The difference between the Greater and Lesser Antilles can be quantified in the following way. In the Greater Antilles, if each ecomorph type had evolved once, followed by colonization (or vicariance) to occupy each island, then five evolutionary transitions would have occurred. Conversely, if each ecomorph class evolved on each island, then at least 17 transitions would have occurred. The observed number is 19; clearly, independent evolution on each island has been responsible for the repeated patterns observed across islands.

By contrast, in the Lesser Antilles, given the different clades in the two regions, the minimum number of evolutionary transitions in body size is four (assuming three size states: small, intermediate, and large). By contrast, if evolutionary divergence in body size has occurred independently on each island bank,[164] then at least 10 transitions would be required. The actual number is 7, exactly intermediate.[165] Thus, in the Lesser Antilles evolutionary divergence has been less important than in the Greater Antilles; conversely, colonization leading to ecological similarity of closely related species on different islands has been more important in the Lesser Antilles.

CHARACTER DISPLACEMENT

But how did the size differences evolve initially? One possibility is that the size differences evolved by character displacement, the phenomenon that when two similar species come into contact, they evolve in opposite directions to minimize resource overlap, thus permitting coexistence (Brown and Wilson, 1956). Character displacement was controversial for many years because some theoretical treatments suggested that it was unlikely to occur (one species was expected to go extinct before substantial evolutionary divergence could occur) and because there were few well documented examples. However, in recent years an abundance of examples has been published and now the evolutionary significance of character displacement is well established (e.g., Schluter, 2000; Dayan and Simberloff, 2005).

Several authors have hypothesized that character displacement is responsible for size divergence in Lesser Antillean anoles (Schoener, 1970b; Williams, 1972; Lazell, 1972; Losos, 1990a). This hypothesis predicts that large and small size evolved at the same time

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164. As in the Greater Antilles, a number of Lesser Antillean islands were united during the last period of lower sea level.

165. In the northern Lesser Antilles, the outgroup, the *cristatellus* Species Group, is primarily intermediate in size. Assuming that intermediate size is ancestral, then three transitions have occurred, to small size in the *wattsi* species group and to large size independently in *A. bimaculatus* and *A. leachii* or, alternatively, to large size in the ancestor of *bimaculatus* + *gingivinus* + *leachii* and back to intermediate size in *A. gingivinus*. The size of the outgroup for the *roquet* Series in the southern Lesser Antilles is unknown. Nonetheless, regardless of whether the ancestor of this clade was small, intermediate, or large, four evolutionary transitions are required to produce the sizes of the extant species.

These estimates are based on the best current phylogenetic hypotheses for these two clades. However, both phylogenies have weakly supported nodes in critical areas that affect the interpretation of size evolution (see discussion in Creer et al. [2001] and Schneider et al. [2001]).

and on the same island.[166] My previous test of this hypothesis supported these predictions for the anoles of the northern Lesser Antilles, but not for those of the southern Lesser Antilles (Losos, 1990a; see also Miles and Dunham, 1996; Butler and Losos, 1997). However, this analysis used a phylogeny which was pieced together based on a variety of pre-DNA studies and which differs in important ways from more recent studies (e.g., Creer et al., 2001; Schneider et al., 2001; Stenson et al., 2004; Nicholson et al., 2005).

Examination of the most recent phylogeny (Fig. 7.7) reveals three possible cases of character displacement:

1. *A. griseus* (large) and *A. trinitatis* (small) on St. Vincent. The species are sister taxa. Uncertainty about the ancestral state makes the scenario somewhat unclear. Nonetheless, at least one species has evolved away from the size of the other; if the ancestor was intermediate in size, then both species have diverged in opposite directions.
2. *A. richardii* (large) and *A. aeneus* (small) on Grenada and elsewhere in the Grenadines. *Anolis richardii* is the sister taxon to a clade composed of *A. aeneus* plus two intermediate-sized species, *A. roquet* (Martinique) and *A. extremus* (Barbados). Two biogeographic scenarios are possible: (i) the ancestor of this clade diverged into two species on Grenada or in the Grenadines, *A. richardii* and the ancestor of *aeneus* + *extremus* + *roquet*, and then the latter species gave rise to a colonist that traveled to Martinique or Barbados; or (ii) The ancestor occurred somewhere in any of these islands; colonization and allopatric speciation then gave rise to two species, *A. richardii* in Grenada and the ancestor of *aeneus* + *extremus* + *roquet* on Martinique or Barbados. Subsequently, colonization to Grenada from the Martinique/Barbados species led to another speciation event producing *A. aeneus*. Given that all of the basal clades of the *roquet* series are in the south of the SLA, this scenario would require a north-to-south dispersal event that runs counter to the general direction of movement (C. Cunningham, pers. comm.).

   These scenarios can then be combined with phylogenetic reconstruction of body size. The ancestor of the clade may have been intermediate-sized. This is supported both by ancestor reconstruction[167] and by the assumption that intermediate size is optimal on one-species islands. Given this assumption, character displacement could have occurred if biogeographic scenario (i) occurred, and, if the ancestor of *aeneus* + *extremus* + *roquet* was small, with intermediate size evolving subsequent to colonization of Martinique/

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[166] Character displacement doesn't have to occur equally in both species (e.g., Grant and Grant, 2006a). However, in the context of the size patterns of Lesser Antillean anoles, the character displacement hypothesis would predict that the evolution of small and large size occurred simultaneously.

[167] If the evolutionary transition from small to large large or vice versa is considered to be twice as great a change as from either large or small to intermediate, then intermediate size is the most parsimonious reconstruction for the ancestor of this clade.

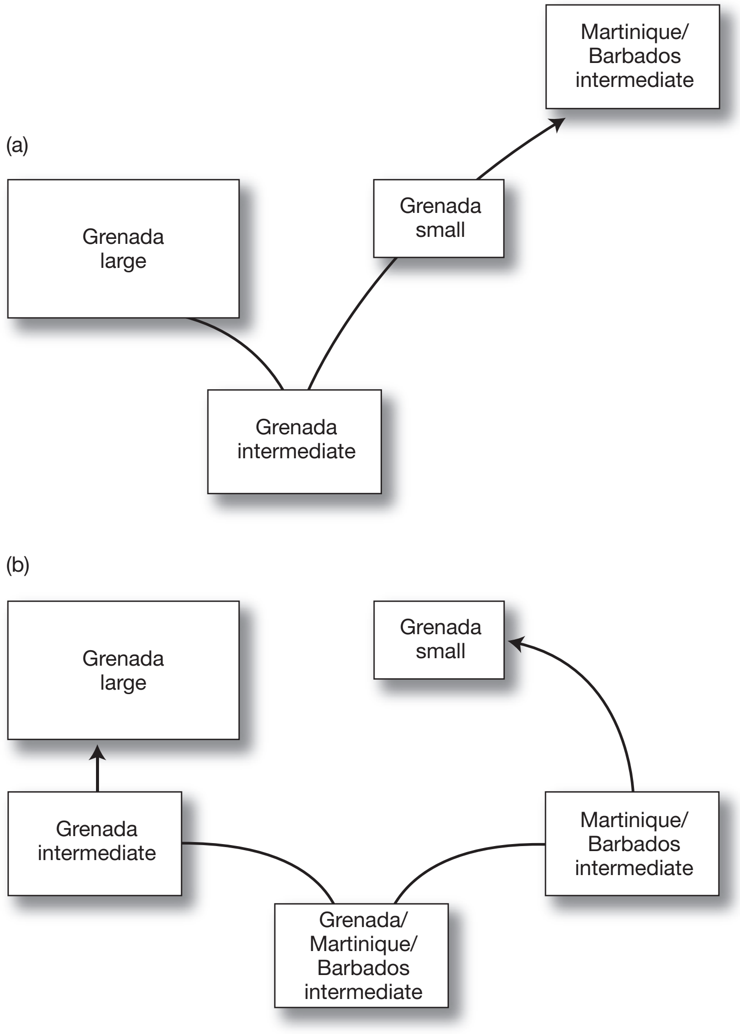

FIGURE 7.8
Two possible scenarios for size evolution in the *richardii* + *aeneus* + *extremus* + *roquet* clade of the southern Lesser Antilles. In (a), character displacement occurs between two species on Grenada. Then, the smaller species, ancestral to *A. aeneus*, gives rise to a colonist which moves to Martinique or Barbados and evolves intermediate size. In (b), allopatric speciation gives rise to two intermediate sized species, one the ancestor to *A. richardii* on Grenada, the other on Barbados or Martinique. This latter species then sends a colonist, the ancestor of *A. aeneus*, back to Grenada, where character displacement occurs between the two initially intermediate-sized species.

Barbados (Fig. 7.8a); or if biogeographic scenario (ii) occurred, the ancestor of *A. richardii* remained intermediate-sized until Grenada was colonized by the ancestor of *A. aeneus*, and the ancestor of *aeneus* + *roquet* + *extremus* was intermediate in size, with small size evolving only when the ancestor of *A. aeneus* colonized Grenada (Fig. 7.8b). Alternatively, other combinations of biogeographic and size evolution scenarios would not be consistent with character displacement.

3. The large and small anoles of the Northern Lesser Antilles. The situation here is uncertain, but in a different way than in the just discussed case of *A. richardii* and *A. aeneus*. The *wattsi* + *schwartzi* + *pogus* clade of small anoles today occurs on the St. Kitts, Antigua, and Anguilla Banks, where it is sympatric with *A. bimaculatus* (large), *A. leachii* (large) and *A. gingivinus* (intermediate), respectively. Given this, it is likely that the small anole clade has been in the presence of another anole species throughout most or all of its evolutionary history, and thus the evolution of small size is consistent with a character displacement hypothesis. But an inconsistency exists: if the ancestor of the other clade was large, then intermediate size subsequently re-evolved in *A. gingivinus,* probably in the presence of small anoles,[168] contrary to what would be expected (Fig. 7.9a). Alternatively, if the ancestral size of this clade is intermediate, then the failure of the ancestor of *A. gingivinus* to evolve larger size is contrary to the character displacement scenario. In this scenario, large size would subsequently have evolved when intermediate-sized colonists were confronted with a smaller anole on the St. Kitts and Antigua Banks (Fig. 7.9b). In either scenario, the coexistence of intermediate-sized *A. gingivinus* and small *A. pogus* is not predicted by the character displacement hypothesis.

In summary, one case, St. Vincent, unequivocally supports character displacement, and the other two cases are ambiguous—character displacement can't be ruled out, but is not definitively supported, either. Although the overall support for character displacement is not overwhelming, it has not been disproven. This is important to keep in mind, because phylogenetic examination could have produced reconstructions entirely inconsistent with character displacement. In summary, the character displacement hypothesis is alive, and has some support; this may be as much as one often can expect from phylogenetic analyses relying on ancestor reconstruction.

Two alternative hypotheses for size evolution must be briefly mentioned. The first is sympatric speciation, in some sense character displacement that occurs within a species, rather than between two species. Certainly, the situation on St. Vincent—sister taxa occurring on the same island—is consistent with sympatric speciation. However, the inferred date of the divergence predates the emergence of the island of St. Vincent, suggesting that these species evolved somewhere else—perhaps the Grenadines?—thus obscuring the geography of this divergence event (C. Cunningham, pers. comm.). Further, in both Grenada and the northern Lesser Antilles, sympatric speciation is consistent with character displacement scenarios, although alternative versions in which

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[168] *A. gingivinus* today occurs on islands on the Anguilla Bank and the small nearby island of Sombrero. *A. pogus* is present on St. Martin and occurred as recently as 1922 on Anguilla. Given that the Anguilla Bank was above seawater during the last ice age, it is probable that *A. pogus* occurred throughout the bank in the recent past.

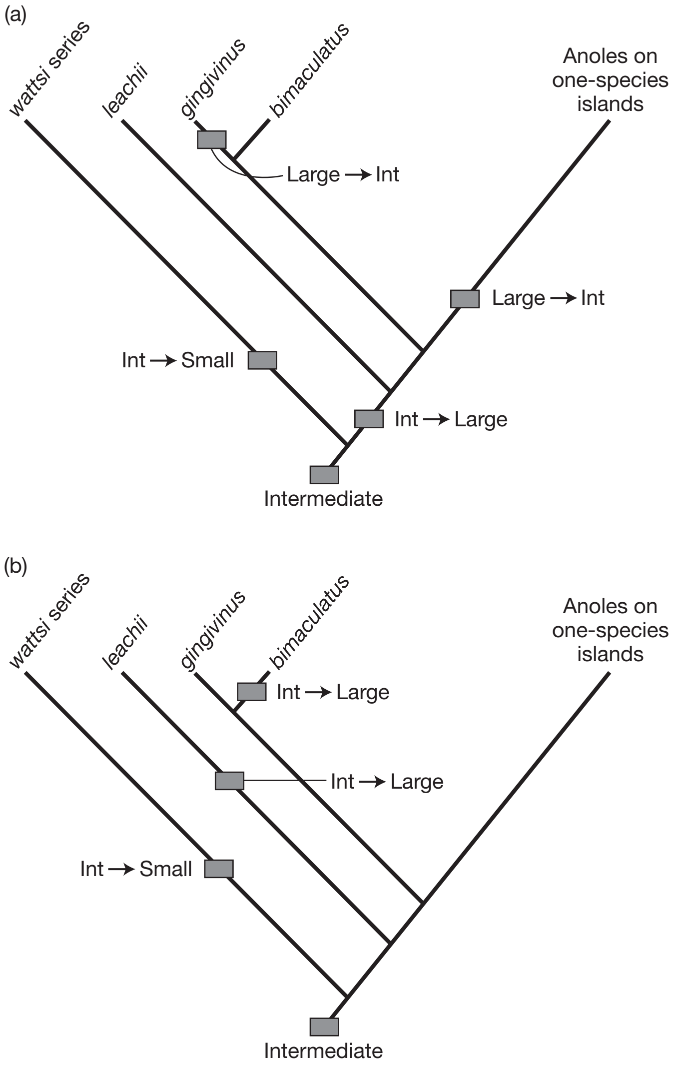

FIGURE 7.9
Two scenarios for size evolution in the northern Lesser Antilles. In (a), character displacement occurs between the two basal clades. Subsequently, intermediate size evolves from large size both in *A. gingivinus* and in the clade of species occupying one-species islands in the southern part of the northern Lesser Antilles. In (b), large size evolves independently in *A. bimaculatus* and *A. leachi* in the presence of a smaller species, consistent with the character displacement hypothesis. In both scenarios, the intermediate size of *A. gingivinus*, whether ancestral or derived, is inconsistent with predictions of the character displacement hypothesis.

speciation occurs in allopatry (e.g., in Grenada and the Grenadines) are possible as well. Sympatric speciation in anoles will be discussed in greater detail in Chapter 14.

The second possibility is the taxon cycle (Roughgarden and Pacala, 1989) or taxon loop (Roughgarden, 1992, 1995) hypotheses. The idea of these hypotheses is that intermediate size is optimal, but that sympatry of large and small species is not produced by divergence in opposite directions, but by a large species invading an island occupied by an intermediate-sized species, which then evolves to smaller size. The only phylogenetic evidence in support of this scenario is the possible evolution from large to intermediate size in *A. gingivinus,*[169] although in the scenario discussed above, this could only have

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[169] In fact, the taxon cycle was inspired by the *gingivinus-pogus* situation, so this doesn't constitute very strong support.

FIGURE 7.10
Mainland aquatic anoles. (a) *A. oxylophus*. Photo courtesy of J.D. Willson. (b) *A. aquaticus*. Photo courtesy of Luke Mahler. Morphological data suggest that these species are sister taxa (Poe, 2004), but molecular data imply that they are more distantly related (Nicholson et al., 2005), raising the possibility that they may have evolved their aquatic tendencies independently.

happened after small size already had evolved in the *wattsi* clade, contrary to the taxon cycle/loop hypothesis. Other criticisms and discussion of this theory can be found in Losos (1992b), Roughgarden (1992, 1995), Schneider et al. (2001) and Stenson et al. (2004).

MAINLAND ANOLES

The mainland is occupied by the Norops clade and the basal anole clade, corresponding to Savage and Guyer's (1989) Dactyloa clade with the inclusion of Phenacosaurus. Both clades exhibit a range of morphologies and ecologies, more so in Norops (Pinto et al., 2008), but that is not surprising given the approximately two-fold greater species richness of Norops. In the absence of more detailed information on the ecomorphological variation of these anoles and greater phylogenetic resolution within each of these clades, statements about patterns of ecomorphological evolution are difficult to make.

I can only come up with two cases in which we can say something definitive about mainland ecomorphological evolution. First, twig anoles seem to have evolved at least twice, once in each clade: *A*. Norops *pentaprion* and close relatives, and the species in the Phenacosaurus clade (Fig. 4.9). Both have twig anole morphology (Beuttell and Losos [1999] for Phenacosaurus; Losos [unpubl. obs.] for *A. pentaprion*) and the scant ecological literature on both species indicates a twig anole lifestyle (Dunn, 1944; Miyata, 1983; Losos, unpubl. for *A. pentaprion*).

Second, aquatic anoles appear to have evolved three times within mainland Norops. These species are different from the West Indian aquatic anoles, but are quite similar to each other in morphology and ecology (Leal et al., 2002; Fig. 7.10).

THE PHYLOGENETIC PERSPECTIVE: WHAT DOES IT TELL US THAT WE DIDN'T ALREADY KNOW AND WHAT HYPOTHESES DOES IT SUGGEST THAT ARE TESTABLE WITH ECOLOGICAL DATA?

Even in the absence of phylogenetic information, ecological interactions would be implicated as an important factor affecting anole communities. The regular size patterns in the Lesser Antilles and the absence of sympatric species occupying the same niche on any island (discussed in Chapter 11) implicate a deterministic factor, the most likely of which is ecological interactions among anole species. Phylogenetic information, however, much more precisely refines this notion.

First, the anole phylogeny makes clear how rarely colonization has occurred in the Greater Antilles, particularly in relatively recent times. We know that this is not for lack of trying: a few species have dispersed widely to unoccupied islands in recent geological time (Chapter 4). It seems most likely that over the course of tens of millions of years, colonists have moved from one Greater Antillean island to another, yet they have failed to become established. The most likely explanation is that they have been repelled by resident species, an example of a "priority effect" (Williams, 1969; MacArthur, 1972; reviewed in Morin, 1999; see also Chase, 2007).

The priority effect is also seen in the Lesser Antilles, where despite the high levels of colonization necessary to populate these oceanic islands, no island contains two species of the same size. Although potential lack of reproductive isolation between similarly-sized species on different islands might be partly responsible for lack of coexistence,[170] the fact that the distantly-related anoles of the southern and northern Lesser Antilles have not been able to cross into each other's domain indicates that this is not the entire explanation.[171] The two-species islands of the northern Lesser Antilles add a twist. The phylogeny indicates that the size difference on these islands has not arisen in situ, but rather results from successful co-invasion of species that evolved their size differences elsewhere. This pattern illustrates the ability of a species to invade successfully in the absence of a similar-sized species.

Second, repeated evolution of the same phenotypes in similar ecological circumstances—ecomorphs in the Greater Antilles, size classes in the Lesser Antilles—implies a deterministic cause. If each phenotype had arisen only once and subsequently had been replicated across islands via colonization, then we could not conclude that these particular phenotypes were specifically well adapted to their environment. Rather, it might be that selection favored the coexistence of any different phenotypes, and the specific ones that evolved were a result of the particular contingencies of history. But repeated evolution of the same phenotypes suggest that the environment is favoring those

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[170] In the absence of reproductive isolation, colonists might simply be subsumed into the native species' gene pool (Losos, 1990a).

[171] Given that these two clades occur on opposite sides of the basal split in anole phylogeny and thus shared their most recent common ancestor at least 40 mya, they almost surely are reproductively isolated; the few cases of hybridization among anoles all occur among much more closely related species (Chapter 2).

specific phenotypes—that, of course, is the basis for the long-held view that convergent evolution is strong evidence of adaptation (see discussion in Chapter 13). Moreover, repeated evolution of the same phenotypes suggests the existence of niches independently of the species that fill them (see discussion in Chapter 16).

Third, the observation that the same ecomorph (Greater Antilles) or size class (Lesser Antilles) has rarely evolved more than once on an island[172] implies that interspecific interactions have a constraining, as well as a driving, role in evolutionary diversification. If island environments favor particular phenotypes, one might expect those phenotypes to evolve repeatedly. The observation that they don't suggests an evolutionary corollary of the priority effect—once an ecological niche is filled by one clade, it is evolutionarily inaccessible to other clades.

These observations lead to the following predictions:

1. Sympatric species interact ecologically.
2. The extent of interspecific competition between species is a function of how ecologically—and morphologically—similar they are.
3. The degree to which a species can colonize a new area is a function of how ecologically similar it is to resident species.
4. Ecological interactions lead to divergence in habitat use.
5. Divergence in habitat use leads to natural selection for phenotypes appropriate to the new habitat.
6. Island environments are similar and favor the evolution of the same phenotypes.

None of these hypotheses is novel, and some of them would have been suggested even in the absence of phylogenetic information. Nonetheless, phylogenetic examination clearly suggests that these hypotheses may be true. Much of the remainder of the book will be devoted to addressing them by studying the extant anole faunas.

FUTURE DIRECTIONS

Future work here echoes that of previous chapters. Pending phylogenetic issues need to be resolved to further understanding of patterns of evolutionary diversification in a number of areas, such as the mainland and the northern Lesser Antilles. Resolution of

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[172] Multiple instances of evolution of an ecomorph on an island may be even rarer than suggested by the 5–7 examples mentioned above (the uncertainty stems from the fact that if twig anole is the ancestral state, then it has not evolved multiple times on Cuba and Hispaniola). Three of those examples—*A. koopmani*, the grass-bush anoles of the *hendersoni* Series, and the twig anole *A. darlingtoni*—are endemic to the South Island of Hispaniola. It is unclear whether this landmass, which has a separate geological history from the North Island, was ever emergent as a separate island (for much of its history, it was underwater [Iturallde-Vinent, 2006]); after merger of the two landmasses, the two regions have been divided many times by high sea levels. Consequently, it is at least conceivable that the South Island clades may not indicate multiple evolution of ecomorph types on the same island, but rather may be the remnants of a separate South Island radiation (R. Glor, pers. comm.).

within-clade relationships will provide insight into how intra-ecomorph diversification proceeds, as well as how unique anoles evolve.

As well as the obvious need to sample more mainland species, a few West Indian taxa are also needed. Most pressing is the Haitian *A. koopmani*, a putative third clade of grass-bush anole from Hispaniola.

8

CRADLE TO GRAVE

Anole Life History and Population Biology

Before tackling the question of how anole species interact (Chapter 11), and how such interactions might drive evolutionary change (Chapter 12), I need to discuss what makes anoles tick. That is, how do anoles interact with their environment? What happens during the course of an anole lifetime and why? These questions will be the focus of this and the next two chapters.

The goal of this chapter is to review the basic aspects of anole population biology and life history, as well as to discuss the role of anoles in the ecosystem. In some sense, much of the information that I will discuss could be categorized as "natural history." In recent years, natural history has not been given a lot of respect—some contend that it does not even qualify as a science. Quite the contrary, I would argue that natural history is not only based on the important scientific foundations of careful observation and inquiry, but that it is essential if we are to formulate meaningful hypotheses about an organism's place in the environment. Moreover, to understand how species interact and evolve through time, knowledge of natural history is indispensable (Greene, 1994, 2005).

Anoles have been intensively studied for more than 40 years, and we know more about anole natural history than we do for most types of organisms. Nonetheless, the amount of information we do not know is staggering. One clear message from this chapter is that many important aspects of anole biology are still little known. As subsequent chapters will illustrate, this lack of information impedes our ability to interpret broad scale patterns of anole ecology and evolutionary diversification. This chapter is meant to be a call to arms: there's much to be discovered and no time like the present!

FIGURE 8.1
Photo of the everted hemipenes of a museum specimen of *A. magnaphallus*. As the name implies, this species' hemipenes are larger than those of most anoles. Only one hemipenis is used at a time: males alternate their use. The hemipenis used depends on whether the male swings its tail over the left or right side of the female. Why some species, such as *A. magnaphallus*, have bilobed hemipenes is not known; the lobes function as a single intromittent organ, rather than being used separately. Photo courtesy of Steve Poe.

The purpose of this chapter is to review the basic aspects of anole biology. In some cases, such as reproductive biology, anoles exhibit little variation (at least of which we are aware), and my goal is simply to report what anoles do.[173] In other cases, such as diet, considerable diversity exists within and among anole species, and my goal is to explore this diversity and to explain its ecological and evolutionary significance.

REPRODUCTION

I'll start at the beginning, with the way a young *Anolis* makes its way into the world. Anole courtship is a highly stereotyped business. Males perform a display in which they bob their heads and extend their dewlaps in a species-specific manner. The stereotypy of the head-bob cadence is important, as it appears to be a means for females to distinguish conspecifics from heterospecifics, a topic to which we will return in Chapter 14. Females respond by headbobbing or dewlapping (or both), and sometimes arch their neck to indicate receptivity. The male often bites the female on the neck and mounts on her back, swinging his tail around to the underside of the female's tail and bringing their cloacae into close proximity. The male then everts one of his two intromittent organs, termed hemipenes and stored in the base of the tail (Fig. 8.1), and inserts it into the female's

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[173] An important caveat is that most generalizations are based on data for relatively few species, most of which are usually West Indian. Even basic aspects of the biology of most of the 361 species of anoles are unknown. Who knows what surprises remain to be discovered?

cloaca (for a review of the reproductive behavior of *A. carolinensis*, which has been studied much more intensively than any other anole species, see Wade [2005]).[174]

Most, but not all, species have a distinct breeding season (e.g., Andrews, 1971; Fitch, 1973a; Jenssen and Nunez, 1994). In the West Indies, seasonal variation in temperature plays a role in determining its length: more northerly species and populations at higher elevations tend to have shorter breeding seasons (Licht and Gorman, 1970; Gorman and Licht, 1974). Some mainland and West Indian species also reduce reproduction in the dry season (Licht and Gorman, 1970; Sexton et al., 1971).[175]

In *A. carolinensis*, the only species whose endocrinology has been studied in detail, long days and warmer temperatures trigger growth of the testes and ovaries. Males begin reproductive behavior before females, and the sight of a displaying male serves as a cue to bring females into reproductive condition.[176] The endocrinological and neurophysiological mechanisms underlying the development and cycling of the reproductive system and governing the expression of reproductive behaviors of the green anole have been extensively studied and are a model system in laboratory research (see references in Crews [1975], Crews and Moore [2005], Lovern et al. [2004], and Wade [2005]); however, little comparative work has been conducted, except for some research on *A. sagrei* (e.g., Tokarz et al., 2002).

Unlike almost all other lizards, females produce only one egg at a time at an average interval of 5–25 days[177] (Andrews and Rand, 1974; Andrews, 1985b). In at least one species, egg size is correlated with female size (Vogel, 1984; see also Jenssen and Nunez, 1994); the only data of which I am aware suggests that inter-egg interval is not a function of female size (Jenssen and Nunez, 1994). Species vary in where they lay their eggs, in places as varied as in the leaf litter; under rocks and logs; in tree holes, rock crevices, and bromeliads; and attached to walls and ceilings of caves (reviewed in Rand, 1967a; see Andrews [1988] for a detailed study of *A. limifrons*). A number of species are known to use communal egg sites, presumably in areas in which appropriate habitat is limited (Rand, 1967a; Novo Rodríguez, 1985; Estrada and Novo Rodríguez, 1986); hatching, or at least dispersal from the communal nesting site, may be synchronized in *A. valencienni* (Hicks and Trivers, 1983).

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174. Anoles (at least *A. carolinensis* and *A. sagrei*, the only species so studied) alternate the use of hemipenes. Each hemipenis is connected to its own testis. If prevented from using one hemipenis (by placing tape over one side of the cloaca), the male transfers significantly fewer sperm when it continually reuses the same hemipenis (Tokarz, 1988; Tokarz and Slowinski, 1990).

175. But see Gorman and Licht (1974), who reinterpreted patterns of reproduction in West Indian species and considered seasonal changes in temperature to be more important than changes in precipitation.

176. But see Jenssen et al. (2001), who argued that some of these conclusions are artifacts resulting from abnormally high densities in laboratory populations. They reported that in the field, males and females emerge simultaneously and become reproductively active more or less in synchrony, with male reproductive development slightly preceding that of females.

177. Although only a single egg is ovulated at a time, alternating ovaries, females retain eggs during times of drought and thus sometimes are found carrying as many as three eggs, two shelled and one in the oviduct (Stamps, 1976). Data on egg-laying intervals are scarce, primarily coming from *A. carolinensis*.

The actual egg laying process is little known. *Anolis carolinensis* begins by selecting a site and then probing it with her snout, followed by digging with the forelegs. An egg is then laid into the hole, pushed deeper with the snout, and then covered with dirt by back-to-forward movements of the forelegs. Eggs not laid in the hole are rolled in with the snout. Periodically, lizards stop digging to probe the hole with their snouts; occasionally the female abandons the hole, presumably because she has determined that conditions are unsuitable (Greenberg and Noble, 1944; Propper et al., 1991). Behavior of *A. aeneus* is very similar; in the laboratory, egg laying behavior didn't culminate in laying until a patch of ground was experimentally watered, which suggests that the lizards were examining whether the soil was sufficiently moist (Stamps, 1976).[178] *Anolis polylepis* has also been shown experimentally to prefer moister soil for egg laying (Socci et al., 2005). Andrews and Sexton (1981) compared eggs of two species that occur in hydrically different habitats and showed that eggs of the species that occupies more xeric habitats, *A. auratus*, have lower rates of water loss than do the eggs of the more mesic *A. limifrons*.

Incubation time is not well documented; in the laboratory it is 3.5–6 weeks for several Caribbean species (Greenberg and Hake, 1990; Sanger et al., 2008a), but may be as long as 130 days for montane species (Schlaepfer, 2003). Offspring are precocial and hatch at a small size (16–42 mm SVL; interspecific variation in hatchling size correlates with adult size [Andrews and Rand, 1974]).

GROWTH

Andrews (1976) measured growth rate and age of maturity of females in 13 anole species. Growth rate varied five-fold among species, with mainland species growing considerably faster than West Indian species. Schoener and Schoener (1978), however, found that some arboreal West Indian anoles had growth rates comparable to mainland species, whereas the terrestrial *A. sagrei*, which has much higher population densities, had growth rates more in line with Andrews' West Indian data. Schoener and Schoener (1978) suggested that population density, which should be related positively to degree of food limitation, may be the primary determinant of anole growth rates (see also Vogel, 1984).

Males generally grow faster than females (Schoener and Schoener, 1978; Vogel, 1984; Schlaepfer, 2006), leading to the sexual size dimorphism seen in many species (Chapter 9). Mean age of sexual maturity of females also shows a five-fold span, from 57–279 days; in line with growth rates, mainland species matured much earlier (Andrews, 1976).

DISPERSAL

Little is known about the dispersal of anoles. One study of *A. limifrons* found that most lizards dispersed very little and that the home ranges of many individuals moved little

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[178] Anole eggs, like those of many other reptiles, are very sensitive to hydric conditions in their incubating medium (Andrews and Sexton, 1981; Socci et al., 2005; Sanger et al., 2008a).

from the juvenile to adult age. The maximum dispersal distance, measured as distance from the center of the juvenile home range to the center of the adult home range, based on 148 individuals, was 45 meters. Both the mean and extremes were greater for males than for females (Andrews and Rand, 1983). *Anolis limifrons* is a small and short-lived mainland species; it is always possible that larger, longer-lived species may disperse further.

The only other data come from *Anolis aeneus*, which moves as much as 150 meters or more after hatching to occupy open clearings (Stamps, 1983b, 1990). Ultimately, the lizards move back into shadier areas when they reach subadult size, although it is not known whether they return to the vicinity of their hatching site.

A number of arboreal species are known to disperse across open ground between trees (Trivers, 1976; Hicks and Trivers, 1983; Losos and Spiller, 2005).

LIFE SPAN AND SURVIVAL RATES

Maximum life spans for most species are not known, but Meshaka and Rice (2005) estimate from growth rates that *A. equestris*, among the largest of anole species, can live for more than 10 years.

Schoener and Schoener (1982b) studied the survival of four species at 12 sites on three Bahamian islands. Some *A. sagrei* survived for at least 48 months (the length of the study), some *A. angusticeps* and *A. distichus* for 36 months, and some *A. smaragdinus*[179] for 24 months. Life expectancy of a newborn lizard varied between 0.9 and 1.9 years for most species/sex classes. In contrast, most mainland species, and some West Indian ones, have substantially lower life expectancy, with a lifespan that rarely exceeds a year (see reviews in Schoener and Schoener [1982b] and Andrews and Nichols [1990]). In the Bahamas, survival was higher on a smaller island with fewer avian predators than on larger islands with more predators; in closed forest compared to scrubby habitat; and, in *A. sagrei*, for females than for males(Schoener and Schoener, 1982b).[180] Variation in survival across sites in Panama for *A. limifrons* is greater than between-site variation in survival in Bahamian species (Andrews and Nichols, 1990).

Another, rarely studied, aspect of survival concerns mortality in the egg stage, which can vary greatly among sites (Andrews, 1988; Schlaepfer, 2003). Andrews (1988) noted that survival of eggs was 2–3 times more variable than survival of adults across the same study sites.

PREDATORS

Anoles are preyed upon by a wide variety of vertebrate and invertebrate predators (Fig. 8.2). I am unaware of any comprehensive review of predation on anoles, but many case studies and some limited reviews are available. Perhaps the most thorough is Henderson and

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[179] Referred to at that time as *A. carolinensis*.

[180] In *A. distichus*, there was a suggestion that males survived better than females.

colleagues' analysis of the diet of West Indian snakes, which shows that most West Indian snakes eat anoles and that, collectively, anoles constitute more than 50% of the diet of West Indian snakes (Henderson and Crother, 1989; Henderson and Sajdak, 1996). By contrast, anoles constitute a much smaller fraction of snake prey on the mainland, 3% in one estimate (Henderson and Crother, 1989).[181] On Guam, the introduced brown tree snake (*Boiga irregularis*) preys heavily on *A. carolinensis* (itself introduced), and appears to have eliminated the anoles from non-urban settings (Fritts and Rodda, 1998).

Some birds, such as the American kestrel (*Falco sparverius*), the pearly-eyed thrasher (*Margarops fuscatus*), cattle egrets (*Bubulcus ibis*) and the aptly named lizard cuckoo (*Saurothera vielloti*) take anoles regularly, and many others take them at least occasionally (Wetmore, 1916; Cruz, 1976; Wright, 1981; Waide and Reagan, 1983; McLaughlin and

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[181] Though some mainland snakes, such as the blunt-headed vinesnakes, genus *Imantodes*, eat anoles in great quantities (e.g., Myers, 1982; Duellman, 2005).

FIGURE 8.2
Anole predators. (a) Predation by a jumping spider on *A. limifrons* at La Selva, Costa Rica. Photo courtesy of Harry Greene. (b) Predation by a basilisk (*Basiliscus basiliscus*), on *A. gorgonae* on Isla Gorgona, Colombia. Photo courtesy of Thomas Marent, www.thomasmarent.com. (c) Predation by *Siphlophis compressus* on *A. nitens* in Brazil. Photo courtesy of Marcio Martins. (d) Predation by a trogon on a green anole, possibly a new species of the *chlorocyanus* Series. Photo courtesy of Eladio Fernández.

Roughgarden, 1989; Gassett et al., 2000; Powell and Henderson 2008a).[182] Forty percent of the bird species at one study site in Grenada were observed eating anoles (Wunderle, 1981), as were many understory bird species in a Panamian rainforest (Poulin et al., 2001).

Lizards, too, can be important predators, and predation by other anole species and cannibalism have been reported in many species (Gerber, 1999). Other predators include monkeys, dogs, cats, mongooses, frogs, katydids, tarantulas, spiders, whip scorpions, and centipedes (e.g., Rand, 1967b; Waide and Reagan, 1983; Corey, 1988; Guyer, 1988a; Mitchell, 1989; Leal and Thomas, 1992; Reagan, 1996).

Probably the best documented effect of a predator on anoles involves the interaction between the curly-tailed lizard, *Leiocephalus carinatus,* and *A. sagrei* (Fig. 8.3). The curly-tailed lizard is a large, lumbering, primarily terrestrial lizard with poor climbing abilities.

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[182] Wetmore (1916) had the right spirit when, in his book *Birds of Porto Rico*, he stated in reference to the American kestrel (p. 32): "The only real criticism of this small hawk is its large consumption of lizards, amounting to 40.4% of its entire food." Similarly, with regard to the lizard cuckoo (p.59): "In consuming such quantities of lizards, this bird must be considered injurious, though to some extent it makes up for this by a diet of pernicious caterpillars . . ."

FIGURE 8.3
Curly-tailed lizard eating an *A. sagrei* in the Bahamas. Photo courtesy of Tom Schoener.

FIGURE 8.4
Tom Schoener on one of the small Bahamian islands near Abaco in the northern Bahamas on which predation studies were conducted. This was the smallest island used in the study.

In 1997, Tom Schoener, David Spiller and I set up an experiment in the Bahamas in which we introduced curly-tailed lizards to six small Bahamian islands, using another six islands as controls (Fig. 8.4; vegetated area of islands: 137–270 m^2).[183]

We did not know what to expect from this experiment. The curly-tailed lizard has a broad diet and is known to eat anoles (Schoener et al., 1982), but we didn't know how often. Possibly such an occurrence is rare and would have minimal population level effects. We contemplated that our experiment might show no effect at all. But we couldn't have been more wrong. The response was immediate and dramatic: within two months, a two-fold difference in lizard density was established between the islands with and without predators, and this difference was maintained for the 2.5 year course of the experiment (Fig. 8.5a). In a second run of this experiment,[184] in which lizards were individually marked, survival rates on the islands in which the curly-tailed lizards were introduced were as low as 6% over the course of six months, whereas on control islands, survival was as high as 91% (Schoener et al. 2005).

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[183] Curly-tailed lizards occur nearby (usually within 200 m) and naturally colonize these islands (Schoener et al., 2002). Moreover, the effects of these experiments are transitory, as hurricanes periodically remove the populations (Schoener et al., 2001).

[184] Initiated after the first experiment was washed away by Hurricane Floyd in 1999. This second experiment, too, was terminated abruptly, by Hurricane Frances in 2004.

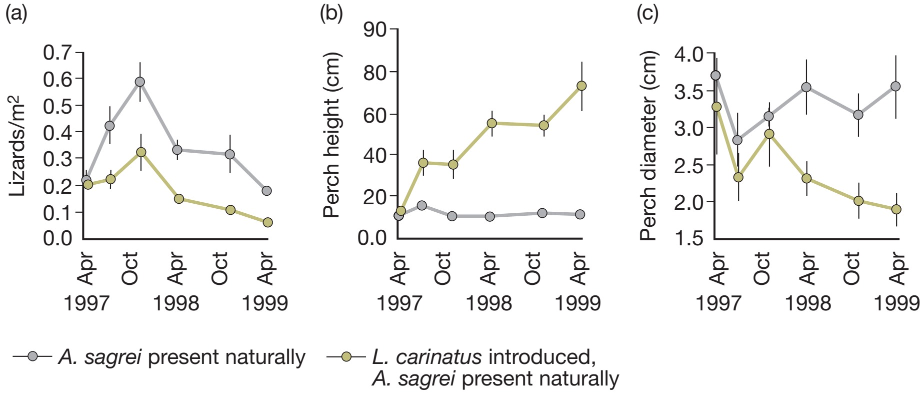

FIGURE 8.5
Effect of curly-tailed lizards on population size and habitat use of *A. sagrei*. Figure modified with permission from Schoener et al. (2002).

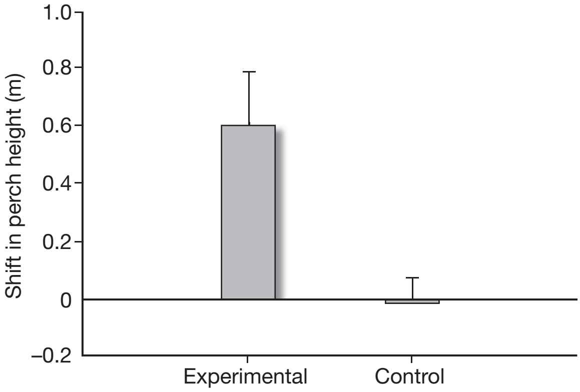

FIGURE 8.6
Immediate behavioral response of *A. sagrei* to newly-introduced curly-tailed lizards. When the predators were introduced to the island, they were placed in front of an anole, which was observed for 10 minutes. As a control, trials with the curly-tailed lizards were alternated with trials in which a piece of wood the size of a curly-tailed lizard was placed in front of an anole. Shifts in perch height were calculated as the height of the anole at the end of the experiment compared to its initial height. Figure modified with permission from Losos et al. (2004).

Behaviorally, anoles responded to the presence of the entirely terrestrial curly-tailed lizards by increasing their use of higher and thinner perches (Fig. 8.5b,c). Focal animal studies conducted when the curly-tails were first introduced revealed that anoles responded immediately to the presence of these predators, even though these islands had been curly tail-free for many generations (Fig. 8.6).

Anoles exhibit similar behavioral shifts in the presence of teid lizards in the genus *Ameiva*, which like curly-tailed lizards are relatively large, entirely terrestrial and known to eat anoles. On both Grenada and some offshore islets near Antigua, several anole species use the ground more often early and late in the day, when the more heliothermic *Ameiva* is not active (Simmons et al., 2005; Kolbe et al., 2008a). Moreover, in comparisons of *A. wattsi* on Antiguan islets with and without *Ameiva*, the anoles on the *Ameiva*-free islands use warmer microsites, are more active at midday and shift upward off the ground to a lesser extent (Kolbe et al., 2008a). These findings strongly suggest a response to the predatory lizard, but experimental manipulations would be useful to rule out other possibilities (e.g., temperature and habitat differences among islands).

Anoles behaviorally react to an approaching predator in many ways. Common responses include running around to the other side of a tree (termed "squirreling"),[185] running up a tree or other vertical object, running or jumping to the ground and running away, and jumping to another structure (Regalado, 1998; Schneider et al., 2000; Cooper, 2006; Larimer et al., 2006). Cryptic species allow a closer approach before fleeing (Heatwole, 1968; Cooper, 2006; Vanhooydonck et al., 2007), and often slowly creep to the other side of a branch or trunk and then quietly slip away (Oliver, 1948); others just hunker down against the surface and hope they will not be detected, a behavior which seems much more common in mainland species (Fitch, 1975; Andrews, 1979; Talbot, 1979). Some mainland species will freeze when a stick—supposedly mimicking a snake—is thrust toward them (Fitch, 1971, 1973a,b; Henderson and Fitch, 1975). Among Greater Antillean ecomorphs, grass-bush anoles tend to flee toward the ground, whereas trunk-crown anoles flee upward; the contradictory data for trunk-ground anoles may reflect a habitat effect: in forests, trunk-ground anoles sometimes flee upward, but in areas with few large trees, they move toward the ground (Collette, 1961; Ruibal, 1961; Rand, 1962; Schoener, 1968; Heatwole, 1968; Losos et al., 1993a; Schneider et al., 2000; Mattingly and Jayne, 2005; Cooper, 2006; Vanhooydonck et al., 2007).

Many anoles will display to an approaching human (e.g., Rand, 1962, 1967b). This behavior has probably been observed by anyone studying anoles in the West Indies (I don't know if it occurs in mainland anoles). I suspect that most workers, like me, dismissed the behavior as non-adaptive and inconsequential—probably the result of some defect in anole neural circuitry and perhaps an artifact of human disruption of the environment. What could be the use of an anole displaying at a potential predator that is so much larger than itself?

In a perceptive series of experiments, Manuel Leal showed that such behavior is adaptive in *Anolis cristatellus*, which displays not only at humans, but also to a common predator, the Puerto Rican racer, *Alsophis portoricensis* (Leal and Rodríguez-Robles, 1997b; Leal, 1999). In laboratory trials, Leal and Rodríguez-Robles (1995) showed that the snake, (which can attain a length of more than), attacked anoles much less often

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[185] A tactic which Wunderle (1981) showed to be markedly less successful when anoles were attacked by a flock of Carib grackles (*Quiscalus lugubris*), rather than by a single individual.

when the lizard displayed. Moreover, they demonstrated that when attacked, the lizards fought back, often biting the snake on the snout for as long as 20 minutes and managing to escape in 37% of the encounters (Leal and Rodríguez-Robles, 1995)—remarkable given the size discrepancy of the snake and the lizard. In field trials, Leal (1999) found that the extent of display behavior toward a snake model correlated with the endurance capacity of the lizard (as determined in subsequent laboratory trials); the greater the endurance capacity of the lizard, the more it displayed to an approaching snake model.

Anole displays to predators may be an example of a pursuit deterrent signal (reviewed in Caro, 2005). By signaling their endurance capability, anoles may be indicating their ability to fight back, escape, and potentially even injure a snake (Leal, 1999). Future work is needed to determine whether other anole species display toward natural predators (Leal and Rodríguez-Robles [1997a] have shown that *A. cuvieri* similarly displays toward a snake model in the field) and whether the pursuit deterrence hypothesis appears generally applicable.

PARASITES

A wide variety of internal and external parasites, including, coccidians, cestodes, nematodes, trematodes, mites and flies, has been reported in many anole species (e.g., Coy Otero and Hernández, 1982; Vogel and Bundy, 1987; Dobson et al., 1992; Cisper et al., 1995; Zippel et al., 1996; Goldberg et al., 1997; Schlaepfer, 2006; Irschick et al., 2006a). In the few cases where it has been investigated, the effect of parasitism on individual lizards appears relatively minor (e.g., Dobson et al., 1992; Schlaepfer, 2006), although infestation by larvae of the parasitic fly, *Lepidodexia blakeae*, which occurred at very high levels in one New Orleans population (Irschick et al., 2006a), is often fatal (Dial and Roughgarden, 1996).

Malaria parasites have been a particular focus of research, and several species are known to afflict anoles (Telford, 1974; Schall and Vogt, 1993; Staats and Schall, 1996; Perkins, 2001; Perkins et al., 2007). However, the individual and population level consequences of such parasitism are not well known. *Plasmodium* infection has detrimental effects on *A. gingivinus* (Schall, 1992), but little or no detectable effect on *A. gundlachi* (Schall and Pearson, 2000) or *A. sabanus* (Schall and Staats, 2002). No direct studies of the population effects of malaria have been conducted, but one correlational study related the prevalence of parasitism in *A. gingivinus* to interspecific interactions (Schall, 1992; see discussion in Chapter 11).

POPULATION DENSITY AND CONSTANCY

Anolis trinitatis has the highest density reported for any anole, more than 32,000 individuals per hectare (Hite et al., 2008), followed by *A. stratulus* (with more than 21,000 individuals per hectare [Reagan, 1992]) and *A. pulchellus* (17,000 individuals per hectare [Gorman and Harwood, 1977]).[186] Among 25 species, mean density of West Indian species (not including either *A. stratulus* or *A. pulchellus*) was five-fold greater than the mainland mean, and 2/3 of the West Indian species had a higher density than any mainland species (Stamps et al., 1997).[187]

Interpopulational variation in density can be great on both the mainland and in the West Indies. Densities exhibit six-fold variation among populations of *A. limifrons* on or near Barro Colorado Island in Panama (Andrews, 1991). Similar or greater variability is seen among populations of four species of Bahamian anoles (Schoener and Schoener, 1980a).

West Indian anole populations generally are quite stable, showing relatively little fluctuation in population size from one year to the next (Schoener, 1985, 1986a).[188] By contrast, mainland anoles show considerably greater year-to-year variability, as much as eight-fold for one population of *A. limifrons* (Fig. 8.7; Andrews, 1991). These generalities should be taken cautiously, however, as they are based on studies of only four mainland and six West Indian species.

DIET

A good place to start a review of the food anoles eat is a discussion of how they procure it. Although prey movement may be required to elicit feeding behavior in some species, others such as the aquatic anole, *A. aquaticus* recognize and rapidly eat non-moving prey (Burghardt, 1964; Goodman, 1971; reviewed in Moermond, 1981). Certainly, recognition of non-moving food occurs in the many anole species that eat fruit (see below).[189]

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[186] This figure is somewhat lower than that given by Gorman and Harwood (1977), whose numbers were inflated by several rounding errors.

[187] Mainland density figures come from Central American species. Few data are available for the density of Amazonian species, primarily because they are so much scarcer even than Central American species (Vitt and Zani, 1998b).

[188] Populations hit by hurricanes being an exception (Schoener et al., 2004).

[189] No discussion of anole frugivory and feeding behavior is complete without mention of the famous Chuckles® experiment. On an expedition to remote Malpelo Island off the coast of Colombia, Rand et al. (1975) noted that the native anole of the island, *A. agassizi*, was attracted to the orange cap of a bottle of suntan lotion and to the orange packaging for Kodak film, and would come running from great distances and in great numbers when half of an orange was placed on the ground. The intrepid biologists wondered whether these anoles had a particular predisposition to the color orange. Fortunately, the expedition was outfitted with packages of Chuckles®—billed as "America's most popular jelly candy" in a 1949 advertisement—which conveniently contain candies in five colors: orange, yellow, red, green, and black. By placing various combinations of these sweets on the ground, the authors found that anoles are most attracted to orange and yellow candies, and least attracted to black ones.

But the story does not end there. In an effort to extend this research program to additional species, a graduate student in my laboratory tested a captive *A. grahami* with differently colored Starbursts®, a non-jellied candy that also comes in different colors (Chuckles® may not have been available in the local vending machine). Unfortunately, this experiment was stymied by other members of the lab, who removed lizard-bite sized pieces from the candies, thus briefly convincing the experimentalist that he was on to a major discovery.

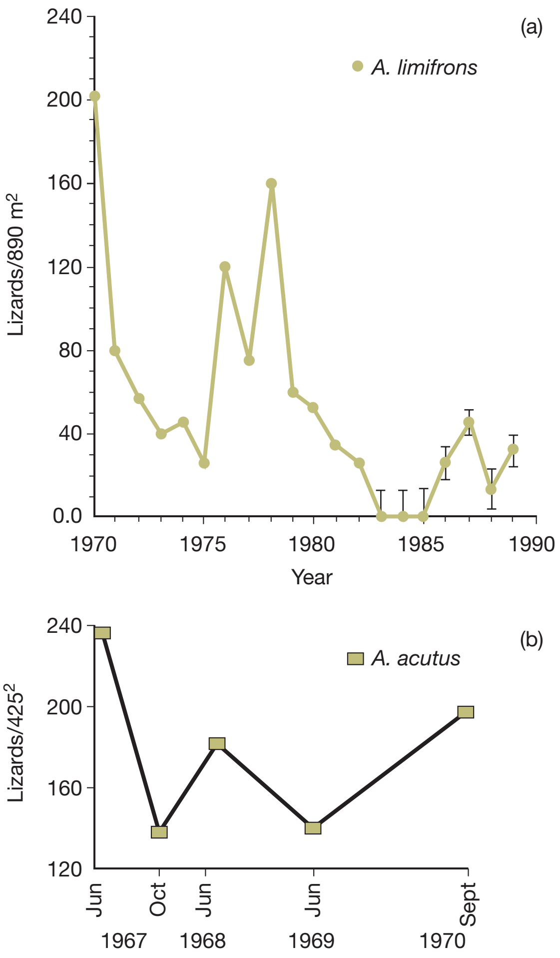

FIGURE 8.7
Population density of *A limifrons* on Barro Colorado Island, Panama over a 19-year period and *A. acutus* from St. Croix over a three-year period. Figure modified with permission from Andrews (1991); data for *A. acutus* from Ruibal and Philibosian (1974).

FORAGING MODE

How lizards forage for prey has been extensively studied (reviewed in Reilly et al., 2007). Two "modes" of foraging are recognized: "sit-and-wait," in which lizards remain in one spot, ready to pounce upon any unsuspecting prey that wanders by, and "active foraging," in which lizards seek out prey items, which oftentimes are immobile and hidden. Much ink has been spilt on whether these modes represent distinct alternatives, as opposed to being endpoints of a continuum (e.g., Perry, 1999; Butler, 2005; Cooper, 2005b, 2007).

Anoles epitomize the different foraging modes. At one extreme, trunk-ground anoles are classic sit-and-wait foragers, surveying the ground from their perches low on tree trunks and rapidly dashing or jumping to the ground to apprehend prey that move within range (e.g., Rand, 1967b). On the other hand, trunk-crown and at least some twig anoles often cruise through the arboreal matrix eating prey they come upon (see, e.g., the description of *A. valencienni* foraging in Hicks and Trivers [1983][190] and the comparison between the trunk-ground anole *A. sagrei* and the twig and trunk-crown anoles *A. angusticeps* and *A. smaragdinus*[191] in the Bahamas [Schoener, 1979]). Quantitative data confirm these impressions. The ecomorphs differ, dividing into active (trunk, trunk-crown) and sedentary (crown-giant, grass-bush, and trunk-ground) groups, with twig anoles being intermediate (Fig. 3.15; Johnson et al., 2008).[192]

Moermond (1979b) proposed that differences in foraging movement rates result from differences in the visibility in different structural microhabitats: lizards sitting in some microhabitats can keep an eye on a larger expanse than lizards in other microhabitats. For example, this hypothesis could account for differences among species that occur primarily on tree trunks; because they survey a larger area (the ground), trunk-ground anoles may need to move less than trunk anoles, which only scan a small area of tree trunk. However, Johnson et al. (2008) measured vegetation structure and found no overall relationship between visibility and movement rates.

An alternative hypothesis is that the costs and benefits of the foraging modes vary among microhabitats, potentially as a result of costs of movement, prey availability, or other factors. Comparisons across lizard families indicate that sit-and-wait foragers have a lower rate of energy acquisition than active foragers (Anderson and Karasov 1981).[193] Behavioral data suggest that the same relationship may exist for anoles; the ecomorphs that move at the lowest rates also eat less frequently (Johnson et al., 2008). Detailed data on rates of energy use and intake, and how they vary among habitats,

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190. Hicks and Trivers (1983) reported on one female A. *valencienni* observed for three hours and forty minutes that moved up from the base of a tree into the vegetation at a height of 11 m, and then back down to the ground, feeding three times along the way.

Some of the danger inherent in an active foraging mode was apparent in another observation of a female moving upside down on a bromeliad, searching for prey (quoting from Trivers' field notes, p. 575): ". . . it seems to spot something on a neighboring bromeliad, also upside down. I too spot something on the second bromeliad. Starts to dart the 5 cm to the neighboring bromeliad but—as if forgetting it is upside down—it steps into thin air and falls 6 m to the ground. It appears to be uninjured."

191. Referred to as *A. carolinensis* in that paper.

192. This conclusion is based on Johnson et al.'s (2008) analysis of data for 31 species. Other studies on smaller numbers of species (Moermond, 1979b; Irschick, 2000; Cooper, 2005a) generally reach similar conclusions, with one key difference: grass-bush anoles generally were found to be among the most active species (e.g., Perry, 1999; Cooper, 2005a); the explanation for this discrepancy is not obvious (reviewed in Johnson et al., 2008).

Some studies of lizard foraging behavior use a second metric, percentage of time spent moving. When species differ in the duration of their movements, this metric is a necessary complement to measuring the number of discrete movements per unit time (Perry et al., 1990; Cooper, 2005b). However, because most movements of anoles are extremely brief, these two measures are highly congruent for anoles (Perry, 1999; Irschick, 2000; Cooper, 2005a): if anything, some of those anoles that move most frequently—trunk-crown and some twig anoles—are also the ones that have longer movement durations (Irschick et al., 2000). Hence, were data available for percentage moving for many species, they would likely reveal even greater differences among the ecomorphs than those shown in Figure 3.15.

193. In comparison to classic active foragers like teid lizards, which spend as much as 87% of their time on the move, all anoles are relatively sedentary (Perry, 1999; Butler, 2005; Cooper, 2005b). Nonetheless, even if the degree of difference is more muted, the sit-and-wait versus active searching dichotomy applies as well to anoles as it does to larger scale differences among lizard families (see discussion in Johnson et al., 2008).

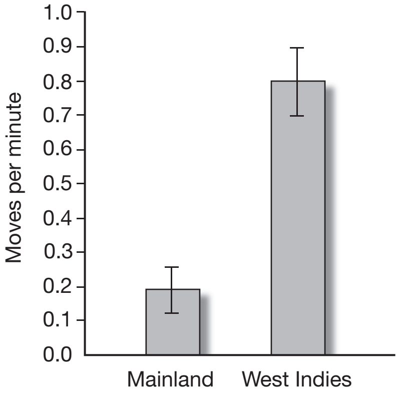

FIGURE 8.8

Differences in movement rate between mainland and West Indian anoles. Differences are statistically significant (Analysis of variance, $F_{1,44} = 41.90$, $p < 0.001$). Data from Perry (1999), Irschick et al. (2000), Cooper (2005a), and Johnson et al. (2008). When multiple values were available for a species, they were averaged. Considerable heterogeneity in methods and results exists among studies. Only Perry's (1999) study contains data for both mainland and West Indian species. Results are nearly significant ($p = 0.091$) if the analysis is confined to only the nine species studied by Perry, thus eliminating effects of inter-study differences in methodology.

could prove useful in understanding the genesis of foraging mode differences among the ecomorphs.

The data in hand also hint at a difference between West Indian and mainland anoles in movement rates. Among 46 species, mean movement rate of West Indian species is three times that of mainland anoles (Fig. 8.8).[194]

Detailed observations of foraging are surprisingly scarce in the literature. One exemplary study focused on the behavior of *A. carolinensis* in Georgia (Jenssen et al., 1995; Nunez et al., 1997). Three foraging styles were observed: sit-and-wait; eat on the run, in which a lizard captured a prey item it encountered as it was moving, usually while patrolling its territory; and active searching, in which the lizard moved very slowly

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[194] As discussed in Chapter 6, the Norops clade of mainland anoles is the result of a single colonization event. Almost all of the ecological and behavioral data for the mainland comes from species in this clade, which accounts for the large majority of mainland species. For this reason, as discussed in Chapter 5, data points from mainland anoles are not statistically independent; consequently, statistical analyses between mainland and island species will suffer from phylogenetic pseudoreplication and, were statistical analyses conducted in a phylogenetic context (not yet possible due to lack of a well supported phylogeny for mainland Norops), most results would be non-significant. This situation does not invalidate the finding that mainland and island anoles are different, but complicates causal explanation of such differences. That is, an analysis of variance between mainland and West Indian anoles tests the hypothesis that geographic location is related causally to foraging rates. However, because mainland Norops represent a single clade, they have inherited from their common ancestor many characteristics other than their geographic location, and thus it is statistically impossible to separate out which factors have been responsible for differences in foraging rate. In an ideal world, we would have many clades that have independently moved from one area to the other, and thus we could investigate whether a statistical association exists between change in geographic location and change in foraging rates. In the real world, however, we are stuck with the distribution of species and clades as they actually occur.

through the habitat, carefully looking for prey by, for example, inspecting the undersides of leaves. Among females, use of the three approaches was correlated with their success rate (Nunez et al., 1997): sit-and-wait (83% of feeding attempts/89% success rate), on-the-run (13%/71%) and active searching (4%/60%). Active searching behavior is also exhibited by the Jamaican twig anole, *A. valencienni*, which seeks out concealed prey items (Hicks and Trivers, 1983; see Fig. 3.9).

My guess is that the foraging behavior of trunk-ground, trunk-crown, and twig anoles conforms to the classic distinction between sit-and-wait versus active foragers: the first group sits on tree trunks and surveys its surroundings, eating what comes along, whereas the latter two move around more frequently[195] and probably search out inactive prey, as well as grabbing whatever passes by (e.g., Schoener, 1979). The other ecomorphs are more mysterious. Although crown-giants do not move at high rates, they do at times cover large distances; they have been seen stalking other anoles (P.E. Hertz, pers. comm.) and take not only fruit, but nestling birds (Dalrymple, 1980), both of which must be sought out. My impression is that crown-giants, though less active overall, are more like twig and trunk-crown anoles in their foraging patterns than they are like the other, less active ecomorphs. In turn, the highly active trunk anoles seem to have a very different strategy than twig and trunk-crown anoles, moving up and down tree trunks, but not through the arboreal matrix. The trunk anoles of the *distichus* Series are probably the most myrmecophagous of all anole species (Schoener, 1968)—an individual actively searches for ants and then "sits passively in front of a trail and gobbles the ants up as they pass by" (Schoener, 1979, p. 484). Unfortunately, the diet and foraging behavior of the Cuban trunk species, *A. loysianus*, is unknown. Finally, it is hard to speculate on the foraging behavior of grass-bush anoles given the disparate results concerning their rate of activity (see footnote 192).[196]

Seasonal shifts in foraging mode have been reported in two species. Male *A. nebulosus* in one of two wet seasons switched from a sit-and-wait to an active foraging mode in which they spent 60% of their time in "slow transit" foraging (Lister and Aguayo, 1992). Similarly, male *A. carolinensis* in the breeding season (May–July) captured prey using a sit-and-wait mode (58% of feeding events) or while they patrolled their territories (eat on the run; 42%); in the non-breeding season (August–September), 22% of feeding events occurred while actively searching for prey as described above and 74% in a sit-and-wait context. The decrease in eating on the run, to 4%, resulted from the substantial decrease in territorial patrolling that occurred in the non-breeding season (Jenssen et al., 1995).

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[195] Although twig anoles are highly variable. Two species, *A. valencienni* and *A. angusticeps*, are among the most active of anoles, but other twig species move considerably less (Johnson et al., 2008).

[196] For completeness, I should point out that little data are available concerning the foraging behavior of West Indian unique, Lesser Antillean and mainland species.

The actual process of anole prey capture has received some study. The most common prey capture behavior is for an anole to rapidly approach a prey item, pause, turn its head toward the prey, and grab it (Moermond, 1981). Some differences in prey attack behavior correspond with morphological differences: the twig anoles *A. insolitus* and *A. angusticeps* use a similar behavior to that just discussed, but their approach is much slower than other anoles, whereas several long-legged species launch themselves toward prey, capturing it as they land (Schoener, 1979; Moermond, 1981).[197] *Anolis carolinensis* uses all of these behaviors; when feeding in the ambush mode, the anoles use the approach-pause-strike method, when feeding on the run they often jump forward to capture prey, whereas while actively searching for prey, they use the slower creeping approach typical of twig anoles (Jenssen et al., 1995; see also Monks [1881]).

One correlate of foraging mode is prey type: across all lizards, sit-and-wait foragers tend to eat active prey, whereas active foragers search out sedentary species (Huey and Pianka, 1981). Whether this trend occurs among anoles is unknown; the dietary information summarized below is insufficient to characterize the attributes of most prey items.

DIET COMPOSITION

Many studies have reported the diet of one or more species from a particular locality at a particular time. Few studies have compared how the diet of a species changes through time or across space, and no comprehensive review of anole diet exists. Most anoles appear to be generalists, eating almost anything they can get their jaws on and swallow, but some exceptions exist (Fig. 8.9).

The diet of Puerto Rican anoles has probably been studied better than the diets of lizards on other islands; these species may be representative of the general situation for anoles, at least in the West Indies. In one of the most thorough studies, Wolcott (1923) examined the stomach contents of large numbers (30–110 for most species) of Puerto Rican anoles; many of his specimens were collected near the campus of the University of Puerto Rico in Río Piedras, but others were collected elsewhere on the island. He found that they ate a wide variety of insects, as well as spiders, millipedes, centipedes, snails, seeds, and other items. Beetles, ants, flies, lepidopterans, hemipterans and homopterans were common prey items for most species, though in varying proportions.

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[197] Examples of this prey-catching behavior were provided for the relatively short-limbed *A. carolinensis* (under the name *A. principalis*) by Lockwood (1876, p. 7): "I have just been watching Nolie eying a fly which was walking on one of the glass panes of his house. He made a noiseless advance of about three or four inches; then followed a spring, when he was seen cleaving to the glass by his feet, and champing the captured fly. I saw him once intently watching the movements of a fly which was walking on the glass. As seemed evident to me by an ominous twitch of that little head, his mind was made up for a spring; but lo, there was a simultaneous make-up of mind on the part of the fly, which at this juncture flew towards the other side of the case. Then came—and how promptly—mental act number two of Anolis, for he sprang as the after-thought directed, and caught the insect on the fly." Dial and Roughgarden (1995) report an anole jumping from a branch one meter above a spider web, catching the spider as it passed by, before landing in the vegetation below.