen. These two variables do a nice job of separating most of

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57. As indicated by direct examination of Euclidean distances between species; this is an example of how a UPGMA phenogram can be misleading by suggesting that all members of an ecomorph class are more similar to all other members of that class than any is to a member of another class.

FIGURE 3.14
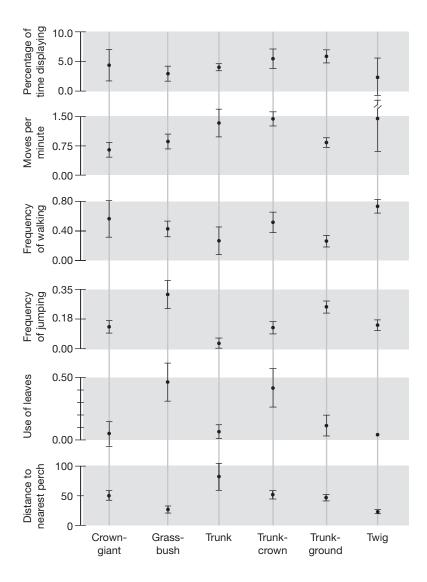Perch height and diameter of ecomorph species.

the ecomorphs, with the exception that crown-giant and trunk-crown anoles are broadly overlapping and that the trunk anoles fall within the space of both trunk-crown and trunk-ground anoles (Fig. 3.14).

Two other, less widely reported, variables serve to further distinguish the habitat use of the ecomorphs. The first is a measure of how cluttered the immediate environment is around a lizard, and correspondingly, how far away a lizard is from a support to which it could jump (Pounds, 1988; Losos, 1990c). This measure (distance to nearest perch) separates twig and grass-bush anoles, which live in highly cluttered habitats, from trunk anoles, which occur on large tree trunks with no other vegetation nearby (Fig. 3.15). The other three ecomorphs are intermediate.
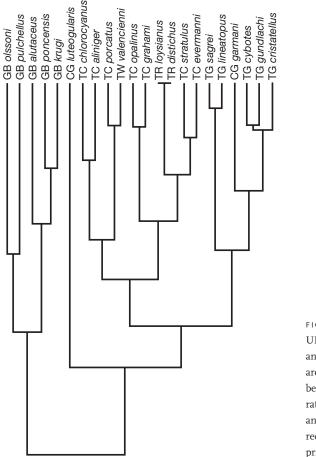
The second measure is the use of leaves and other herbaceous vegetation (e.g., grass) during locomotion. This measure clearly separates the trunk-crown anoles, which often move onto leafy vegetation, from the other arboreal ecomorphs, which tend to stay on the woody branches and trunk. It also distinguishes grass-bush from trunk-ground anoles (Fig. 3.15).

The ecomorphs also differ in their locomotor and display behavior (Fig. 3.15). As a proportion of all of their movements, twig anoles walk much more often than the other ecomorphs, whereas trunk and trunk-ground anoles walk least often. Trunk-ground and grass-bush anoles are the most frequent jumpers, whereas the other ecomorphs jump relatively little. In terms of overall movement rate, the ecomorphs group into those ecomorphs that move frequently (trunk, trunk-crown, and twig), and those that move much less (the others). Display frequency also differs among the ecomorphs.

Ecological and behavioral differences among ecomorphs. Use of leaves is the proportion of individuals observed to use leaves or other herbaceous structures during behavioral observations. Distance to nearest support is a composite measure of the distance to the nearest object to which a lizard could jump. Frequency of walking and jumping are the proportion of all movements that were categorized as walks or jumps. Moves per minute is the number of movements per minute. Values are means plus one standard error. Data on use of leaves and distance to nearest support were not collected for all species; leaf use data were available for only one twig anole (hence, the lack of an error bar). Values are means for each ecomorph based on mean values for each species.

As would be expected given these ecomorph differences, interspecific variation in morphology, ecology, and behavior are related. For example, among species, relative hindlimb length is correlated positively with perch diameter and negatively with rate of walking. Similarly, the more often a species is observed using leaves, the greater the

FIGURE 3.16
UPGMA phenogram of behavioral and ecological data. Similar results are obtained when ecological and behavioral data are examined separately, and when different ways of analyzing the data are used (e.g., reducing data dimensionality with principal components analysis).

number of its toepad lamellae, relative to body size. These relationships are discussed in greater detail in Chapter 13.

Overall, these data make a strong case that the ecomorphs represent a syndrome of morphologically, ecologically, and behaviorally distinctive types. Indeed, just as with the morphological data, a discriminant function analysis on behavioral and ecological data also classified all species to the correct ecomorph class.[58] Nonetheless, when a multidimensional ecological or behavioral space is examined, species do not sort out precisely along ecomorph lines. A representative UPGMA phenogram is presented in Fig. 3.16; the general groupings correspond to the ecomorph classes, but there are exceptions.

58. The analysis is based on 22 species for which the following data are available: percentage of movements that are runs and walks; movement rate; perch height and diameter; degree of clutter; and use of leaves. All data were log- or arcsine-square root transformed as appropriate. The analysis was highly significant (p less than 0.0001).

This result could be viewed in two ways. On one hand, it could be taken to indicate that the ecomorphs are defined primarily by morphology—ecology and behavior are related to morphology, but with so much variability that the ecomorphs do not represent discretely different ecological and behavioral entities. On the other hand, the field data I have analyzed were for the most part collected from few populations (often just one) over a short period of time. As I will discuss in Chapters 8 and 11, anoles alter their behavior and habitat use seasonally and as a result of many factors, such as which other species are present. Moreover, structural habitat use strongly depends on what habitat is available at a particular site (Johnson et al., 2006): in areas with many big trees, perch diameter of many species will be much greater than if the same species is studied in a scrubby area. For example, in the Bahamas, average perch diameter of *A. sagrei* varied four-fold across islands that differed in vegetation type (Losos et al., 1994). Given this variability, perhaps it is not surprising that ecomorphs are not found to cluster perfectly in ecological or behavioral space; the noise resulting from the limited extent of sampling of many species may have obscured otherwise clearer distinctions among the ecomorphs. More extensive sampling would be useful to get a more precise characterization of the habitat use and behavior of ecomorph species, both across their geographic range and over seasons and years.

ECOMORPH CLASS AND INTERSPECIFIC VARIATION

The ecomorph classes were initially defined based on a limited number of morphological characters, most of which obviously relate to an anole's position in and movement through the habitat, as well as its habitat use and foraging behavior (Williams, 1972; 1983). Recent work, however, has shown that the ecomorphs differ in a wide variety of other characteristics, including head dimensions, pelvic and pectoral girdle shape (Harmon et al., 2005), limb muscle mass (Vanhooydonck et al., 2006a), and sexual dimorphism in both size and shape (Butler et al., 2000; Butler and Losos, 2002; Losos et al., 2003a). Although variation in the girdles and limb muscle mass probably has functional significance relevant to locomotion (Peterson, 1972; Vanhooydonck et al., 2006a; Herrel et al., 2008), head shape variation probably is related more to other activities, such as eating and fighting (although species that use narrow surfaces may need narrow heads for balance and crypsis [Harmon et al., 2005]). Differences in sexual dimorphism among ecomorphs, particularly in size, also probably aren't related to sexual differences in locomotor ecology (Butler, et al., 2000; Losos et al., 2003a; see Chapter 9). These findings indicate that the morphology-ecology-behavior ecomorph syndrome likely results from more than the demands and constraints on locomotion determined by different structural microhabitats, a point that will be explored in Chapter 15.

Despite the seeming pervasiveness of ecomorph class as an explanation for interspecific differences, variation in many traits does not fall out along ecomorph lines.

Examples of morphological traits that vary tremendously among species, but for which ecomorph class does not explain a statistically significant portion of the variation, include tail crest height (Beuttell and Losos, 1999) and dewlap size, color and pattern (Losos and Chu, 1998; Nicholson et al., 2007). An important ecological trait that is independent of ecomorph class is microclimate; i.e., the temperature and humidity of the microhabitat used by a species. That microclimate does not vary by ecomorph should not be surprising, because the structural microhabitats themselves do not correspond to climatic microhabitats. Trunk-ground anoles, for example, occur in open, hot and sunny parts of the environment, but also in cool, shady, and mesic areas. Moreover, the spatial scale at which microclimate varies is great enough that lizards in a particular spot have relatively little latitude to select a preferred microclimate; for example, a trunk-ground anole in the deep forest does not have within its territory a large range of different microclimates from which to choose. The result is that substantial variation in microclimate occurs among populations and between species within all of the ecomorph classes.

An interesting, but surprisingly understudied, question concerns whether ecomorphs differ in prey type and size. Prey use could differ among ecomorphs for two reasons: either the prey available may differ among structural microhabitats or, because of behavioral or morphological adaptations, ecomorphs may utilize different portions of the prey resource spectrum, even if prey availability were the same in different structural microhabitats. Certainly, the diet of crown-giants and grass-bush anoles would differ in prey size and at least to some extent in prey type, even if prey availability were the same in their microhabitats. More generally, foraging behavior differs among the ecomorphs, predisposing them to encounter and attack different types of prey. Nonetheless, other than effects attributable to body size, little evidence of consistent differences among ecomorphs in diet has been found, although this question has not been studied in detail (see Chapter 8).

SPECIES DIVERSITY WITHIN ECOMORPHS

Most of the ecomorph classes are represented by more than one species per island,[59] although some ecomorph classes have greater species richness than others, a topic I will discuss in Chapter 15. Species within ecomorph classes on an island sometimes are ecologically distinct, even though they share the same structural microhabitat. This diversity occurs in several ways:

1.   Some species are restricted to particular habitat types, such as pine forests, semi-deserts, or xeric rock outcrops.[60]

59. A list of all ecomorph species can be found in the Afterword at the back of the book.
60. Glor et al. (2003) refer to these as "macrohabitats."

2. Species co-occur by partitioning climatic microhabitats. In Cuba, for example, the widespread trunk-ground anoles *A. sagrei* and *A. homolechis* co-occur throughout the island, with *A. sagrei* always using hotter and more open microhabitats than *A. homolechis* (Ruibal, 1961; Hertz et al., in prep.).

   Climatic microhabitat partitioning has both a spatial and an elevational component. In xeric southeastern Cuba, for example, *A. jubar* occurs in the hottest, most open microclimates, *A. sagrei* occurs in open shade, and *A. homolechis* occurs in deep shade. Conversely, at higher elevations, *A. sagrei* is absent and *A. homolechis* occurs in the open, with other species in more closed microhabitats (Hertz et al., in prep.).

3. Co-occurring species differ in body size. In a number of cases, two members of the same ecomorph class occur in sympatry without dramatic differences in microclimate, but with substantial differences in body size. Because prey size strongly correlates with body size in anoles (Chapter 8), these coexisting species probably differ in diet. Diet data are only available for one pair of sympatric ecomorphs that differ in size, the trunk-crown anoles of Puerto Rico, *A. evermanni* and *A. stratulus*. As expected, these species differ in prey type and size (Lister, 1981; Dial and Roughgarden, 2004).

Sympatry of pairs of species within the same ecomorph class occurs on all islands. The only cases in which sympatric species are not known to differ substantially in some aspect of ecology (microclimate, body size, or in a few cases, specialization to particular structural microhabitats)[61] involve either species at contact zones (e.g., Webster and Burns, 1973; Williams, 1975; Hertz, 1980a) or species for which almost nothing is known of their natural history.[62] Although in most cases the maximum number of sympatric members of the same ecomorph class is two, as many as three trunk-crown (Díaz et al., 1998; Garrido and Hedges, 2001) and grass-bush (Garrido and Hedges, 1992, 2001) and four trunk-ground species (Losos et al., 2003b) can be found in sympatry.[63]

The means by which resource partitioning occurs among sympatric members of the same ecomorph class differs among the ecomorphs. Ecomorphs that occur near the ground—trunk-ground and grass-bush—divvy up the habitat along microclimate lines and exhibit little difference in body size. By contrast, arboreal ecomorphs—primarily

61. Primarily rocks. In western Cuba, for example, the trunk-ground *A. allogus* and *A. mestrei* both occur in deep shade, but *A. mestrei* is always found either on or in close proximity to large boulders or rock walls (Rodríguez Schettino, 1999).
62. For example, almost nothing is known about the ecology of the many recently described grass-bush anoles from eastern Cuba (e.g., Garrido and Hedges, 1992).
63. Garrido and Hedges (2001) suggest that four grass-bush species may occur in sympatry on the northern slope of the Sierra Maestra in Cuba.

trunk-crown, but in a few cases twig and crown-giant anoles[64]—exhibit the opposite pattern. Although sympatric trunk-crown anoles do exhibit some differences in microclimate preferences (e.g., Reagan, 1996), they still substantially overlap in habitat use and can often be seen in close proximity, in contrast to the situation for trunk-ground and grass-bush anoles, which tend to be more segregated within a locality (Schoener and Schoener, 1971b). This phenomenon is discussed in greater detail in Chapter 11.

IS SIX THE RIGHT NUMBER OF ECOMORPH CLASSES?

In 1983, Williams expanded upon his original concept, suggesting that several of his ecomorph classes should be split in two, producing nine classes. In particular, he divided both the trunk-crown and twig ecomorphs into giants and dwarves, and divided the grass-bush ecomorph into grass and bush ecomorphs. All of this was done without explanation.
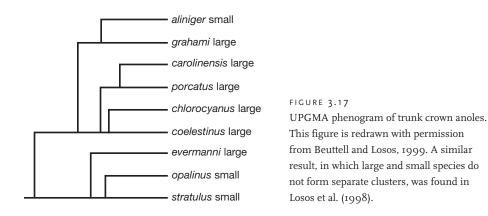
My feeling is that the data do not strongly support this proposition. Williams' (1972) definition of ecomorphs, implying discretely different groups recognizable on the basis of morphology, ecology, and behavior, accurately describes the six original ecomorph classes.[65] By contrast, the division of trunk-crown and twig anoles into large and small ecomorphs is based only on one morphological difference, and the division of grass-bush into grass and bush ecomorphs is based only on ecology. Closer examination of these three cases reveals that none of them result in groupings that are distinct in morphology, ecology, and behavior.[66]

I will go through each of these ecomorph classes in turn. With regard to trunk-crown anoles, the quantitative morphological comparisons reported earlier in the chapter indicate that small and large trunk-crown species do not form morphometrically distinct groups. Some small species cluster together in morphological space, as do some of the larger species, but, overall, small and large species do not form distinct clusters (Fig. 3.17).

64. Size differences occur among trunk-crown anoles on all four Greater Antillean islands. Similar examples are rarer among the other arboreal ecomorphs. Specifically, the inaptly named crown-giant *A. pigmaequestris* co-occurs with *A. equestris* on Santa Maria. The two species of large twig anoles, *A. valencienni* on Jamaica and *A. darlingtoni* in Haiti, are not known to coexist with smaller species; although smaller twig anoles do occur on Hispaniola, they have not been recorded in *A. darlingtoni*'s range. In Cuba, the unusual anoles in the *Chamaeleolis* clade, which might be considered twig giants (as discussed in the next chapter), coexist with more typical twig anoles (e.g., *A. angusticeps*) that are several orders of magnitude smaller in mass.

65. Even the two most similar ecomorphs, crown-giants and trunk-crown anoles, differ not only in morphology (primarily size), but also in some aspects of ecology and behavior.

66. Some readers may consider the discussion in this section particularly arcane, even by the standards of this book. However, given the central role that discussion of ecomorph evolution plays in understanding anole diversity, I feel that it is important to clearly delineate the case for recognizing the specific number of ecomorph classes that are discussed throughout this book. Moreover, some papers and websites casually refer to additional ecomorph types beyond the six recognized here, usually on the basis of structural microhabitat use. As mentioned at the outset of this chapter, the "ecomorph" concept is more than shorthand for species using the same structural microhabitat or those similar in morphology; it refers to groups of species that have independently evolve similarities in ecology, morphology, and behavior. In this regard, I consider it essential to clearly identify exactly how many such entities exist, and what the evidentiary basis is for such a claim.

FIGURE 3.17
UPGMA phenogram of trunk crown anoles. This figure is redrawn with permission from Beuttell and Losos, 1999. A similar result, in which large and small species do not form separate clusters, was found in Losos et al. (1998).

Ecologically, few consistent differences exist between the smaller and larger trunk-crown anoles. In general, all trunk-crown anoles can be characterized as occurring at eye level and above on tree trunks, branches, and leaves. One difference in Jamaica and Puerto Rico is that the larger trunk-crown anoles use leaves much more than the smaller trunk-crown anoles (Schoener and Schoener, 1971a,b), but the smaller trunk-crown anole of Cuba, *A. isolepis*, appears to move on leaves quite often.[67] Movement patterns of large and small trunk-crown anoles also seem broadly similar (e.g., Losos, 1990c), and none of the small trunk-crown anoles exhibit the unusual movement patterns characteristic of the Hispaniolan trunk anoles.

I have heard some workers take a slightly different tack and suggest that the small Puerto Rican and Jamaican trunk-crown anoles, *A. stratulus* and *A. opalinus*, should be considered trunk anoles because they are superficially similar to members of that ecomorph category in morphology and habitat use. However, the data do not provide much support for this idea. Morphometrically, both species cluster with other trunk-crown anoles. Ecologically, both species use leaves to some extent, whereas trunk anoles rarely venture onto green matter (e.g., Schoener, 1968; Moermond, 1979a; Rodríguez Schettino, 1999).[68] *Anolis opalinus* does tend to be found at relatively low heights and in this regard is similar to trunk anoles (Rand, 1967c; Jenssen, 1973; Schoener and Schoener, 1971a; Losos, 1990c). On the other hand, detailed studies from canopy towers at the El Verde Field Station in Puerto Rico clearly demonstrate that *A. stratulus* is found on branches much more than on tree trunks (Reagan, 1992). Overall, both species appear to be good trunk-crown anoles, and the trunk-crown class as a whole does not seem to be readily divisible into small and large species.

67. I make this statement based on a comment by Williams (1969) to this effect and my unpublished observations of several *A. isolepis* from La Gran Piedra, Cuba, that repeatedly used leaves as they moved through the canopy.
68. The habitat use of the Cuban trunk anole *A. loysianus* is little known. Rodríguez Schettino (1999) does not mention use of leaves when summarizing its habitat use, but no data are provided. My unpublished data reveal that none of the 27 *A. loysianus* observed at Soroa was on a leaf (as opposed to 8 of 34 of the trunk-crown *A. porcatus* at that site); it would be interesting to know what *A. loysianus* does when it is high in the canopy, where it seems to spend a lot of its time.

Twig anoles are perhaps the least well known of the ecomorphs. It is true that most twig anoles are quite small (mean size of males less than 50 mm SVL), but *A. valencienni* of Jamaica and *A. darlingtoni* of Haiti are substantially larger (70–80 mm SVL). Unfortunately, *A. darlingtoni* is very poorly known, so it is not possible to examine whether it and *A. valencienni* share morphological, ecological and behavioral similarities relative to smaller twig anoles.

Grass-bush anoles are species which use narrow diameter vegetation near the ground, such as grass blades or the branches of bushes. One could imagine that species might adapt to one or the other, supporting Williams' (1983) decision to separate them into "bush" and "grass" ecomorph classes; alternatively, it is easy to see how the structural similarity in such supports and the fact that grasses and bushes are often found in close proximity might have led to one morphological type that is adapted to use both (the original "grass-bush" ecomorph). Although some anoles are found primarily in grassy habitats (e.g., *A. ophiolepis* of Cuba), and others usually use low-lying, narrow diameter vegetation such as bushes (e.g., *A. krugi*, Puerto Rico; *A. bahorucoensis*, Hispaniola), many grass-bush anoles use both types of habitat. Moreover, some grass-bush anoles are often found using ferns or vines (Fig. 3.18), which in some ways are structurally intermediate between grass and bushes.

The evidence upon which Williams (1983) assigned species as either "bush" or "grass" anoles is not clear to me. For example, he classified *A. pulchellus* of Puerto Rico as a bush anole, but I associate it as much with grassy as with bushy habitats (e.g., Gorman and Harwood, 1977). Morphometrically, the Puerto Rican grass-bush anoles, which Williams (1983) assigned to the "bush" category, do cluster with the bush-dwelling *A. bahorucoensis*. However, the grass-inhabiting *A. ophiolepis* clusters with this group, rather than with Williams' other putative "grass" anoles (Losos et al., 1998). For these reasons, I conclude that the case for the existence of distinct grass and bush ecomorph classes is weak.

FIGURE 3.18
The Cuban grass-bush anole, *A. alutaceus,* clinging to a fern.

In conclusion, I see no compelling evidence for subdividing any of the ecomorph classes. None of the divided groups are as discretely distinct and recognizable in the way the original six ecomorph classes are. Williams (1972) got it right the first time!

FUTURE DIRECTIONS

Whether the ecomorphs differ in a wide variety of other important ecological factors, including abundance, parasite load, rates of predation, social structure and foraging behavior, has yet to be studied. Making *a priori* predictions is difficult because in many cases pertinent data (e.g., whether abundance of predators or parasites varies across structural microhabitats) is unknown. Moreover, because morphology, ecology, and behavior are tightly interwoven, ecomorph differences may exist for traits that at first blush would seem unrelated to structural microhabitat. Abundance, for example, might be a function of degree of territoriality, which in turn might result from foraging mode, which is related to limb morphology, which in turn evolves adaptively in response to differences in structural microhabitat use (see Chapter 15).

By the same token, whether some aspects of morphology differ among ecomorphs also remains to be investigated. For example, no study has looked at tooth or claw morphology or aspects of the musculature (see Chapter 13). As mentioned in Chapter 2, examinations of the fine structure of the toepads suggests some differences (more terrestrial species having less developed setae), but more detailed studies are needed.

In addition, the natural history of many ecomorph species with small ranges is poorly known, particularly for species that occur in Cuba. Data on these species is needed to fully understand the ways in which the great species richness of some ecomorphs is attained on some islands.

APPENDIX 3.1

A BRIEF HISTORY OF THE STUDY OF *ANOLIS* ECOLOGICAL MORPHOLOGY

Credit for the discovery and documentation of the anole ecomorphs goes to Ernest E. Williams, who arrived at Harvard in 1950 and served as Curator in Herpetology at the Museum of Comparative Zoology from 1957–1980. Students working under his supervision detailed the ecological, morphological, and behavioral aspects of the ecomorph phenomenon, and Williams painted the bigger picture in several synthetic papers that were in many respects well ahead of their time.[69] Indeed, one might argue that Williams' 1972 *Evolutionary Biology* paper played an important role in the development of the field of ecological morphology.[70]

Morphological and ecological differences among anoles were noted by early researchers (e.g., Oliver, 1948; Ruibal, 1961), but quantitative and comparative studies date initially to the work of a college undergraduate who made observations on anoles while visiting his parents in Cuba (Collette, 1961).[71] This work was followed by Rand's

69. For example, in the use of phylogenetic "tree thinking" in interpreting the evolution of anole ecomorphs in his 1972 paper, well before the phylogenetic revolution initiated by papers like Gittleman (1981), Lauder (1981), and Felsenstein (1985).

70. Ecological morphology has become a vibrant, multidisciplinary field that incorporates field and laboratory studies of ecology, behavior, and functional morphology, often in a phylogenetic context (e.g., Wainwright and Reilly, 1994). "Ecomorph," the term Williams coined that refers to species that share a similar set of morphological and ecological features, thus shares obvious relationships to "ecological morphology" or "ecomorphology," which is the study of the relationship between ecology and morphology.

A search of the terms "ecological morphology," "ecomorphology," and "ecomorph" in JSTOR revealed that the terms were rarely used prior to Williams' 1972 paper. In contrast to its frequent use in recent years (JSTOR reported 32 papers using the term in the period 1990–2000), "ecomorph" was only used once before Williams' definition of the term: in a 1954 paper in *Systematic Zoology*, J.G. Edwards proposed the term "ecomorph" for sympatric and synchronic interbreeding populations showing morphological and ethological differences. The term was proposed to distinguish these populations from allopatric, allochronic populations, for which the term "subspecies" would be appropriate. Why the prefix "eco" was employed was not explained.

"Ecological morphology" and "ecomorphology," too, were rarely used before Williams' work (which does not use either of those terms). JSTOR reported that "ecological morphology" was used five times prior to 1972: in a book in German by H. Fitting in 1926, *Die Ökologische Morphologie der Pflanzen*, which is about environmental forces on plants, according to a review in the *Quarterly Review of Biology* in 1927; in an obituary of the Russian plant ecologist Boris Aleksandrovich Keller published in *Science* in 1946; in a paper by Luckan in 1917 discussing the anatomical traits that allowed a plant, the velvetleaf (*Abutilon theophrasti*), to withstand a drought with little apparent ill effect; in an obscure paleontology paper that I did not look up (Kireeva, 1958); and in van der Klaauw's (1948) lengthy article, "Ecological morphology" which anticipated much of what is currently studied under the same name.

JSTOR only cites one use of the term "ecomorphology" prior to 1972, in a paper from 1902 in which I could not find "ecomorphology" (although I did find "geomorphology"). By contrast, the term was found in 153 papers from 1990–2000 (admittedly, a number of these were in the references section citing a book by that name). Of course, much of the credit for popularizing the term and the approach should go to Karr and James (1975), who were the first to use "ecomorphological," and who apparently came upon the term independently of Williams (his work was not cited). Prior to Karr and James' work, "ecomorphological" was only used, according to JSTOR, in a 1957 review of a book on Scandinavian ecology in *Ecology*, in which the term was used without explanation or definition.

71. Bruce Collette became a distinguished ichthyologist at the National Museum of Natural History, Smithsonian Institution, and is the recipient of many awards and honors. Despite his many ichthyological contributions, his 1961 paper on anoles is the second most cited of his papers. Although Collette never studied at Harvard, he was encouraged by Williams, who saw to it that the paper was published in Harvard's *Bulletin of the Museum of Comparative Zoology*.

pioneering community-wide studies on differences in microhabitat use among sympatric species in Hispaniola (Rand, 1962; Rand and Williams, 1969), Puerto Rico (Rand, 1964a) and Jamaica (Rand, 1967c), which in turn led to more detailed and sophisticated studies by Schoener and colleagues (e.g., Schoener, 1968, 1974; Schoener and Gorman, 1968; Schoener and Schoener, 1971a,b).

Rand and Williams' (1969) study of the anoles of La Palma in the Dominican Republic provided the names of the different ecomorphs, leading Williams (1972, 1983) to propose the ecomorph concept—linking morphological, ecological, and behavioral evolution—and to discuss the evolution of communities of ecomorphs.[72]

Moermond (1979a,b), working in Haiti, was the first to quantify morphological differences among sympatric anoles and to examine the relationship between morphology and behavior, an approach followed by Pounds (1988)[73] in Costa Rica. Mayer (1989) extended this quantitative approach across islands, showing that members of an ecomorph class are morphologically more similar to each other than they are to members of other ecomorph classes from their own island. I integrated these approaches by quantitatively examining the relationship between morphology, habitat use, and behavior across islands (Losos, 1990b,c,d; Irschick and Losos, 1999), and by examining the evolution of the ecomorphs in a phylogenetic context (Losos, 1992a; Losos et al., 1998).

A more detailed history of the development of anole research is provided by Rand (1999), and even greater detail can be gleaned by perusing the *Anolis* Newsletters. Starting as a 29-page grant summary report to the National Science Foundation, the idea blossomed into lengthy and informal summaries of the current work of *Anolis* researchers. Newsletters, which range in length from 29–144 pages and contain reports from 13–30 researchers, are available online.[74]

The past 15 years have seen an explosion of research investigating many aspects of ecomorph biology. The list has become too numerous to summarize here, but this work is discussed in appropriate places throughout the book.

72. No discussion of Ernest Williams would be complete without mentioning the two principles he articulated, well known to *Anolis* workers, but otherwise not widely appreciated (Williams, 1977a): "It was while walking along a hedge row in the Dominican Republic, listening to a complaint that I and some of my co-workers did not frame hypotheses every day while in the field, that I invented (or recognized) the Principle of Unsympathetic Magic. This states that, if one arrives at any firm and vivid conviction about matters of fact or theory in the field, the NEXT observation will provide a contradiction. . . . Note, however, that nature is not deceived. No opinion merely pretended to, i.e. not held with fierce conviction, will be responded to by a conclusive observation. The Malice of Nature prohibits the Principle of Unsympathetic Magic from being a source of satisfaction to the field worker."

73. J. Alan Pounds and Bruce Collette (footnote 71) are the only two researchers mentioned in this appendix who did not study under Williams, either as an undergraduate (me) or as graduate students (the rest). Pounds conducted his doctoral work on Costa Rican anole ecomorphology at the University of Florida, but he spent the summer after receiving his degree at Harvard working with Williams.

74. The URL may not remain constant, so I won't provide one. My advice is to Google them.

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