A variety of other aspects of anole biology could, in theory, affect rates of species diversification. Other factors such as environmental stability and seasonality or trophic position might plausibly have an effect. As discussed in Chapter 14, degree of sexual selection has been suggested recently as one factor that may affect rate of species diversification. If ecomorphs differ in extent of sexual selection (which remains to be determined [Chapter 9]), then this hypothesis would be worth investigating.

SEXUAL DIMORPHISM AND ADAPTIVE RADIATION

Despite the tremendous amount of research over the past several decades on both sexual dimorphism and adaptive radiation, little attention has been paid to the relationship between these two topics. Most research on sexual dimorphism has focused on its causes and consequences within single species and has considered neither the role that sexual dimorphism may play in adaptive radiation, nor how dimorphism might evolve during the course of a radiation.

THE EVOLUTION OF SEXUAL DIMORPHISM DURING AN ADAPTIVE RADIATION

Imagine the first anole species occupying a Greater Antillean island. Presumably, resources would be abundant and many different ways of making a living—corresponding to the different ecomorph types—would be available. What's a species to do? One possibility is that disruptive selection could drive adaptive radiation as all of the ecomorph types evolve *in situ*. I've already argued in Chapter 14 that sympatric speciation doesn't seem to occur in anoles, so—for whatever reason—this option appears to be out.

Another possibility is niche expansion. As discussed in Chapter 11, anole populations in species-poor localities tend to have broad resource use. An evolutionary response to such wide niche breadth is the evolution of increased intra-population phenotypic variation in which individuals are adapted to use different parts of the resource spectrum. At the extreme, these differences could take the form of discrete morphs, as in the African fire-cracker finch (*Pyrenestes ostrinus*), in which large- and small-billed morphs are adapted to eat seeds of different sizes (Smith, 1993). However, as discussed earlier in this chapter, quantitative analysis indicates that broad resource use is not generally accompanied by increased phenotypic variation within a population, but rather by phenotypically similar individuals with broader resource use (Lister, 1976b); moreover, few examples of ecologically relevant, non-sex-linked polymorphisms exist in anoles.

An alternative response is for populations to evolve sexual dimorphisms in which the sexes use different parts of the ecological spectrum (Schoener, 1986b). Such sexual dimorphism in both size and shape is rampant in anoles and varies by ecomorph (Chapter 9). Consequently, we might predict that the hypothetical initial Greater Antillean anole population would be comprised of individuals with broad resource use and that substantial ecological differentiation would occur between the sexes leading to the evolution of sexual dimorphism in morphology.

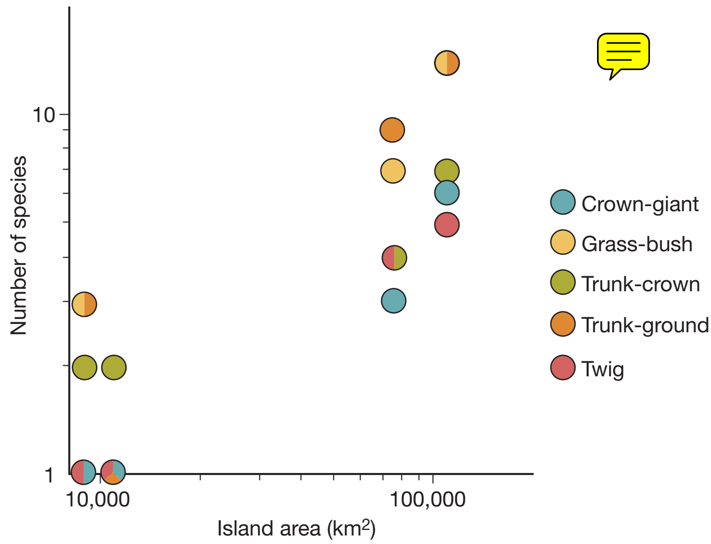

FIGURE 15.10
Sexual size dimorphism as a function of number of coexisting species on an island. Each point represents the median value of sexual size dimorphism for all of the species on one island. Values on the x-axis represent number of described species per island in the mid-1970s. Many species have been discovered since then, particularly on the larger islands. Modified with permission from Schoener (1977).

Eventually, however, more anole species evolve, probably in allopatry, and then become sympatric. As a result, ecological contraction—the opposite of ecological release—should occur, leading to diminished sexual dimorphism. Moreover, as more and more species join the community, this decrease should continue and the extent of sexual dimorphism should get steadily smaller.

This prediction has been tested most thoroughly with regard to size dimorphism. In comparisons both among species and among populations within species, the degree of sexual size dimorphism is negatively correlated with the number of sympatric species (Fig. 15.10; Schoener, 1977). This inverse correlation has several components:

1. Species in depauperate communities on landbridge islands have high levels of dimorphism due to ecological sorting. As landbridge islands decrease in size, ecomorphs drop out in a predictable sequence, and the ecomorphs that tend to persist, trunk-ground and trunk-crown anoles, tend to have high dimorphism (Chapter 4). One possibility is that these ecomorphs are successful in persisting on depauperate islands because of their high dimorphism; however, an alternative is that these ecomorphs are the best adapted to conditions on small islands, unrelated to their great degree of sexual dimorphism.
2. Size dimorphism increases after colonization of solitary islands. Colonizers of empty islands tend to have relatively high levels of size dimorphism, but subsequently evolve even higher levels (Poe et al., 2007). For example, in the Greater Antilles, solitary anole species all have as their sister taxa either

trunk-crown or trunk-ground anoles; comparison to estimates of ancestral size dimorphism indicates increased size dimorphism in these solitary species.[409]

3. Size dimorphism decreases during adaptive radiation with increased species number. Jamaica, the island with the fewest anole species, has the highest median size dimorphism, whereas the two most species-rich islands, Cuba and Hispaniola, have the lowest dimorphism. This trend has several causes. First, among the ecomorphs common to all four islands, size dimorphism within each ecomorph is inversely related to species number on an island (analysis of covariance, heterogeneity of slopes non-significant, island species number effect, $F_{1,11} = 3.97$, $p = 0.036$, one-tailed). Second, the ecomorphs found only on the larger, and more species-rich, islands—grass-bush and trunk—have relatively low dimorphism. Third, most Greater Antillean unique anoles, which occur only on the two largest islands (with one exception), also tend to have intermediate-to-low dimorphism.[410]

The relationship between sexual shape dimorphism and number of species has only been examined in one comparison: the species in the Jamaican radiation have a higher mean shape dimorphism than the anoles of Puerto Rico (Butler et al., 2007). Whether, as would be predicted, Lesser Antillean anoles have even greater dimorphism, and Hispaniolan and Cuban anoles even less dimorphism, remains to be tested.

These trends support the hypothesis that sexual dimorphism evolves adaptively in response to the presence or absence of other species, presumably as a result of resource competition. Moreover, they indicate that the degree of dimorphism decreases during adaptive radiation, both because species within microhabitats evolve decreased dimorphism and because the microhabitats occupied only in species-rich radiations tend to be filled by species with low dimorphism.

THE RELATIVE IMPORTANCE OF SEXUAL DIMORPHISM VERSUS INTERSPECIFIC DIFFERENTIATION IN ADAPTIVE RADIATION

A second question about sexual dimorphism concerns how substantial a role it plays in adaptive radiation. Most research has implicitly assumed that sexual dimorphism is a minor contributor to the ecomorphological diversity within an adaptively radiating clade. In theory, however, there is no reason that much of the niche differentiation that occurs within a clade could not be manifested as differences between the sexes within species (Fig. 15.11). No study to date has examined the role that sexual dimorphism plays in adaptive radiation.

409. This analysis was limited to species endemic to solitary islands and did not consider populations of species also found on islands with other species.

410. Data from Schwartz and Henderson (1991) and Butler et al. (2000). The Cuban aquatic anole, *A. vermiculatus* and its sister taxon, the rock-wall anole, *A. bartschi,* are conspicuous exceptions to the generalization that unique anoles have low dimorphism.

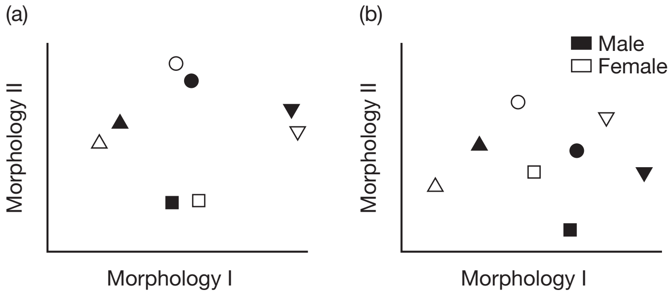

FIGURE 15.11
The role of sexual dimorphism in adaptive radiation. Sexual dimorphism could be a minor (a) or a major (b) component of morphological differentiation. Symbols represent different species, shaded symbols are males and open symbols are females.

Butler et al. (2007) examined the positions of both sexes of Puerto Rican and Jamaican anoles in multivariate morphological and ecological space. They found that the lion's share of the variation was accounted for by consistent differences among the ecomorph classes. Nonetheless, a substantial additional portion of the variation was explained by sexual differences within species, as well as a small amount due to variation that occurred between sexes in some ecomorphs and not others.[411] Moreover, because of sexual dimorphism, morphological and ecological space were much more fully occupied than if no sexual differences had existed—the morphospace volume occupied by both sexes on these two islands is 59% greater than that occupied just by females and 88% greater than that occupied by males. Similarly, both sexes occupy 33% more multivariate ecological space than females alone and 47% more than males.

These data indicate that sexual size and shape dimorphism play an important role in anole adaptive radiation. In islands with few species, much of the ecomorphological variation among anoles is partitioned between the sexes. As radiation proceeds, dimorphism decreases as species' niches become compressed by the presence of competitors, but it still accounts for an important part of the ecological and morphological variation.

Clearly, work is needed on patterns of shape dimorphism on islands both larger and smaller than the two studied to date. In addition, experimental studies on the evolutionary dynamics of sexual dimorphism could prove quite interesting. One would predict, for example, that the addition of a second species to a site previously occupied by only one species would lead to selection for the sexes to become more similar in the original species. Alternatively, patterns of selection might differ among the sexes, with the sex more similar to the introduced species being affected more greatly.[412] Anoles could prove to be a model system for the study of the evolution of sexual dimorphism, as well as of its role in adaptive radiation.

411. The ecomorph-by-dimorphism interaction term.
412. Alternatively, the same questions could be investigated by looking at the effect of introduced species on the sexual dimorphism of native species.