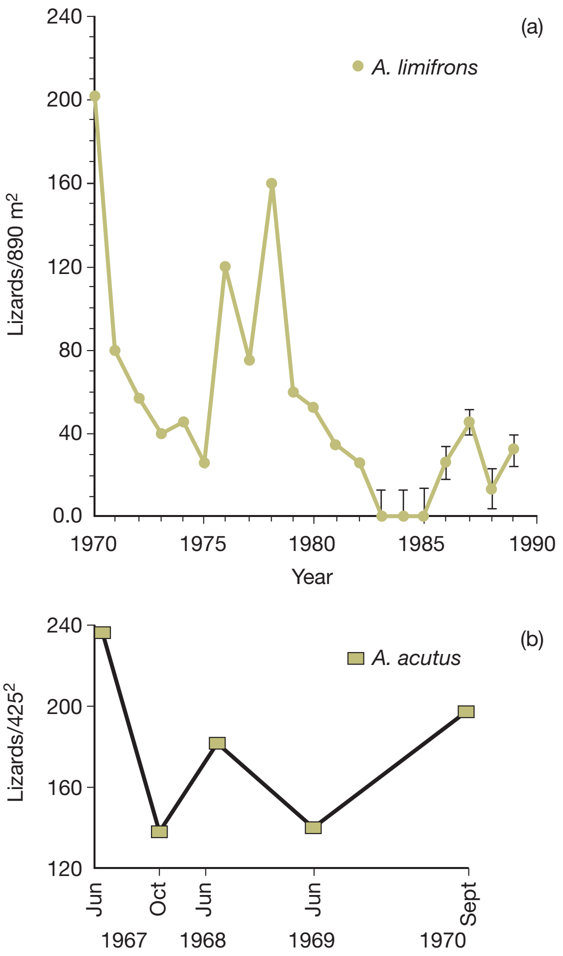

FIGURE 8.7 Population density of *A limifrons* on Barro Colorado Island, Panama over a 19-year period and *A. acutus* from St. Croix over a three-year period. Figure modified with permission from Andrews (1991); data for *A. acutus* from Ruibal and Philibosian (1974).

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).

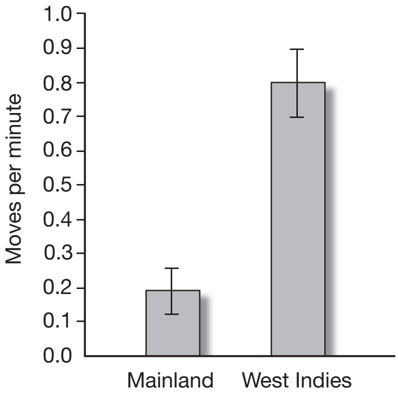

FIGURE 8.8
Differences in movement rate between mainland and West Indian anoles. Differences are statistically significant (Analysis of variance, $F_{1,44} = 41.90$, $p < 0.001$). Data from Perry (1999), Irschick et al. (2000), Cooper (2005a), and Johnson et al. (2008). When multiple values were available 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.