

10

HABITAT USE

A key factor in understanding anole biological diversity is habitat use. Within localities, coexisting species invariably differ in some aspect of habitat use. Across the landscape, species replace each other as the environment changes. Through time, habitat use evolves within clades in predictable ways. These will be important themes throughout the remainder of the book. In this chapter, I will discuss the various aspects of the environment that are important to anoles, as well as the extent to which habitat use shifts through time.

I have already discussed how sympatric anole species partition the environment by using different structural microhabitats: trunks, twigs, ground, grass and so on. However, there are other aspects of the environment that vary within and among localities and to which anoles specialize. This specialization allows anole species to adapt to extreme habitats, and permits sympatric species to coexist while occupying the same structural microhabitat.

Two important environmental factors are temperature and moisture: anoles can be found across the broad range of habitats that occur throughout their range, from deserts to cool mountaintops and rainforest interiors. The latter half of the twentieth century saw a flowering of the field of physiological ecology and work on reptiles, and particularly anoles, played an important role. I will begin this chapter by discussing the extensive knowledge of anole thermal biology, and then will move on to other aspects of habitat use.



FIGURE 10.1

A male *A. valencienni* having its body temperature taken with a cloacal thermometer. In the heyday of anole thermal ecological studies, researchers measured the temperatures of hundreds of lizards throughout the course of the day. According to a—perhaps apocryphal—story (R.B. Huey, pers. comm.), Stan Rand was once engaged in such research and attracted a crowd of curious onlookers. Finally, one gentleman stepped forward and asked “Excuse me, sir; are the lizards sick?” Photo courtesy of Luke Mahler.

TEMPERATURE THERMOREGULATION

ANOLIS AND THE HISTORY OF THERMAL BIOLOGY

The 1960s and 1970s might well be termed the “noose ‘em and goose ‘em” decades in herpetology. The invention of the rapid-reading cloacal thermometer, combined with a growing appreciation of the importance of thermal biology to ectotherms, led every able-bodied herpetologist to head out to the field, Schultheis® thermometer in hand, to measure the body temperature of unsuspecting reptiles (Fig. 10.1). The result was a golden era in the study of reptile thermal biology and a wealth of data on how reptiles regulate their body temperature. Perhaps no group of reptiles was studied as intensively or was as important for the development of the field as were anoles (reviewed in Huey, 1982).

Following Cowles and Bogert’s (1944) pioneering work, it was widely believed that all lizards bask in the sun to regulate their body temperature precisely. Ruibal’s (1961) study on several Cuban anoles was the first to contradict that idea by showing that some species do not bask or otherwise attempt to regulate their body temperature. Initially Ruibal’s study was treated as an exception, but subsequent work by Rand (1964a; Rand and Humphrey, 1968) and Ruibal and Philibosian (1970) confirmed that a variety of tropical forest lizards, and not just anoles, are thermoconformers. Subsequent work on *A. cristatellus* by Huey (1974) led to the development of a conceptual framework for understanding when thermoregulatory behavior should be favored. In sum, early anole

studies played an important role in the history of thermal biology, as these studies forced a reinterpretation not only of the complexities of the thermoregulatory behavior of lizards, but also of the paradigm of homeostasis as being central to an animal's ecology (Huey, 1982).

COSTS AND BENEFITS OF THERMOREGULATION

Physiologists have long believed that thermoregulation is adaptive because it allows animals to regulate their body temperature within the range in which they function best (Cowles and Bogert, 1944; Huey, 1982). A wealth of data for *Anolis* (summarized in Chapter 13), as well as for other lizards and ectotherms, generally supports this conclusion (Huey, 1982). Why, then, do some lizards not thermoregulate?

The reason is that thermoregulation has costs, such as the energy required to move into and out of the sun and the concomitant increased exposure to predators. Huey and Slatkin (1976) pointed out that, given these costs, thermoregulation is only beneficial in some circumstances. In particular, in situations in which thermoregulation is costly because the distance between different environmental patches (e.g., shaded areas versus sunny areas) is too great, lizards should not attempt to thermoregulate and instead should passively adopt the temperature determined by their surroundings.²⁴⁷ As predicted by this theory, populations that live in deep forest tend not to bask and instead are thermoconformers, whereas those that occur in open or edge habitats tend to bask frequently (Fig. 10.2; reviewed in Huey and Slatkin, 1976).

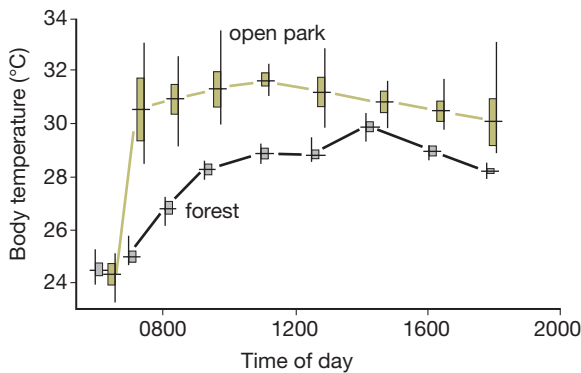


FIGURE 10.2

Anole thermoregulation. Body temperature of *A. cristatellus* in open and forest habitats. Note that in the open area, temperature rises rapidly early and then is maintained at a fairly constant rate throughout the course of the day; this pattern is commonly seen in lizards with ready access to basking sites. By contrast, body temperatures in the forest vary more through the course of the day as air temperatures rise and fall. Figure modified with permission from Huey (1983).

247. A related issue is the difference in temperature between different patches. In thermally extremely heterogeneous environments, the difference may be so great that the benefit of thermoregulating (and thus avoiding much lower body temperatures) may outweigh the costs even when distances between patches are great (cf. Blouin-Demers and Nadeau, 2005).

Although the thermal biology of a large number of anole species has been studied (see below), only recently has a conceptual framework been developed to quantitatively investigate the extent to which individuals within a population are thermoregulating (Hertz et al., 1993; see discussion in Christian and Weavers [1996]; Currin and Alexander [1999]; Hertz et al., [1999]). An important idea is that of the “operative environmental temperature” (T_e), which is the temperature to which a non-thermoregulating animal would equilibrate in a particular environment (see Appendix 10.1 regarding methods in thermal biology). By comparing the temperatures of real lizards in an environment to the distribution of T_e values that a non-thermoregulating lizard would attain in that environment, the extent of thermoregulation can be quantified.

Hertz’s (1992b) study of *A. cristatellus* and *A. gundlachi* in Puerto Rico illustrates this approach. In many habitats, *A. cristatellus* spent more time in direct sunlight than lizard models randomly placed in the environment, and as a result had higher body temperatures than the mean T_e measured for the models. Moreover, *A. cristatellus* basked more often in January than in August and at higher compared to lower elevations, with the result that mean body temperature varied little between seasons and elevations. By contrast, *A. gundlachi* did not bask more frequently than expected at random, and its body temperature did not differ significantly from the T_e of randomly placed models in any season or at any elevation. *Anolis cristatellus* is a thermoregulator and *A. gundlachi* is a thermoconformer.

As yet, few comparable studies have been performed on anoles (see also Hertz [1992a]). One exception is a study of the leaf-litter dwelling South American species *A. nitens* (Vitt et al., 2001). These lizards avoid basking and maintain a body temperature that does not differ from air or substrate temperature at the particular sites they occupy. However, by choosing relatively warm sites, they are able to maintain body temperatures approximately 1–3° C higher than the T_e that lizards randomly placed at the study site would attain (Fig. 10.3).²⁴⁸ Anoles in the Lesser Antilles also use perches with warmer T_e values than random and the extent of this non-random habitat selection varies by species and elevation (Buckley and Roughgarden, 2005b).

A related question concerns the effectiveness of thermoregulatory behavior. Laboratory studies—in which lizards are placed in a thermally heterogeneous chamber or trackway with homogeneous illumination—confirm that, given a choice, anoles (and many other types of ectotherms) regulate their temperature within a particular range (reviewed in Huey, 1982; Hertz et al., 1993). But are they able to do so in nature?

The effectiveness of microhabitat selection for regulating body temperature can be seen in the thermoregulating species *A. cooki* and *A. cristatellus*: body temperatures attained in the field by these species are closer to the preferred temperature range selected in the lab than would be expected if they selected sites randomly (Hertz et al.,

248. Similarly, at montane sites in Hispaniola, *A. shrevei* often rested under logs and planks in warm, decomposing sawdust and attained body temperatures higher than air temperature (P.E. Hertz, pers. comm.; see Hertz and Huey [1981]).

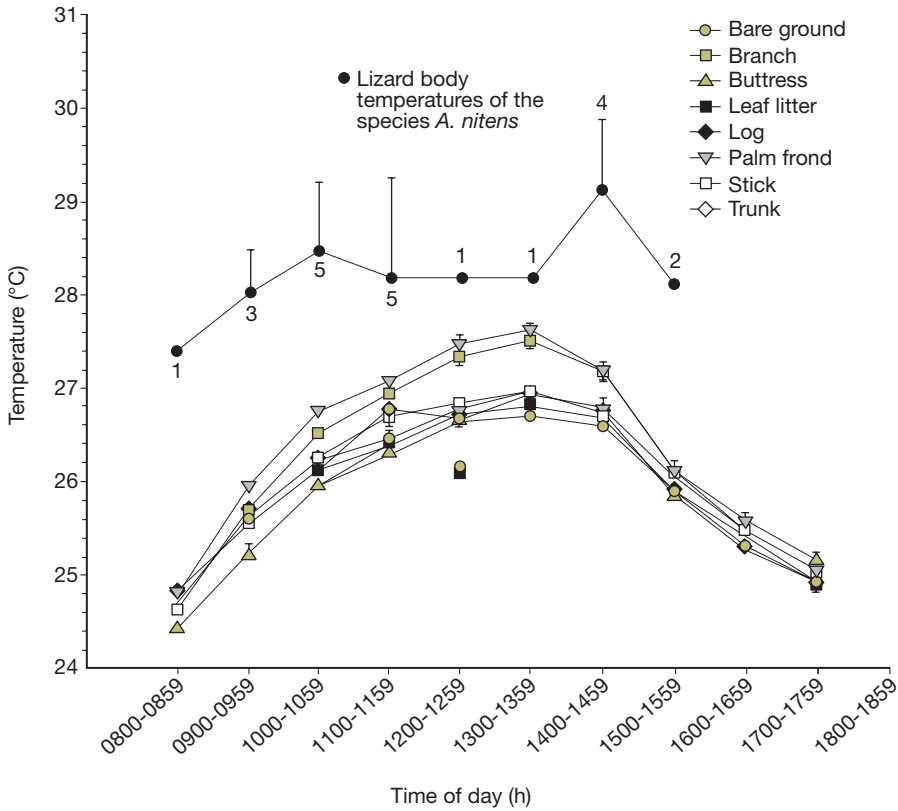


FIGURE 10.3

Body temperature of *A. nitens* through the course of the day, relative to body temperatures that would be attained by lizards randomly selecting perch sites on a variety of substrates. Figure modified with permission from Vitt et al. (2001).

1993). Of course, habitat selection is not always required to attain body temperatures within the preferred range. Lowland populations of *A. gundlachi* occur in forests where the ambient temperature is often within their preferred range, and thus body temperatures fall within this range even though the lizards use the habitat randomly with respect to T_e . However, this thermoconforming behavior causes populations of *A. gundlachi* in high elevation forests to experience body temperatures substantially below those they select in the lab (Hertz et al., 1993).

INTERSPECIFIC AND INTERPOPULATIONAL VARIATION

Given that anoles occur in many habitats, elevations, and latitudes and that they differ in extent of basking, we might expect anole species and populations to vary in the body temperatures they attain. On the other hand, most clades of lizards show relatively little variation in body temperatures (Huey, 1982; Hertz et al., 1983; but see Castilla et al. [1999] for

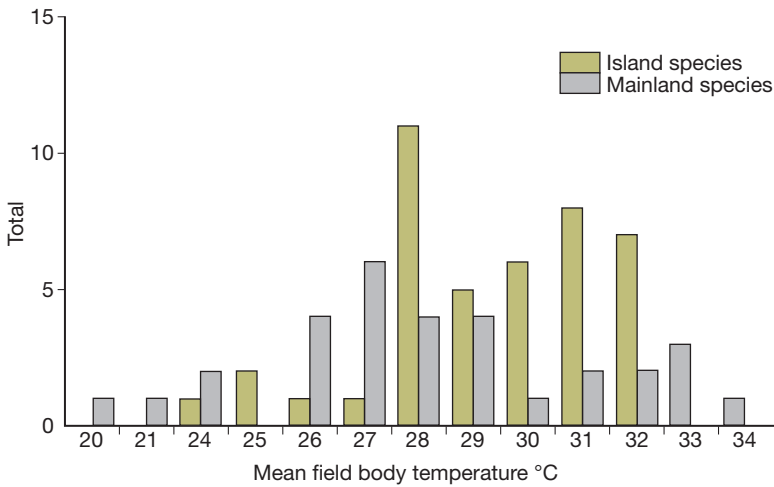


FIGURE 10.4

Mean field body temperature of anoles. Island anoles have higher temperatures than mainland species ($F_{1,71} = 12.75$, $p = 0.001$). As in Chapters 8 and 9, mainland versus island analyses do not incorporate phylogenetic information, although in this case, *A. agassizi* from Malpelo Island represents an additional island colonization event. Data from Hertz et al. (in prep.).

one exception); *Sceloporus* is a particularly good comparison to *Anolis*, being a species-rich clade that occurs in many habitats and elevations in North and Central America, yet demonstrates little variation in field body temperatures (Bogert, 1949; Andrews, 1998).

In contrast to *Sceloporus*, anole species exhibit considerable variation in field body temperature, with species' mean values ranging from 20.5–34.2°C (Fig. 10.4). To a large extent, this variation reflects differences in both macro- and microhabitats: species living at high elevations tend to have lower body temperatures than species in the lowlands, and species which live in deep shade have lower temperatures than species out in the open (Clark and Kroll, 1974). The predominance of higher temperatures in island species reflects the fact that most island species occur in open, lowland habitats (Fig. 10.4).

Field body temperature does not vary by ecomorph type (Fig. 10.5), which makes sense given that all ecomorph classes are represented in just about all habitats (e.g., open versus deep forest) and elevations. By the same token, because closely related species often occur in different habitats and elevations, field body temperature is an evolutionarily labile trait with no detectable phylogenetic signal (Hertz et al., in prep.).

These phenomena are clearly exhibited by the trunk-ground anoles of Cuba. At Soroa in western Cuba, four species of the *sagrei* Series co-occur (Fig. 2.8). *Anolis sagrei* is found out in the open in the sun, with an average field temperature of 30.6°C; at the other extreme, *A. allogus* in the deep shade of the forest interior—some times a mere

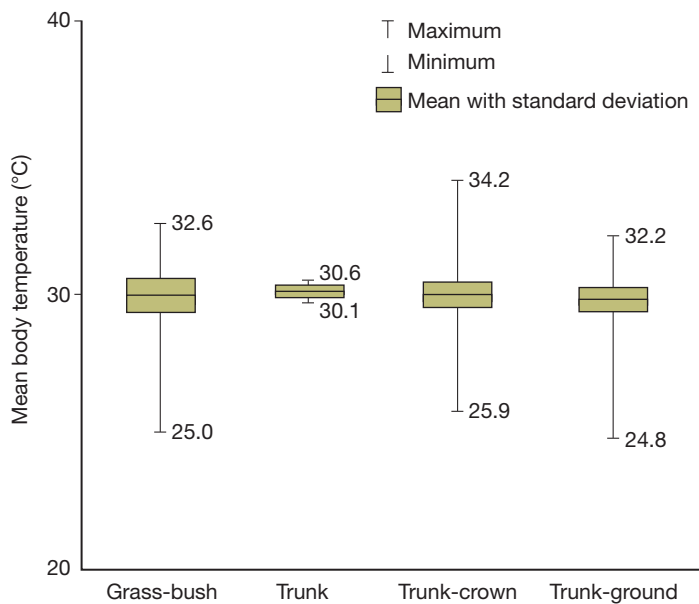


FIGURE 10.5

Body temperatures of ecomorphs. Ecomorphs vary little in mean body temperatures of constituent species; the range of variation is also comparable for most ecomorphs. Data from Hertz et al. (in prep.).

stone's throw away—maintains a temperature of 27.0°C (data from Losos et al. [2003b]; see also Ruibal [1961]).²⁴⁹

Intraspecific studies also demonstrate the lability of anole thermal biology. All anole species show a decrease in mean body temperature among populations with increasing altitude (reviewed in Huey and Webster, 1976; Hertz, 1981, 1992a). Most species bask more at higher elevations, thus behaviorally minimizing the decrease in body temperature that would otherwise result from decreasing air temperatures; however, the thermoconforming deep forest *A. gundlachi* bucks this trend and does not increase its basking rate at higher elevations (Huey and Webster, 1976; Hertz, 1981; Hertz and Huey, 1981; Sifers et al., 2001). Anoles also generally alter their activity times elevationally, being inactive at midday in xeric, lowland areas and restricting activity to midday at high elevations (Hertz and Huey, 1981).

On an evolutionary time scale, interspecific comparisons show a strong match between the temperature a species selects in the lab and the temperature that the species attains in the field: for the nine West Indian species for which data are available,

249. Unfortunately, after a proliferation of thermal studies in the 1970s and early 1980s, relatively little research has been conducted on anole thermal ecology, particularly in the West Indies.

preferred temperatures, which range from 25.1–34.0°C, correlated strongly with field body temperatures (Hertz et al., in prep.). This correlation may suggest that species are generally quite good at attaining the body temperatures which they prefer; alternatively, however, the data might suggest that preferred temperatures evolve to adapt to the thermal environment in which a species occurs, a topic which will be revisited in Chapter 13.

MOISTURE

As with the thermal environment, anoles occupy a wide variety of hydric environments from xeric deserts to mesic rainforests. Elevationally, water stress should be greatest at lower elevations where conditions of high temperature and low rainfall often prevail (Hertz, 1980b). The organismal consequences of living in habitats differing in aridity are straightforward; particularly for small organisms, the risk of dehydration increases with decreasing moisture content of the air. Thus, one would expect that in the lab, species that live in xeric habitats should have lower rates of water loss than species from more mesic areas. For the most part, this prediction is confirmed, as will be discussed in Chapter 13.

No precise analogue to T_e exists to measure variation in hydric environment among sites within a habitat. Whether the hydric environment is more homogeneous than the thermal environment is unclear; nonetheless, variation in moisture probably exists in most habitats, and anoles may alter their microhabitat use to hydroregulate (Hertz, 1992b). For example, the small Central American species *A. limifrons*, which loses water at high rates (Sexton and Heatwole, 1968), basked less and maintained a lower body temperature in the dry season, presumably staying in cooler, moister sites to limit water loss (Ballinger et al., 1970).²⁵⁰ Similarly, *A. gundlachi* does not use open habitats at high elevations, even though the thermal environment is suitable; Hertz (1992b) attributes this species' confinement to closed habitats at high elevations to the risk of dehydration, to which it is vulnerable (Hertz et al., 1979).

As with thermal biology, the hydric ecology of anoles shows no phylogenetic or ecomorphic signal: closely related species can occur in very different environments. For example, the trunk-ground anole clades on Cuba, Puerto Rico, and Hispaniola all include representatives living in desert environments and others occurring at high elevations, and the clades on Cuba and Puerto Rico also contain deep forest shade species.

LIGHT

Recently, Leal and Fleishman (2002) have suggested that microhabitats in close proximity may differ in their light intensity and spectral qualities, providing the opportunity for species to partition these microhabitats. In particular, they showed that the two sympatric trunk-ground species in southwestern Puerto Rico, *A. cristatellus* and *A. cooki*, use perches

250. An alternative possibility is that insect abundance is reduced during the dry season and that lizards consequently reduced their body temperature to minimize metabolic energy expenditures (Huey, 1982; Christian and Bedford, 1995).

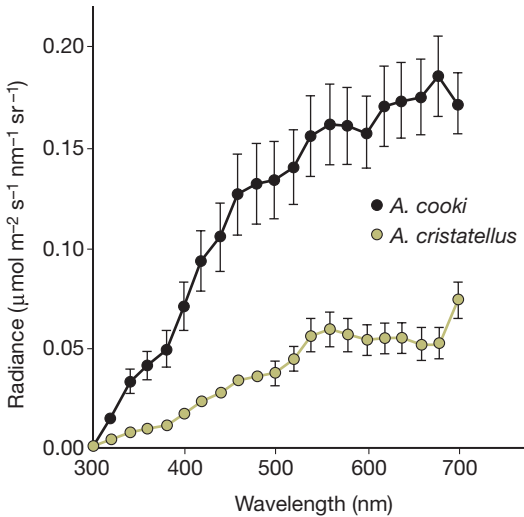


FIGURE 10.6 Differences in light environment for *A. cooki* and *A. cristatellus*. In locations occupied by *A. cristatellus*, the light spectrum peaks at 550 nm, which is green, whereas *A. cooki* sites have a more broad-based light spectrum with much higher levels in the low spectra, where ultraviolet occurs. Modified with permission from Leal and Fleishman (2002).

differing in light environment. *Anolis cooki* uses perches that are more open, with less vegetation, whereas *A. cristatellus* is found in more vegetated areas. In the vegetated areas used by *A. cristatellus*, plants tend to absorb short and long wavelengths, producing a light environment which peaks in the green region of the spectrum. By contrast, the areas used by *A. cooki* are more open to blue sky and thus not only have greater light intensity, but also a broader light spectrum, including ample light in the UV region (Fig. 10.6).

Of course, light and thermal environments will be correlated in many cases, so disentangling their effects on anole habitat use will be difficult. For example, in sympatry, *A. cristatellus* and *A. cooki* exhibit different body temperatures (Huey and Webster, 1976; Hertz, 1992a), and at a more mesic study site, light intensity and T_e were strongly correlated among perch sites of *A. cristatellus* (Hertz et al., 1994). On the other hand, light intensity and thermal environment are not always related. In a closed forest site near to the *A. cristatellus* mesic site, no relationship existed between light intensity and T_e for perch sites used by *A. gundlachi* (Hertz et al., 1994).

The role of the light environment in driving evolutionary divergence in signaling behavior and structures is potentially very important and will be discussed in Chapter 14. The possibility that species can diverge to adapt to different light environments as a means of partitioning the habitat is an exciting new possibility, the generality of which remains to be investigated.

REMOTE SENSING APPROACHES TO INVESTIGATION OF SPECIES' HABITAT REQUIREMENTS

The integration of satellite data and distributional records to understand the habitat factors shaping a species' distribution has taken off in recent years (e.g., Guisan and Zimmerman, 2000; Peterson, 2001). To a large extent, these Geographic Information Systems (GIS) approaches are useful in elucidating the role of temperature and

moisture (e.g., maximum, minimum, seasonality) in determining where species occur. However, these approaches are too coarse-grained to shed light on the factors that affect microhabitat partitioning within local communities.

Although rich in potential for understanding ecological and evolutionary aspects of anole distribution, GIS approaches are just beginning to be applied to anole data. Knouft et al. (2006) studied the *A. sagrei* group on Cuba and found that ambient temperature, precipitation, and seasonality all were important determinants of species' distributions. As for thermal and hydric biology (discussed above), no phylogenetic effect is apparent in the environmental niches of different species: some closely related species have similar environmental niches and some have highly divergent niches; distantly related species also can be very similar or very divergent.

ONTOGENETIC AND SEASONAL SHIFTS IN HABITAT USE

Anoles change their habitat use both as they grow and across seasons. Ontogenetic habitat shifts have been reported in many species; anoles generally shift to higher and wider perches as they get older (reviewed in Stamps, 1983b). These size-related shifts probably have a variety of causes (Huey and Webster, 1975; Scott et al., 1976; Moemond, 1979a; Stamps, 1983b; Jenssen et al., 1998; Ramírez-Bautista and Benabib, 2001). Larger lizards have greater locomotor capabilities—including the ability to jump across larger gaps and to capture prey and escape to a refuge from a greater distance (Chapter 13)—and require broader surfaces to support their mass; in addition, larger lizards need to use wider surfaces to minimize their visibility to predators approaching from the opposite side of the object upon which they are perching.²⁵¹ In addition, larger lizards are dominant over smaller ones (Chapter 9) and thus able to secure the most desirable microhabitats.

Ontogenetic habitat shifts have been particularly well documented in *A. aeneus* (Stamps, 1983b). In this species, juveniles move into open clearings, then return to shady areas when they reach subadult size. Presumably, the juvenile shift is to avoid predation by the larger *A. richardii*, which is not found in open clearings and which poses a threat particularly to smaller *A. aeneus* (Stamps, 1983b).

Seasonal changes in habitat use have received relatively little attention. Not surprisingly, many species bask more in the winter to compensate for lower air temperature (e.g., Hertz, 1992a,b) and as mentioned above, *A. limifrons* basked less in the dry season, perhaps to minimize water loss (Sexton and Heatwole, 1968).

251. Lizards have a blind spot behind and underneath their heads, and the size of this blind spot is a function of head size. As a result, a predator approaching from the other side of a tree may not be visible to a lizard. Consequently, lizards should choose surfaces broad enough that they can't be seen by a potential predator located in their blind spot on the other side of the surface. Larger species, being wider, require broader surfaces.

Upward shifts in perch height in the non-breeding season occurred in three Puerto Rican rainforest anoles and *A. carolinensis*.²⁵² Two mainland species, *A. nebulosus* and *A. cupreus*, also exhibited shifts in perch height, but in the opposite direction, from near the ground in the non-breeding dry season to much higher in the vegetation in the wet season. In both species, the upward shift was substantially greater for males, which at the same time greatly increased their territorial behavior, than for females (Fleming and Hooker, 1975; Lister and Aguayo, 1992).²⁵³

Seasonal shifts in perch height also lead to shifts in foraging location. *Anolis nebulosus* changed from foraging almost entirely on the ground in the dry season to foraging mostly in arboreal situations in the wet season. Comparable shifts in foraging location occurred in male, but not female, *A. cupreus* (Fleming and Hooker, 1975) and in *A. stratulus* (sexes not differentiated [Reagan, 1986]).

Puerto Rican rainforest anoles also shifted their perch diameter use across seasons, but the direction of changes differed among species, and even among sexes (Lister, 1981; Jenssen et al., 1995; Dial and Roughgarden, 2004).

Habitat shifts as a result of the presence of other species have been commonly reported and are discussed in Chapter 11.

HABITAT SELECTION

The segregation of species into different microhabitats suggests that species can select the appropriate microhabitat, but little work has investigated how this selection occurs (Sexton and Heatwole, 1968; Kiester et al., 1975; Talbot, 1977). Several studies suggest that anoles may use conspecifics as cues when settling into new habitats (Kiester, 1979; Stamps, 1987, 1988).

That anoles use temperature in habitat selection is suggested by the data on thermoregulation discussed above. The physiological mechanisms underlying temperature detection and response in ectotherms are an area of active research and have not received much attention in anoles (reviewed in Seebacher and Franklin, 2005). *Anolis cristatellus* may use light intensity as a cue for habitat selection. In the open habitats that it uses, warmer sites are more brightly illuminated, and in a laboratory experiment, lizards of this species use light as a cue when attempting to thermoregulate (Hertz et al., 1994).

252. Thermoregulating lizards also shift perch height over the course of the day to avoid hotter temperatures near the ground at midday (e.g., Huey, 1974), as well as to avoid predators that are most active at midday (Chapter 11).

253. In a study on *A. nebulosus* that commenced just as Lister and Aguayo's (1992) study at the same site was ending, Ramírez-Bautista and Benabib (2001) found somewhat different patterns of seasonal change in perch height.

NIGHT-TIME HABITAT USE

Anoles are almost entirely diurnal. The only exception is that many species have been reported active after dark on walls near electric lights, feeding on the insects attracted to the light (e.g., Rand, 1967b; reviewed in Perry et al., 2008).

Many anoles sleep on leaves or on the ends of branches (Fig. 10.7).²⁵⁴ The presumed function of this behavior is that any potential predator approaching the lizard will cause the branch or leaf to vibrate, alerting the lizard in time to escape by jumping into the void. This behavior may work well against such predators (as far as I am aware, no one has ever studied the efficacy of this behavior), but at least some arboreal snakes have thwarted this defense by adopting an airborne approach, stretching across from another branch to pluck the unsuspecting lizard while it still slumbers (Fig. 10.8; Henderson and Nickerson, 1976; Yorks et al., 2004). The presence of anole remains in owl pellets suggests the existence of another threat to sleeping anoles, although another possibility is that crepuscular owls nabbed still-active anoles just as they were preparing for bed (Hecht, 1951; Etheridge, 1965; Buden, 1974; McFarlane and Garrett, 1989; Gerhardt, 1994; Debrot et al., 2001).²⁵⁵

For many years, just about every field biologist I knew who worked on anole ecology or behavior contemplated the idea of studying whether sympatric anoles partition their sleeping sites as they do their diurnal haunts. Many workers, myself included, set out to collect the relevant data, only to discover that this was a full time project in itself. Finally, such a study has been conducted. For three Jamaican species, sleeping perches are generally higher, narrower and more horizontal than diurnal perches (Singhal et al.,



FIGURE 10.7

Typical anole sleeping postures. (a) *A. lineatopus* from Jamaica on a leaf; (b) *A. transversalis* from Brazil on a narrow branch.

Photo courtesy of Marcio Martins.

254. But not all. Jenssen (1970b) described a population of *A. nebulosus* that slept in the leaf litter.

255. Sleeping on leaves and at the end of branches also makes sleeping anoles vulnerable to nocturnal biologists and other rapsallions: many anoles blanch in color at night and stand out quite vividly against the background in the beam of a flashlight.



FIGURE 10.8
A Brazilian blunt-headed vinesnake (*Imantodes cenchoa*) eating an anole captured while sleeping. Photo courtesy of Marcio Martins.

2007).²⁵⁶ Females increased height at night substantially more than males and day and nighttime habitat use was significantly different for each sex within all three species (except for *A. grahami* males). Despite these shifts in habitat use, interspecific differences in habitat use occurred at night, just as they did during the day (Fig. 10.9).

The implication of these findings is that community and functional biologists should consider the potential importance of sleeping sites. Could species be partitioning sleeping sites as a resource? Perhaps more importantly, could the morphological differences among species represent adaptations for using different microhabitats at night, as well as during the day? The narrowness of nighttime perches is particularly notable and might make strong biomechanical demands on lizards snoozing on such perches (see discussion of competition and adaptation in Chapters 11 and 13). Another question concerns whether perch sites are chosen for their thermal properties, either at night or early in the morning, when lizards may need to raise their body temperature quickly. Finally, could nocturnal predation exclude anoles from some microhabitats, thus affecting their diurnal microhabitat use (Chandler and Tolson, 1990)?

Anolis lineatopus individuals use sleeping sites that are within their diurnal home ranges (Singhal et al., 2007).²⁵⁷ Some anoles appear to use the same perch repeatedly,

256. Some or all of these patterns have been reported for many other species (e.g., Ruibal and Philibosian, 1974b; Vitt et al., 2002; Vitt et al., 2003b; Poche et al., 2003).

257. Comparable data are not available for the two other species in this study.

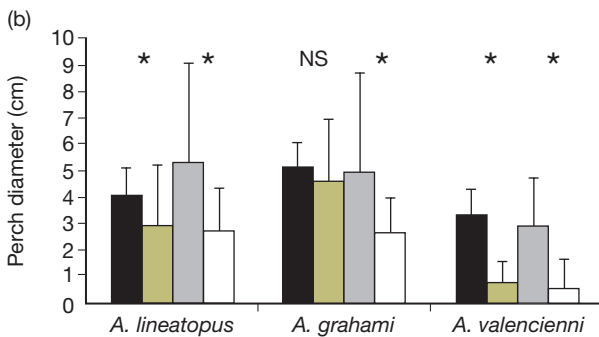
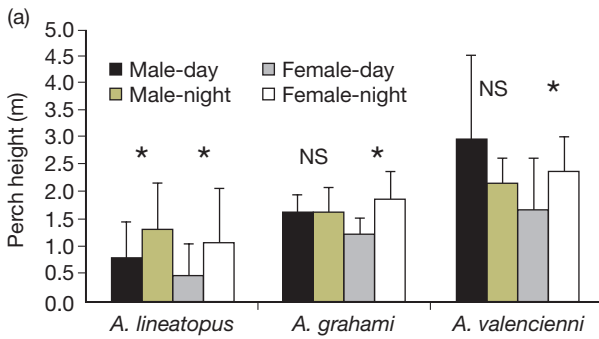


FIGURE 10.9 Shifts in (a) perch height and (b) perch diameter between day and night for three Jamaican species. Values are means + 1 standard error. Asterisks indicate significant differences between daytime and nighttime habitat use. Modified with permission from Singhal et al. (2007).

but others do not (Rand, 1967b; Kattan, 1984; Clark and Gillingham, 1990; Shew et al., 2002; Poche et al., 2005; Singhal et al., 2007).

FUTURE DIRECTIONS

As with the data on population biology reported in Chapter 8, it is remarkable how little we know about habitat use of most species. Even for thermal biology, which has been extensively studied, few clades or communities have been well sampled. Moreover, most of the work on anole thermoregulation was conducted prior to the development of modern methods for assessing the extent to which anoles nonrandomly regulate their body temperature. Thus, despite a great number of studies on many species, we cannot quantitatively assess the extent of thermoregulation in most species. Now that the tools are in hand, a re-blossoming of anole thermal biology—mostly dormant since the early 1980s other than work on several Puerto Rican species—would be welcome.

The situation for other aspects of habitat use is much worse. The hydric and light ecology of only a few species have been studied. Now that remote sensing methods are available, such data will be critical to cross-validate the conclusions concerning the environmental factors that determine anole distributions (e.g., Kearney and Porter, 2004).

APPENDIX 10.1

APPROACHES TO THE STUDY OF THERMAL BIOLOGY

The history of the study of thermoregulation in ectotherms is a long one, and studies on lizards—especially on anoles—have played an important role (reviewed in Avery, 1982; Huey, 1982; Angilleta et al., 2006). A variety of early ideas concerning how to study the extent of thermoregulation have proven too simplistic: for example, neither the slope of the regression line between air temperature and body temperature nor the variance in body temperature among individuals in a population are good indicators of the extent of thermoregulation (Huey, 1982; Hertz et al., 1993).

The body temperature of a small ectotherm is a function of air temperature, wind speed, whether the animal is in the sun, the temperature of the surface on which it is sitting and a variety of other factors. Sophisticated biophysical models have been developed to calculate what the equilibrium temperature of a lizard occupying a particular spot with particular parameter values should be (Porter et al., 1973; Roughgarden et al., 1981; Waldschmidt and Tracy, 1983). However, a much easier approach is simply to build a model lizard, of appropriate size and with appropriate reflectance, conductance and other thermal properties, and place it in the environment (Fig. 10.10; Bakken and Gates, 1975; Bakken, 1992; Grant and Dunham, 1988; Hertz, 1992b; Dzialowski, 2005; see comparison of approaches in Huey [1991]). The temperature to which the model equilibrates is an estimate of the temperature a live lizard would attain if sitting in the same spot and not using any behavioral or physiological means to alter its body temperature (See Hertz [1992b] for review).

This approach can be taken one step further. By randomly placing many such models in the environment and monitoring them, one can estimate both the mean and the variance in body temperature that a population of lizards would attain if they were using the environment randomly and thus not behaviorally thermoregulating. By comparing real lizard temperature data to those generated by models, we can determine the extent to which lizards are actively thermoregulating (Figure 10.3).



FIGURE 10.10

Photo of lizard models. Instead of models cast from a real lizard, other researchers have used cylindrical tubes plugged at either end or small temperature sensors (e.g., Van Berkum et al., 1986; Vitt et al., 2001). Photo courtesy of Kevin de Queiroz.

Moreover, from such data we can also estimate the extent to which lizards might need to thermoregulate in a particular environment. Laboratory choice experiments (usually conducted by placing a lizard in a thermally heterogeneous gradient and seeing what temperature it selects) can determine the preferred temperature range of a species. Comparisons with the temperature that models attain in the field can indicate how far non-thermoregulating lizards would be from their preferred temperature (that is, how much thermoregulation is needed). The precision of thermoregulation can then be defined as the extent to which real lizards are closer to their preferred temperature than they would be if they were randomly sampling the environment (Hertz et al., 1993; Blouin-Demers and Nadeau, 2005).