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A COMPARATIVE STUDY OF POPULATION DENSITY AND SEXUAL SIZE DIMORPHISM IN LIZARDS

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Abstract.—Two hypotheses predict a positive relationship between population density and sexual size dimorphism (SSD) among species of *Anolis* lizards; these hypotheses focus on food competition and male-male competition for breeding territories, respectively. We first tested an underlying assumption of the food competition hypothesis, using data on the prey consumed by *Anolis aeneus*. This assumption is that SSD reduces intersexual food competition relative to the amount of competition expected if males and females are the same size. Contrary to this assumption, estimates of food competition were lower if males and females were the same size than if males were larger than females or vice versa. Next, we tested the prediction from both hypotheses that SSD should be positively related to female density, using data from 25 taxa (24 species) of anoles. Statistically significant relationships between these two variables were obtained in the vast majority of potentially correct phylogenies for the species in this data set, based on either a gradual or a speciation model of evolution. In addition to documenting a relationship between SSD and density, this study shows how comparative questions can be pursued in taxa that currently lack a definitive phylogeny.

Despite the current interest in the evolution of sexual size dimorphism (Hedrick and Temeles 1989; Shine 1989; Fairbairn and Preziosi 1994), surprisingly little is known about relationships between population density and sexual size dimorphism (herein abbreviated SSD; see the appendix for a list of the terms in this article). Many authors have suggested that SSD might be related to mating systems and sexual selection (e.g., Clutton-Brock and Harvey 1978; Alexander et al. 1979; Bondrup-Nielsen and Ims 1990; Bjorkund 1990; Heske and Ostfeld 1990; Webster 1992) or that mating systems and sexual selection might be related to population density (e.g., Warner and Hoffman 1980a; Schwagmeyer 1988; Clutton-Brock 1989; Ostfeld 1990; Davies 1991; Sandell and Liberg 1992). When combined, these lines of reasoning imply that sexual dimorphism in body size or other anatomical traits might vary as a function of population density. To date, however, relatively few workers have pursued this idea.

Ghiselin (1974) was among the first to consider seriously the possible impact of density on the evolution of SSD. He argued that sexual selection might favor relatively large males in taxa that evolved at high densities, because of frequent

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encounters among competing males under those conditions. Conversely, he suggested that selection might favor relatively small (dwarf) males in taxa in which females are sedentary and sparsely distributed, for example, because small males mature earlier and have more modest metabolic requirements than larger members of the same sex (Ghiselin 1974).

Of course, sexual selection is not the only selective pressure associated with the evolution of SSD (Selander 1972; Slatkin 1984; Shine 1989, 1991), and other types of selection affecting body size might also vary as a function of population density. For instance, selection favoring SSD might occur if males and females use different habitats, in which they are exposed to different predators, thermal regimes, or food items (Selander 1966; Shine 1989; Shuster 1990; Vollrath and Parker 1992; Houston and Shine 1993). Alternatively, sex differences in the size of trophic structures might reduce dietary overlap between males and females that forage within the same microhabitats (Schoener 1967; Selander 1972; Shine 1989, 1991). If intersexual habitat segregation or intersexual food competition were more likely to occur at high population densities, then ecological factors could also encourage the evolution of relationships between SSD and density.

Empirical studies of relationships among density, selection on body size, and SSD are still rare and their results often contradictory. In some species, large males are most strongly favored at high densities (Zeh 1987; Zeh and Zeh 1992), in others the reverse is true (Warner and Hoffman 1980a, 1980b; McLain 1982; Conner 1989; Madsen and Shine 1993; Rowe et al. 1994), and in still others no discernible relationship exists between density and selection on male body size (Cade and Cade 1992). Of three interspecific comparative studies of relationships between SSD and density, two have reported positive relationships between density and SSD without controlling for phylogeny (lizards: Stamps 1983; pseudoscorpions: Zeh 1987), whereas a third study controlled for phylogeny but did not obtain a significant correlation between SSD and density (*Sceloporus* lizards: Martins 1994).

This article focuses on interspecific relationships between SSD and population density among lizards in the genus *Anolis*. The first portion discusses two alternative hypotheses that predict positive relationships between density and SSD among anoles: these are termed the food competition hypothesis and the territory defense hypothesis. Next, we use diet samples collected from one species of *Anolis* to test an underlying assumption of the food competition hypothesis, namely, that SSD reduces dietary overlap and food competition between the sexes, relative to the degree of competition expected if males and females are the same size. In the next section, we test the hypothesis that SSD and female density are positively related among the species in this genus. Because a definitive phylogeny does not yet exist for anoles, we employ two methods recently developed to deal with the problem of unresolved polytomies in comparative studies (Purvis and Garland 1993; Losos 1994). The first method repeats the same comparative analysis using many different phylogenies (Losos 1994; cf. Martins 1996). In the current study, we use simulations to generate a large number of possible phylogenies for those species for which reliable estimates of density and SSD are currently available, and then we use each of these phylogenies to explore the

relationship between population density and SSD for the members of this genus. We also employ a second method, recently proposed by Purvis and Garland (1993), which reduces the degrees of freedom in a comparative analysis to compensate for unresolved phylogenetic relationships.

POPULATION DENSITY AND SSD IN ANOLES

Two hypotheses have been offered to explain interspecific variation in SSD among anoles. These hypotheses focus on food and sex, respectively. The earliest discussions of the evolution of size dimorphism in anoles emphasized relationships among body size, jaw size, and prey size (Schoener 1967, 1968, 1977). Anoles eat a wide range of arthropods, and food has been shown to limit *Anolis* growth rates, rates of egg production, and/or fat storage (Andrews 1976, 1979, 1982; Stamps and Tanaka 1981; Rose 1982; Guyer 1988, 1994). Within species, males and females forage in the same locations and take broadly overlapping sizes and types of prey (Schoener 1967, 1968, 1977; Schoener and Gorman 1968; Andrews 1971, 1979; Sexton et al. 1971; Stamps 1977a; Floyd and Jenssen 1983). Hence, it is unlikely that male and female body sizes are subject to different selective pressures because they live in different habitats, eat different types of food, or otherwise have different ecological roles, as has been suggested for other types of animals (see, e.g., Slatkin 1984; Shine 1989, 1991). However, in sexually size-dimorphic anoles, the members of the larger sex sometimes take larger prey than do the members of the smaller sex, which suggests that size dimorphism might reduce dietary overlap and food competition between the sexes within species of anoles (Rand 1967; Schoener 1967, 1968, 1977; Schoener and Gorman 1968).

By extension, intersexual food competition might also lead to a positive relationship between SSD and population density among the species in a taxon. The food competition hypothesis for interspecific variation in SSD rests on two key assumptions. First, it assumes that SSD reduces intersexual dietary overlap and food competition, relative to the situation expected if males and females were the same size. Second, it assumes that species living at high densities experience stronger intersexual food competition than equivalent species living at lower densities. If both of these assumptions are true, then SSD should be positively related to population density among the species in a taxon. Note that this hypothesis does not specify the direction of SSD (e.g., whether males should be larger than females or vice versa).

A second line of reasoning argues that variation in SSD among anoles is a consequence of intrasexual selection, as a result of the processes by which males compete for access to mates. *Anolis* males compete for access to breeding territories that overlap the smaller home ranges of one or more females (Schoener and Schoener 1982; Stamps 1983; Jenssen et al. 1995; Tokarz 1995; but see Hicks and Trivers 1983). Within species, territory ownership, mating success, and/or the number of females per territory are positively correlated with male body size (Rand 1967; Fleming and Hooker 1975; Trivers 1976; Stamps 1977a, 1983; Ruby 1984; Andrews 1985), which suggests that male-male competition for mating op-

portunities may have favored larger-male SSD in anoles (Trivers 1976; Schoener and Schoener 1980; Stamps 1983, 1995). Conversely, because female body size is unrelated to egg size or clutch size within species of anoles (Andrews and Rand 1974), evolutionary explanations for SSD that emphasize relationships between female size and fecundity are less likely to apply to this taxon (Shine 1988).

By extension, the territory defense hypothesis suggests that intrasexual selection might lead to a positive relationship between SSD and density across species. This hypothesis assumes that males can more economically defend multiple females in species with short interfemale distances than in species in which females are far from one another (Stamps 1983). In turn, this hypothesis is based on several underlying assumptions, one of which is that female spacing patterns do not vary as a function of population density across species. In fact, adult female anoles typically live in relatively exclusive home ranges or territories, with no indication that female dispersion patterns vary as a function of population density within or among species (Stamps 1977*a*, 1983; Schoener and Schoener 1980, 1982; Tokarz 1995).

The defense of breeding territories by male anoles makes sense in light of the reproductive patterns of the females of this genus. Females produce single-egg clutches at 1–2-wk intervals over an extended 6–12-mo breeding season (Andrews and Rand 1974; Andrews 1985). Each female comes into a brief behavioral estrus when an egg is ovulated, females typically mate once per estrus period (Crews 1973; Stamps 1975; Trivers 1976; Jones et al. 1983; but see Hicks and Trivers 1983), and field observations suggest that females mate more readily with familiar males who have courted them repeatedly in the past (Trivers 1976; Stamps 1977*a*). Males seem unable to predict when females are in estrus; perhaps, as a result, breeding males spend appreciable amounts of time visiting and courting the adult females within their territories (e.g., see Jenssen et al. 1995). Given the spacing and reproductive patterns of female anoles, a male's reproductive success is likely to be affected by his ability to quickly detect and expel intruding males and to visit each of the females in his territory regularly. In this situation, economic models of territoriality suggest that the costs of territory defense should monotonically increase as a function of the distance between adult females (Schoener and Schoener 1980; Stephans and Dunbar 1991), because travel costs and the probability of detecting male intruders should both increase (all else being equal) as a function of the distances between the females in the territory. Conversely, the benefits of territory defense are expected to increase as a function of the number of females per territory (Schoener and Schoener 1980, 1982; Stamps 1983; Hixon 1987). Thus, for the same number of females per territory, the costs of territory defense would be higher in species with large interfemale distances than in species with small interfemale distances. Viewed another way, the defense of territories containing many females should be more economical when females are closely spaced than when females are widely scattered across the landscape. In turn, to the extent that male-male competition for multiple-female territories favors large male body size (see earlier discussion), intrasexual selection for large male size should be stronger in species in which females are closely spaced than in those in which they are widely scattered.

Hence, the territory defense hypothesis predicts that SSD should be inversely related to interfemale distances among anole species. Data on interfemale distance are not available for most anoles. However, because female anoles have relatively uniform spacing patterns, interfemale distances should be inversely related to the square root of female density across species. Thus, this hypothesis predicts that SSD should be positively related to the square root of female density. In contrast to the food competition hypothesis, the territory defense hypothesis also specifies the direction of SSD: SSD should be positively related to the square root of female density among the species in this genus.

TESTING AN ASSUMPTION OF THE FOOD COMPETITION HYPOTHESIS

The food competition hypothesis assumes that sex differences in body size reduce dietary overlap between the sexes, relative to the amount of overlap expected if males and females were the same size (see previous discussion). This intuitively attractive idea stems from another underlying assumption, namely, that sex differences in body size map directly onto sex differences in prey size. That is, within a given species, members of the larger sex should eat larger prey than members of the smaller sex, and males and females of the same size should eat same-sized prey.

Unfortunately, support for these assumptions has proven elusive for anoles. In some species, males and females are the same size, but females eat significantly larger prey than males (*Anolis limifrons*: Andrews 1979). In other species, males and females are of different sizes, but both sexes eat same-sized prey (*Anolis polylepis*: Andrews 1971; *A. cupreus*: Fleming and Hooker 1975). In *Anolis opalinus*, members of the smaller sex (females) eat larger prey than members of the larger sex do, a reversal of the expected pattern (Floyd and Jenssen 1983).

Because anoles mature at small sizes relative to asymptotic size (Stamps et al. 1994; Stamps and Krishnan, in press), one can compare the prey size distributions for adult males and females of the same length in species in which males grow to a larger asymptotic size than do females. Contrary to the expectation that males and females of the same size should eat same-sized prey, most of these studies have reported sex differences in prey size at the same body length. In some species, males take larger prey than do females of the same size (*Anolis conspersus*, *Anolis angusticeps*: Schoener 1967, 1968, respectively; *Anolis aeneus*, *Anolis richardi*: Schoener and Gorman 1968), whereas in others, males take smaller prey than same-sized females (*Anolis sagrei*, *Anolis distichus*: Schoener 1968; *Anolis occulatus*: Andrews 1979). Indeed, it is difficult to find any sexually dimorphic anoles that satisfy both of the criteria listed previously (but see *Anolis smaragdinus*: Schoener 1968; *Anolis roquet*: Schoener and Gorman 1968). As a result, several workers have questioned whether anoles would exhibit the relationship between body size and prey size assumed if SSD were a consequence of intersexual food competition (Andrews 1979; Floyd and Jenssen 1983; Preest 1994).

Although intriguing, none of the foregoing studies have attempted to test the assumption that SSD reduces dietary overlap and food competition relative to

TABLE 1

ANOLIS AENEUS LIZARDS USED TO ESTIMATE INTERSEXUAL FOOD COMPETITION AS A FUNCTION OF SNOUT-VENT LENGTH (SVL)

GROUP	SEX	NUMBER OF LIZARDS	SVL (mm)			NUMBER OF PREY ITEMS
			Range	Mean	SD	
1	F	34	47-51	49	1.15	342
2	M	18	47-51	49	1.19	112
3	F	13	38-42	40.5	1.39	108
4	M	34	58-62	60	1.43	226

size monomorphism. Here, we use information on the prey taken by *A. aeneus* to estimate the amount of potential food competition if males and females of the same size or of different sizes share the same foraging area.

For a variety of reasons, *A. aeneus* is an excellent candidate for studying potential food competition between males and females. First, the food competition hypothesis assumes that individuals compete for food and that food limits growth, survival, or reproduction. *Anolis aeneus* occurs at high population densities, a situation that encourages food competition in anoles (Andrews 1976, 1979). In addition, food has been shown to limit growth in *A. aeneus* under natural conditions (Stamps and Tanaka 1981). Second, the food competition hypothesis assumes that males and females forage in the same place and time on the same prey items, hence depleting the food available to one another. In *A. aeneus*, males and females have overlapping home ranges throughout the year and forage on the same types of prey in the same microhabitats (Schoener and Gorman 1968; Stamps and Crews 1976; Stamps 1977a). Other basic assumptions of the food competition hypothesis also seem reasonable for this species. For instance, the food competition hypothesis assumes that males and females must satisfy their resting metabolic requirements before allocating nutrients to growth, reproduction, fat storage, or behavior such as courtship or territorial defense.

Because the point of this analysis is to test whether SSD reduces dietary overlap and food competition relative to sexual size monomorphism, we assume a priori that *A. aeneus* males and females compete for food. That is, the goal of this analysis is not to determine whether male and female anoles actually compete for food but rather to see whether SSD would reduce intersexual food competition, assuming that interspecific food competition exists in this species.

MATERIAL AND METHODS

Gut samples from adult males and females with a wide range of snout-vent lengths (SVLs) were collected from July to September 1975 at Grand Anse, Grenada (see Stamps 1977a), and the contents were assigned to a series of prey volume classes. Males and females were collected at the same times and in the same microhabitats, and the adult size distributions in the sample reflected the size distributions typical for this habitat (Stamps 1977a). Adult lizards were divided into four groups (table 1). Adult females averaging 49-mm SVL were used

as the "baseline," and adult males averaging 49 mm were used to investigate potential dietary overlap when males and females had the same SVL. Males of 60 mm were relatively abundant in this habitat, so this size class was used to estimate dietary overlap when males were larger than females (in this case, 22% larger, by length). For a symmetric study of intersexual food competition, we also needed to estimate intersexual food competition when males were 22% shorter than females. However, male *Anolis aeneus* averaging 40.5 mm are both rare and immature. Because males and females are similarly proportioned at this SVL, we used gut samples from 40.5-mm adult females to estimate the degree of food competition that might be expected if 49-mm adult females and 40.5-mm adult males foraged in the same area. Adult male *A. aeneus* eat larger prey than do females of the same size (Schoener and Gorman 1968; Stamps 1977a), so this method provided a conservative estimate of the degree of intersexual food competition expected when males were smaller than females.

For each group of lizards, we calculated the fraction of the total prey volume in each prey size category, producing an initial prey utilization function, in which the volume of prey in each size category is proportional to the area in the prey size distribution histogram (see Roughgarden 1972; Stamps 1977a). These initial prey utilization functions were then weighted to reflect the proportionally larger energy demands of large versus small individuals. The resting metabolic rates of lizards of different sizes were estimated using an equation generated empirically for another member of the genus, *Anolis bonairensis*: $RMR \propto M^{0.55}$, where RMR is resting metabolic rate and M is mass (Bennett and Gorman 1979; see also Andrews and Pough 1985). Because $M \propto SVL^{3.0}$ in *A. aeneus* (reduced major axis method, $N = 277$ adults, SE of the slope = 0.05, $r = 0.96$), we assumed that in *A. aeneus* $RMR \propto SVL^{(0.55 \times 3.0)}$, that is, that $RMR \propto SVL^{1.65}$. By extension, sex differences in $RMR \propto (\text{male SVL}/\text{female SVL})^{1.65}$. Hence, to estimate the metabolic requirements of 60-mm males relative to 49-mm females, we multiplied the prey utilization functions of the 60-mm males by 1.40 ($[60/49]^{1.65}$). Similarly, we divided the prey utilization functions of 40.5-mm lizards by 0.73. Finally, we estimated the degree of competition between lizard size classes by computing the amount of overlap between the weighted prey utilization functions for adult size classes (e.g., 49-mm females vs. 60-mm males). The degree of food competition between two groups X and Y was estimated by

$$\alpha_{XY} = \frac{O_{XY}}{A_X},$$

where α is the competition coefficient between X and Y, O_{XY} is the area of overlap between the prey utilization functions of X and Y, and A_X is the total prey utilization area of X. A more complete discussion of this method can be found elsewhere (Roughgarden 1972; Stamps 1977a).

This method of estimating intersexual competition coefficients is subject to several possible errors. For instance, the exponent relating metabolic rate to SVL might be somewhat higher or lower than 1.65. Studies of lizard resting metabolic rates have yielded intraspecific mass exponents ranging from 0.55 to 0.79 (Andrews and Pough 1985), but these estimates are themselves subject to various

types of statistical and measurement errors. Similarly, the exponent relating SVL and M in *A. aeneus* might be slightly higher or lower than 3.00. To be as conservative as possible, we reran the analysis twice, assuming that resting metabolic rate was proportional to either $SVL^{1.00}$ or $SVL^{3.00}$. Both exponents are more extreme than any value likely to be valid for this species.

Along the same lines, we initially assumed that male and female anoles had the same metabolic rate at a given SVL. Because no data exist on sex differences in resting metabolic rates for anoles, we reran the analyses assuming that males had resting metabolic rates either 33% higher or 33% lower than females at the same snout-vent length, where female metabolic rate was proportional to $SVL^{1.65}$.

This method also assumes that the prey eaten by the lizards in our study accurately reflect the typical prey size distributions for the adults of this species. Support for this assumption comes from several sources. First, the size distribution of prey suitable for adult *A. aeneus* does not change on a seasonal basis (Tanaka and Tanaka 1982), which implies that dietary overlap measured from July to September is comparable to that exhibited during other months of the year. Second, Schoener and Gorman (1968) studied *A. aeneus* dietary overlap in a different locality, year, and type of habitat. Even so, the prey size distributions taken by the adult size classes in our study were indistinguishable from those reported for the same size-sex groups of *A. aeneus* by Schoener and Gorman (1968, figs. 3, 4, 6; see also Stamps 1977a) (prey size distributions compared using Kolmogorov-Smirnov two-sample tests; all P values $> .50$). To test this assumption another way, we scanned our prey size distributions to determine whether any of them included rare, large prey items that might skew estimates of competition coefficients. One such "outlier" was detected: a 49-mm male ate a single large prey item that was significantly larger than any other prey item in the study (fig. 1). Hence, we ran the analyses again, omitting this particular item from the prey size distribution of 49-mm males.

RESULTS

From the perspective of both sexes, competition coefficients were lower when males and females were the same size than when females were larger than males or vice versa (see table 2). Several factors contributed to this counterintuitive result. First, adult male *Anolis aeneus* ate much larger prey than adult females of the same SVL, as previously reported (Schoener and Gorman 1968; Stamps 1977a). The dramatic difference between the prey size distributions for 49-mm males and females was partly a result of a single large prey item eaten by a 49-mm male (see fig. 1). However, when we reran the analysis without this outlier, 49-mm males still ate considerably larger prey than did 49-mm females (in this case, $\alpha = 0.55$ for both sexes). Males of 60 mm had prey size distributions similar to those of 49-mm males, but the larger males were assumed to require more food per unit time to satisfy their basic metabolic needs. As a result, our estimates indicated that 60-mm males took more food from the prey size classes used by 49-mm females than did 49-mm males. Conversely, small (40-mm) lizards had prey size distributions that overlapped extensively with those of 49-mm females.

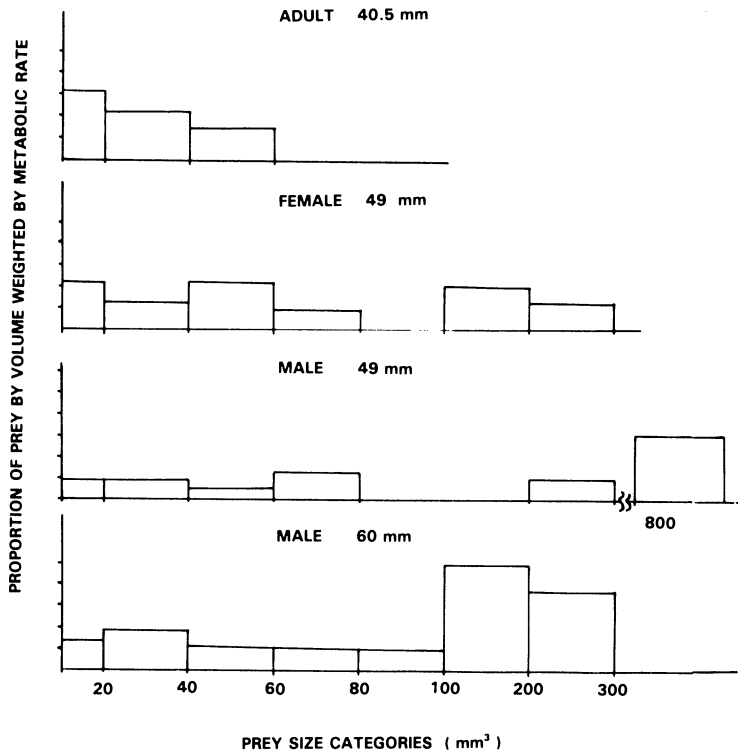


FIG. 1.—Prey sizes found in stomachs of lizard size classes (SVL, in millimeters). Weighted prey utilization functions for each size class were constructed by calculating the proportion of the total prey volume that came from various prey size classes. These proportions were adjusted to reflect the larger energy requirements of larger lizards and are represented as probability density functions for each lizard size class (see the text).

TABLE 2

FOOD COMPETITION COEFFICIENTS FOR PARTICULAR MALE-FEMALE SIZE COMBINATIONS, BASED ON THE WEIGHTED PREY UTILIZATION FUNCTIONS ILLUSTRATED IN FIGURE 1 FOR THE GROUPS IN TABLE 1

MALES-FEMALES (MEAN SVLS)	AVERAGE MALE SVL/ AVERAGE FEMALE SVL	COMPETITION COEFFICIENTS	
		Females	Males
49-mm female and 49-mm male	1.00	.42	.42
49-mm female and 60-mm male	1.22	.80	.57
49-mm female and 40.5-mm male	.82	.49	.67

NOTE.—Results for 40.5-mm males were estimated using data from females with the same snout-vent length (SVL); see the text.

Hence, even though we assumed that 40-mm lizards required less food than 49-mm lizards to support their resting metabolic needs, the extensive overlap in the prey sizes taken by 40- and 49-mm lizards produced higher estimates of food competition than those obtained when males and females were the same size.

These arguments can be summarized as follows. Large males require large amounts of food, much of which comes from the prey size classes used by females. Small males require small amounts of food, virtually all of which comes from the prey size classes used by females. Same-sized males require the same amount of food as females but take most of their food from prey size classes larger than those used by females. As a result, estimates of intersexual food competition were lower when males and females were the same size than when males were larger than females or vice versa.

Recall that we used 40.5-mm adult females to estimate the prey consumed by (hypothetical) 40.5-mm adult males. If anything, this method would err in the conservative direction. If 40.5-mm males followed the same pattern as their larger male counterparts and consumed larger prey than females at the same SVL, the competition coefficients for 40.5-mm males versus 49-mm females would have been even higher than those obtained in the current study.

Varying the parameter values used to estimate the competition coefficients had no effect on the qualitative results of the analysis. The alternative analyses listed in Material and Methods produced different estimates of α for each male-female combination than those shown in table 2, but in every analysis, competition coefficients for both sexes were lowest when males and females were both 49 mm and higher for both sexes when males were larger than females or when females were larger than males.

In summary, all of the analyses produced the same conclusion. From the perspective of minimizing intersexual dietary overlap and food competition, the best option for *A. aeneus* appears to be sexual size monomorphism rather than sexual size dimorphism. In this species, either male-larger or female-larger size dimorphism yielded higher estimates of intersexual food competition for both sexes than those obtained when males and females were the same size.

DISCUSSION

Inspection of male-larger versus female-larger SSD in table 2 implies that the members of the smaller sex would be more severely affected by food competition than would the members of the larger sex. Previous studies of food competition functions in relation to body size in anoles also suggest that large individuals have a greater impact on smaller ones than vice versa (Roughgarden 1972, 1974; Schoener 1977; Stamps 1977a). The intuitive explanation for this pattern is straightforward. Lizards of different sizes take prey from an underlying available prey size distribution that is skewed in favor of small prey items. Large animals not only require more food per unit time to satisfy their basic metabolic needs, but they also take most of this food from the small prey size categories that form the entire diet of smaller individuals. Conversely, small individuals require less

food in toto to satisfy their resting metabolic requirements, and they are unable to take rare but profitable large items that are accessible to larger individuals.

Asymmetric food competition functions are interesting because they imply that the direction of SSD (e.g., male-larger or female-larger) is likely to affect the amount of food competition experienced by the members of each sex. From the female perspective, female-larger dimorphism leads to less intersexual food competition than an equivalent degree of male-larger dimorphism, whereas the reverse is true for males (e.g., see table 2). In anoles, the female perspective is probably more important than that of males when investigating the effects of food competition on fitness, because the reproductive success of males is directly affected by the egg production rates and survival of the females with whom they share a territory, whereas female reproductive success is largely independent of the growth or survival of the male owner of the territory (see above; Arnold 1994; Arnold and Duvall 1994). That is, a male's reproductive success is influenced not only by the amount of food available for his own growth and survival but also by the amount of the food available to his mate(s). In contrast, a female's fertility would be little affected if food shortages reduced the growth or survival of her current mate, given the number of other males ready to replace him.

Hence, in contrast to earlier suggestions that food competition hypotheses do not specify the direction of SSD (e.g., Schoener 1977; Slatkin 1984; Hedrick and Temeles 1989; Shine 1989; but see Gilbert and Williamson 1983), situations may exist in which intersexual food competition would favor the evolution of female-larger rather than male-larger SSD. In particular, the evolution of female-larger dimorphism from a size-monomorphic ancestor would be favored if (1) food competition functions are asymmetric with respect to body size, so that intersexual food competition is more severe for the members of the smaller sex, (2) female survival and fecundity have a stronger effect on male reproductive success than male survival and fecundity have on female reproductive success, and (3) males and females forage in the same areas when females are accumulating nutrients to provision eggs or neonates.

Most present-day anoles exhibit male-larger SSD (Fitch 1981; Shine 1988), and it is not known whether the members of this genus evolved from a monomorphic ancestor. Because of the current uncertainty about the origins of SSD in the genus, the most relevant question for our purposes is whether an increase in the intensity of food competition would select for an accentuation or a reduction in SSD, in a species that already exhibited either male-larger or female-larger SSD. In the case of *Anolis aeneus*, it seems clear that strong food competition would, if anything, lead to a reduction in SSD. It remains to be seen whether the same is true for other dimorphic anoles.

Many anoles share with *A. aeneus* the conditions that would produce less intersexual food competition under monomorphism or female-larger dimorphism than under male-larger SSD. One necessary precondition is that resting metabolic costs should increase as a function of body size, a pattern that is as ubiquitous in lizards as it is in other animals (Andrews and Pough 1985). A second necessary condition is that males and females of the same snout-vent length should eat prey

of different sizes; as noted earlier, this pattern has been observed in most of the sexually size-dimorphic anoles studied so far. It might be interesting to repeat this analysis for other anoles in which males eat significantly larger or smaller prey than same-sized females.

Anoles are not the only squamate reptiles in which there is reason to question a direct functional relationship between body size and prey size. Many other squamates exhibit sex differences in allometric relationships between jaw size and body size (Schoener et al. 1982; Vitt and Cooper 1985; Shine and Crews 1988; Cooper and Vitt 1989; Shine 1989, 1991; Vial and Stewart 1989; Anderson and Vitt 1990; Hews 1990; Griffith 1991; Mouton and van Wyk 1993), and, in some species, males and females take prey of different types or sizes even after controlling for body or jaw size (e.g., Simon 1976; Houston and Shine 1993; Perez-Mellado and De la Riva 1993). As was true for anoles, sex differences in diets at the same body size imply that SSD may not be the only, or even the most efficient, way to reduce intersexual dietary overlap and food competition.

RELATIONSHIPS BETWEEN SSD AND DENSITY AMONG SPECIES OF ANOLES

Material and Methods

Estimates of adult female population density and sexual size dimorphism were gathered from the literature and unpublished studies (table 3). When estimates varied temporally or spatially, we used the average density for a given area. Data from different populations of the same species were not combined; if estimates of female density were available for different populations of the same species (e.g., *Anolis sagrei* studied by Schoener), we used the locality with the largest sample size. One population per species was used in the analysis, with the exception of *Anolis limifrons*, for which we included data from two populations, from Costa Rica and Panama, respectively. The largest adults per sample were used to estimate male and female asymptotic snout-vent length (ASVL; see Stamps and Andrews 1992), and these estimates were used to compute SSD based on asymptotic size (male ASVL/female ASVL; see Stamps et al. 1994). Because the territory defense hypothesis predicted a relationship between interfemale distance and SSD, we used the square root of female density (SDEN) to estimate average interfemale distances for the species in this analysis.

Relationships between SSD and SDEN among *Anolis* lizards were estimated using two different methods. The first used simulations to generate large numbers of possible phylogenies for the 25 taxa (24 species) in the data set; the relationship between SSD and SDEN was then analyzed for each phylogeny using independent contrasts (Felsenstein 1985; Losos 1994; see below for details). In addition, we compared the results produced by the simulation method with those produced by a different method that adjusts degrees of freedom (Purvis and Garland 1993).

In theory, at least, relationships between SSD and SDEN could be confounded by variation in body size among the species in a comparative data set. We considered two methods to control for relationships between body size and other vari-

TABLE 3

ESTIMATES OF ANOLIS POPULATION DENSITY, ASYMPTOTIC SIZES, AND SEXUAL SIZE DIMORPHISM

SPECIES	LOCALITY	FEMALES/ HECTARE	ASYMPTOTIC SVL (mm)		SSD	REFERENCE
			Female	Male		
<i>acutus</i>	St. Croix	2,633	49.0	64.0	1.31	Ruibal and Philibosian 1974; Philibosian 1975
<i>aeneus</i>	Grenada	1,163	50.0	70.0	1.40	J. A. Stamps, unpublished data
<i>angusticeps</i>	Bimini	580	45.5	51.5	1.13	Schoener and Schoener 1980; T. W. Schoener, unpublished data
<i>auratus</i>	Panama	517	51.0	51.0	1.00	Fleishman 1986, 1988
<i>bimaculatus</i>	St. Eustatius	780	64.0	84.5	1.32	Rummel and Roughgarden 1985
<i>capito</i>	Costa Rica	11	97.0	88.0	.91	R. M. Andrews, unpublished data
<i>carolinensis</i>	Louisiana	536	57.5	70.5	1.23	Gordon 1956; Ruby 1984
<i>cupreus</i>	Costa Rica	71	47.0	49.0	1.04	Fleming and Hooker 1975
<i>distichus</i>	Bimini	310	46.0	50.0	1.09	Schoener and Schoener 1980; T. W. Schoener, unpublished data
<i>frenatus</i>	Panama	18	120.0	150.0	1.25	R. M. Andrews, unpublished data
<i>garmani</i>	Jamaica	38	95.0	132.0	1.39	Trivers 1976
<i>humilis</i>	Costa Rica	192	43.0	40.0	.93	C. Guyer 1988, unpublished data
<i>limifrons</i>	Panama	350	51.0	50.0	.98	Sexton et al. 1971; R. M. Andrews, unpublished data
<i>limifrons</i>	Costa Rica	33	43.0	41.0	.95	Lieberman 1986; R. M. Andrews, unpublished data
<i>lineatopus</i>	Jamaica	1,604	45.5	67.0	1.47	Rand 1967
<i>lionotus</i>	Panama	245	70.0	76.0	1.09	Campbell 1973
<i>nebulosus</i>	Mexico	470	46.0	49.0	1.07	Jenssen 1970
<i>oculata</i>	Dominica	1,776	63.0	79.0	1.25	R. M. Andrews, unpublished data
<i>poecilopus</i>	Panama	245	66.0	74.0	1.12	Campbell 1973
<i>polylepis</i>	Costa Rica	140	48.0	53.0	1.10	R. M. Andrews, unpublished data
<i>sagrei</i>	Bimini	2,200	45.0	58.5	1.30	Schoener and Schoener 1980; T. W. Schoener, unpublished data
<i>smaragdinus</i>	Bimini	223	50.0	61.0	1.22	Schoener and Schoener 1980; T. W. Schoener, unpublished data
<i>tropidonotus</i>	Honduras	43	52.0	56.0	1.08	Jackson 1973
<i>valencienni</i>	Jamaica	213	74.0	85.0	1.15	Hicks and Trivers 1983
<i>wattsi</i>	St. Eustatius	1,550	41.0	47.0	1.15	Rummel and Roughgarden 1985

ables of interest in comparative studies. The first, simpler method involves regressing the variables of interest against body size, and then using the residuals from these linear regressions in subsequent analyses. In the current study, we regressed SSD and SDEN against female ASVL, and then used the residuals from each regression to estimate SSD and SDEN after controlling for body size. However, several authors have recommended that residuals from log male size against log female size be used to control for relationships between body size and SSD, to correct for statistical artifacts that might occur when regressing female body size against a ratio that contains female body size in the denominator (e.g., Fairbairn and Preziosi 1994). Hence, before proceeding further, we asked whether these two methods of controlling for the effects of body size on SSD would yield different results.

We addressed this question by calculating two sets of residuals for the taxa in our data set: residuals from a regression of SSD against female ASVL and residuals from a regression of log male ASVL against log female ASVL. Then, we calculated the correlation coefficient between these two sets of residuals. The residuals were strongly correlated with one another ($r = 0.998$, $N = 25$ taxa), a correlation coefficient so high that either method would produce the same results in any further analyses. Because the two methods yielded interchangeable estimates of SSD controlled for female size, in the current study we used the simpler of the two methods (residuals from a linear regression of SSD against female asymptotic SVL).

For logistical reasons, it was not feasible to calculate residuals based on the phylogenetically independent contrasts generated within each simulation. Instead, we computed residuals using values for each taxon, in which the residuals from SDEN against female ASVL were used to estimate interfemale distances after controlling for female size, and the residuals of SSD against female ASVL were used to estimate SSD after controlling for female body size. In addition, we used the Purvis and Garland (1993) method to determine whether calculating residuals before computing independent contrasts might have biased our results. Analyses were run two ways, either calculating residuals before using the contrast method or calculating residuals by regressing contrasts of one variable on contrasts of a second variable. The results produced by the two analyses were virtually identical, indicating that for this data set, estimates of relationships between SSD and interfemale distance were robust with respect to the methods used to control for the effects of body size on other variables.

We derived our phylogeny for *Anolis* from several sources (fig. 2). The basic tree is from Cannatella and de Queiroz (1989, their fig. 4). In addition, we resolved additional relationships as follows: *carolinensis* and *smaragdinus* are both members of the *carolinensis* species group, relationships in the *bimaculatus* group are from Roughgarden and Pacala (1989), and Jamaican anoles (*valencienni*, *garmani*, *lineatopus*) are from Burnell and Hedges (1990). The "series" within the "beta" group of anoles (taxa from *sagrei* to *lineatopus* on the tree in fig. 2; see Guyer and Savage 1986, 1992; Williams 1989) were assumed to be monophyletic.

For each analysis, we used computer simulations to generate 10,000 phylogenies for these 25 taxa, with the stipulation that each simulation produce a phylog-

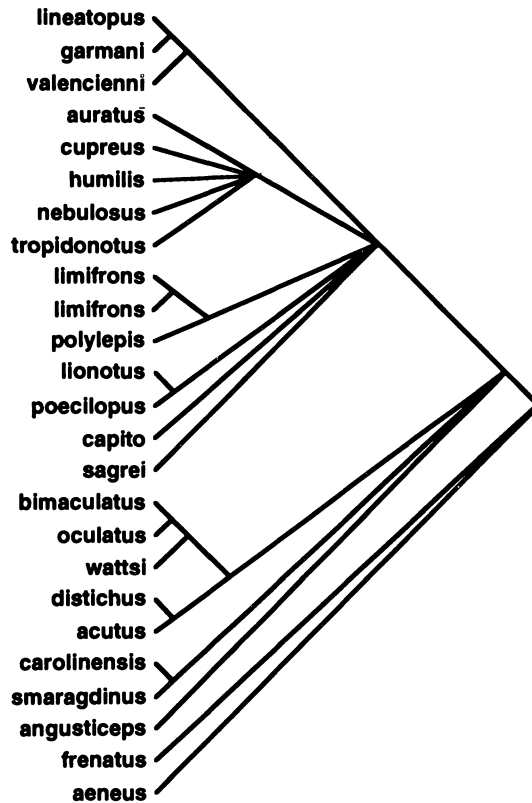


FIG. 2.—Phylogeny of *Anolis* from Cannatella and de Queiroz (1989), Burnell and Hedges (1990), and Roughgarden and Pacala (1989) (see text).

eny that was consistent with the phylogeny in figure 2 but with polytomies resolved. We thus assume that polytomies in figure 2 represent lack of information rather than simultaneous speciation (i.e., “soft” polytomies, sensu Maddison 1989). Briefly stated, the method works as follows (see also Losos 1994). Initially, a simulation begins with 25 taxa at a time of zero. In each subsequent “time interval,” a random number is drawn for each taxon. If the number is below a small but nonzero threshold, then that taxon is chosen. The threshold number is the same for all taxa and varies according to the number of taxa remaining in the simulation, such that the probability of a speciation event remains constant through time. If no taxon is chosen, then the time counter is increased by one, and the process is repeated. If a taxon is chosen, then another taxon is randomly chosen and the two taxa are replaced by their ancestor, which thus reduces the number of taxa by one. The number on the time counter is then recorded as the time of divergence for this ancestral node. If pairing the two taxa will produce a phylogeny inconsistent with known relationships, then the pairing does not occur and the simulation proceeds until an acceptable pairing occurs. In this manner,

the simulation proceeds until the taxa have coalesced into a single remaining ancestral node. At this point, a phylogeny has been created that is consistent with figure 2 but with all polytomous nodes fully resolved.

For each simulated phylogeny, we then used the independent contrasts method (Felsenstein 1985; Garland et al. 1992) to estimate relationships between the variables reflecting SSD and SDEN (note that the phylogenetic relationships among the taxa potentially differed in each simulation, but their character values remained unchanged). The independent contrasts method requires information on trait values for each taxon, phylogenetic relationships among taxa, and branch lengths in units of expected variance of character evolution for each branch on the tree.

Two alternative models of evolutionary change were assumed to obtain branch lengths (Garland et al. 1992). The speciation change model assumes that change occurs only at speciation events; consequently, the amount of change expected along each branch of the tree is the same, and all branch lengths are set to one. The gradual model assumes that the expected amount of change along a branch is proportional to length of the branch in units of time. In this situation, the simulated phylogenies provide estimates of branch lengths (the number of time intervals along each branch of the tree), which are then used to standardize the contrasts (i.e., remove the expected relationship between contrasts and their branch lengths). In the event that a standardization was unsuccessful (i.e., a relationship still existed between the absolute value of standardized contrasts and their standard deviations [= branch lengths]), we recalculated the analysis after transforming the branch lengths by taking natural logs (see Garland et al. 1992). If this standardization was also unsuccessful, we excluded this simulation from further analysis (Losos 1994). Diaz-Uriarte and Garland (1996) have illustrated other means by which branch lengths could be transformed (see also Garland et al. 1992), but attempting a whole suite of different transformations would have been too computationally intensive. Further study is needed to determine what bias, if any, results from the exclusion of trees that could have been rendered compatible with a gradual model by such transformations.

Martins (1996) argues that branch lengths generated in simulations that have been constrained in some way, as our method does, are not equivalent to the branch lengths generated with a standard branching process algorithm. In effect, the branch lengths thus generated model evolution in which the rate of phenotypic evolution and speciation are different for different clades in the phylogeny rather than follow a single gradual model. Consequently, the simulations might not represent a random subset of all of the possible phylogenetic trees. We recognize this limitation but point out that there is no other feasible means of generating trees that are compatible with current information about the phylogeny of the group in question. The alternative would be to use unconstrained simulations producing trees that contradict available information about the group's phylogeny. The value of considering analyses conducted on such trees would seem to be minimal. Although our method thus does contain some biases (e.g., trees in which *aeneus* and *richardi* are sister taxa occur much more frequently in the

simulations than those containing either taxon as a sister group to the remaining 23 species), further study is required to indicate what effect, if any, this bias may produce.

A second method has recently been proposed in which independent contrasts can be used with polytomous phylogenies (by contrast, the tree simulation method can be used in concert with any statistical method). Initially, Grafen (1989) and Pagel (1992) suggested that a single contrast should be calculated for each polytomous node. Purvis and Garland (1993) expanded on this idea, arguing that one should calculate all possible contrasts but set the internode branch lengths for polytomous nodes to zero. Then, by using the number of nodes on the tree minus one as the degrees of freedom, an analysis would not inflate the degrees of freedom. Consideration of greater degrees of freedom would indicate the appropriate statistic if some of the nodes were truly polytomous. This method allows unbiased statistical estimation and also may provide a conservative means of hypothesis testing when the minimal degrees of freedom are employed. We employed this method using three possible means of setting branch lengths: all branches set equal to one (i.e., a punctuated model of evolution), and two methods of setting branch lengths that roughly correspond to a more gradual model of evolution (Grafen 1989; Pagel 1992). The two latter methods differ in that Grafen's model produces greater disparity in branch lengths among taxa, whereas branch lengths are more homogeneous in the Pagel model.

Results

In the nonphylogenetic analysis, the relationship between SDEN and SSD was strongly positive, after controlling for body size using residuals ($r = 0.68$, $P < .001$, $N = 25$ taxa; fig. 3).

If we grant the assumptions of the speciation model, then the relationship between residual SSD and residual SDEN estimated by independent contrasts was significant at $P < .05$, one-tailed for 9,998 of the 10,000 simulated trees, with $P < .10$ for the other two trees (fig. 4). Similarly, under the assumptions of the gradual evolution model, 622 trees were successfully standardized for independent contrasts. Of these, 608 were significant at $.05$, with $P < .10$ for the remaining trees (fig. 5).

Analyses using the unresolved polytomies and the method of Purvis and Garland (1993) gave significant results regardless of the method used to assign branch lengths (speciation model: $r = 0.60$, $F = 12.81$, $df = 1, 13$, $P < .005$; Grafen model: $r = 0.53$, $F = 8.90$, $df = 1, 13$, $P < .025$; Pagel model: $r = 0.56$, $F = 10.38$, $df = 1, 13$, $P < .01$).

GENERAL DISCUSSION AND CONCLUSIONS

The current study shows that clear results can be obtained from interspecific comparative studies, even in the absence of a well-established phylogeny. All of the simulated trees yielded results that were statistically significant or nearly so. In addition, an alternative method that reduced degrees of freedom rather than

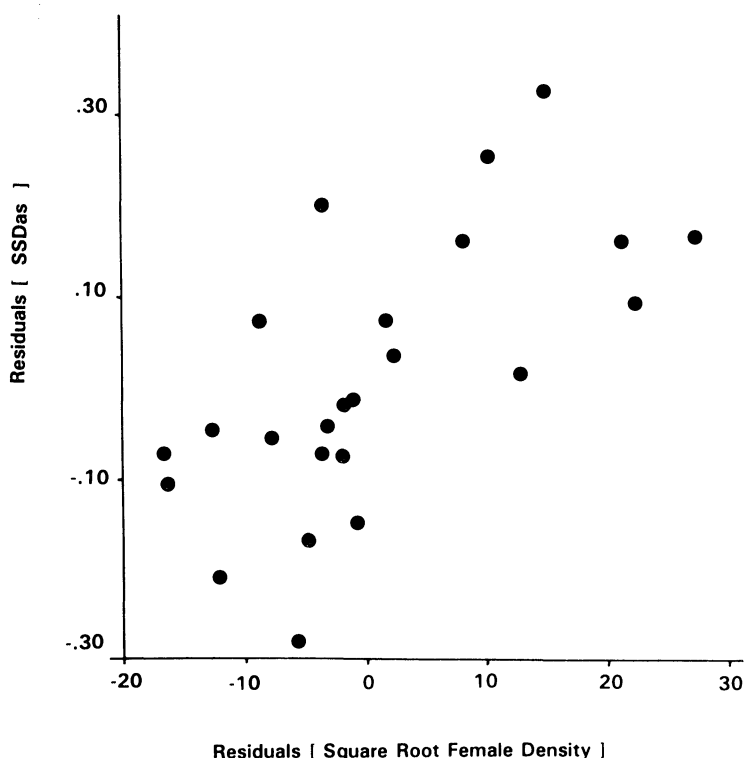


FIG. 3.—Relationship ($r = 0.68$) between an estimate of interfemale distance (SDEN) and SSD for the 25 taxa listed in figure 2 and table 3. Based on a nonphylogenetic analysis of residuals from regressions on asymptotic female SVL, $P < .001$.

resolved polytomies also yielded significant results. We therefore conclude that SSD is positively related to the square root of female density in anoles.

This is the first time that simulation (Losos 1994; Martins 1996) and reduced degrees of freedom (Purvis and Garland 1993) approaches have been applied to the same data set. The ease of calculation of the latter relative to the more laborious simulation method, and the similarity in results between the two methods, may prompt others to use the Purvis and Garland method. In this light, we should emphasize the differences between the two methods.

With respect to evaluating a null hypothesis, the simulation method asks whether trees exist that are compatible with current information about phylogeny and that produce nonsignificant results. Implicit in this approach is the idea that if many trees produce nonsignificant results, then one cannot adequately evaluate whether a relationship exists between the variables of interest until a better phylogeny is in hand. In this sense, the simulated trees method is highly conservative. The reduced degrees of freedom approach may not be as conservative, because this method may yield a lower P value than exists for some of the possible phylogenies for the taxa in a comparative analysis. For example, in the current

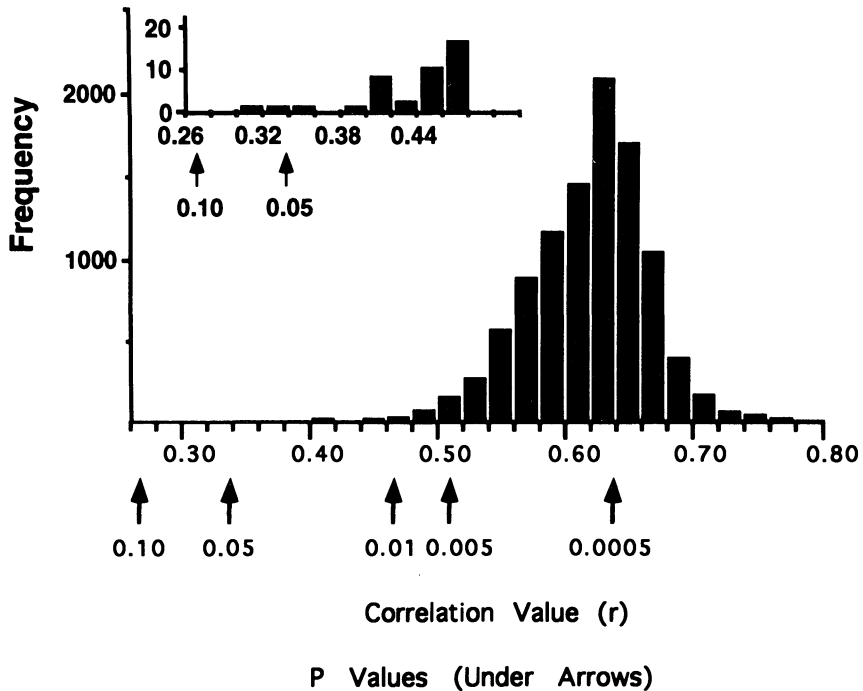


FIG. 4.—A frequency histogram of independent contrasts correlation coefficients between residual SDEN and residual SSD for 10,000 simulated trees based on a speciation model of evolution. Larger numbers on the abscissa indicate r values; smaller numbers under the arrows indicate P values for various levels of significance ($N = 25$ taxa, one-tailed test). The insert is a magnification of the left-hand tail of the frequency histogram.

study, the reduced degrees of freedom speciation change analysis yielded a higher significance level than was obtained in 10% of the simulated trees (see fig. 4). Hence, although both methods yielded the same conclusion about the relationship between density and dimorphism in anoles, in other situations the reduced degrees of freedom method might yield a statistically significant result even if many potentially correct trees did not.

On the other hand, the simulation method is more cumbersome and time-consuming than the reduced degrees of freedom method, and the latter can answer a variety of questions quickly and easily. For instance, we used this method to determine whether different methods of computing residuals to control for body size were likely to affect estimated relationships between SSD and density. Future research should focus on the advantages and limitations of each method. Certainly, the ease of use of the Purvis and Garland (1993) method will make it attractive in many contexts.

All of our analyses indicate a statistically significant relationship between female density and SSD among species of lizards in the genus *Anolis*. This result is consistent with both the territory defense and the food competition hypothesis for the evolution of SSD in *Anolis* lizards. As we emphasized in the previous section, however, several key assumptions of the food competition hypothesis

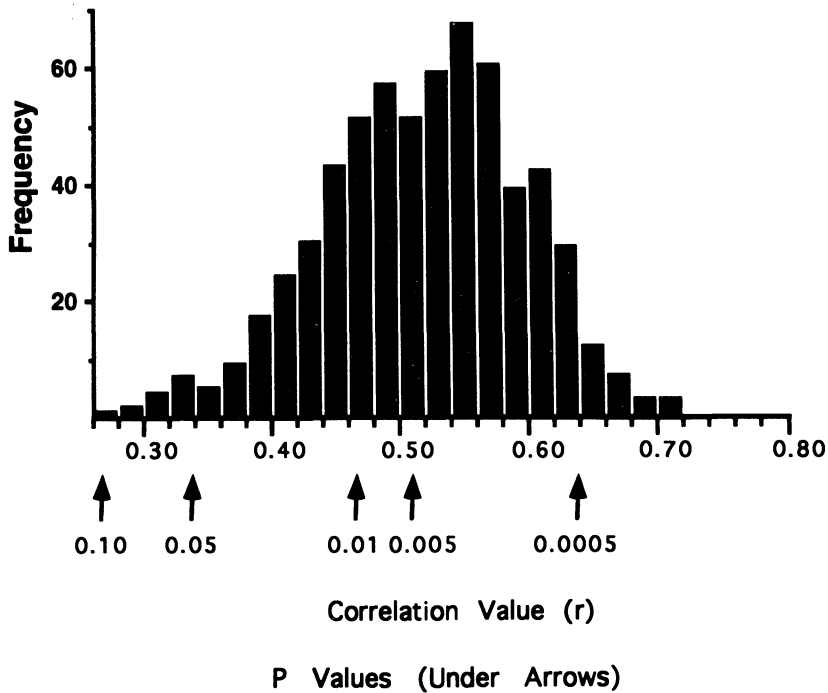


Fig. 5.—Independent contrasts correlation coefficients between residual SDEN and residual SSD for the 622 successfully standardized simulations based on a gradual model of evolution. Of these, 608 yield correlation coefficients that exceed the nominal critical value of 0.337 for a one-tailed test with an N of 25. See figure 4 for notation on r and P values.

may not apply to the members of this genus. Many workers (we included) have not found the simple relationships between SVL and prey size that are assumed by the food competition hypothesis, and estimates of intersexual food competition in one species (*Anolis aeneus*) indicate that overlap in prey size distributions is less extreme when males and females are of the same size than when males are larger than females or when females are larger than males.

Although intuitively attractive, the food competition hypothesis for SSD has yet to be rigorously tested for any animal. A field experiment along these lines could be conducted with anoles, for example, by enclosing or isolating patches of habitat containing the home ranges of a free-living adult male and female, removing the original residents, and then introducing a new male and female into each enclosure. Each enclosure should be visually isolated from conspecifics, and the combined mass of the introduced male and female should be the same for each enclosure. However, one set of enclosures would each house a small female and a large male, whereas the other set would house a male and female of the same size. If conducted under food-limited conditions during the breeding season, this experiment could reveal whether rates of growth or egg production differ for dimorphic and monomorphic pairs of adults, while controlling for the types of behavioral interactions related to territory defense and sexual selection.

Until such experimental results are available, however, the evidence (albeit indirect) more strongly supports the territory defense hypothesis than the food competition hypothesis for the members of this genus.

Because the territory defense hypothesis is based on general economic models of territoriality, it might apply to taxa other than *Anolis* lizards. All else being equal, if males can defend breeding territories that provide them with relatively exclusive access to fertile females, then SSD should be positively related to female density. Generally speaking, these conditions may apply more easily to species in which travel is costly than to highly mobile animals. For instance, some polygynous birds bear a superficial resemblance to lizards, in that males defend breeding territories containing the nests of several females (Orians 1969; Davies 1991; Webster 1992). However, extrapair fertilizations are common in birds (Dunn and Lifjeld 1994), in part because females have the option of flying outside the territory to mate (Smith 1988; Heg et al. 1993). As a result, the number of females per territory may be uncorrelated with the number of offspring fathered by the territory owner (Gibbs et al. 1990). In addition, extrapair paternity in birds may increase as a function of density (Gowaty and Bridges 1991; but see Dunn et al. 1994), further eroding the potential reproductive advantages of multifemale territories at high population densities. Hence, the territory defense hypothesis is more likely to apply to animals that walk than to those that fly.

Another caveat is implied by the phrase "all else being equal" in the previous paragraph. The males of some microtine rodents defend territories that overlap the home ranges of one or more sedentary females, and it is assumed that males have relatively exclusive reproductive access to the females in their territory (Ostfeld 1985, 1990; Heske and Ostfeld 1990). However, interspecific variation in female dispersion patterns and the degree of female reproductive synchrony is common in this subfamily, and both of these factors may affect microtine mating systems, sexual selection, and SSD (Ostfeld 1985, 1990; Ims 1987, 1988; Ostfeld and Heske 1993). Hence, it might be possible to apply the territory defense hypothesis to this group, but only after controlling for interspecific variation in female reproductive synchrony and dispersion patterns.

Sceloporine lizards seem to fit many of the assumptions for the territory defense hypotheses (Stamps 1977b, 1983), so it is interesting that Martins (1994) did not obtain a significant relationship between SSD and density in a comparative study of *Sceloporus* that controlled for phylogeny ($r = -0.35$, $P < .33$). Differences in methodology may have contributed to the discrepancy in results. For example, Martins used average male and female sizes to estimate SSD, and such estimates vary more within species than do estimates of SSD based on asymptotic size (Stamps 1993, 1995). Other differences include a smaller sample size for the *Sceloporus* (12 taxa vs. 25 in the current study), a smaller range of SSD values among the species in that sample, and a correlation coefficient heavily influenced by a single outlier. A particularly striking difference between the two data sets is that the variance in population density among anoles was nearly 200 times greater than that in Martins's (1994) sample ($F = 177.5$, $df = 24, 11$, $P < .001$). Because population densities often vary substantially within populations on a spatial or temporal basis (e.g., Schoener and Schoener 1982), it might be useful

to focus on groups with extreme variation in population density among species when studying relationships between SSD and density using a comparative approach.

The current study also suggests a mechanism by which interspecific competition might influence the evolution of SSD in anoles and other animals. Experimental field studies show that congeners can reduce density, growth rates, feeding rates, and egg production for the species in this genus (Pacala and Roughgarden 1982, 1985; Schoener 1983), and the current study suggests that SSD is positively related to female density. In combination, these results imply that SSD should be inversely related to the number of congeners with which a population has shared a habitat over evolutionary time. In fact, anoles are frequently more dimorphic on depauperate islands than on islands containing many congeners (Schoener 1969, 1977).

Traditionally, negative correlations between species richness and SSD in anoles have been interpreted as supporting the food competition hypothesis for the evolution of size dimorphism (Schoener 1977; Slatkin 1984; Shine 1989). As was noted earlier, however, support for several assumptions of the food competition hypothesis is equivocal for anoles. In addition, intraspecific variation in SSD among populations living on different islands is primarily caused by variation in male body size (Schoener 1969, 1977), a pattern that is more consistent with the territory defense hypothesis than with the food competition hypothesis. Hence, observed relationships between species richness and SSD in anoles and possibly other animals may actually reflect underlying relationships between both variables and population density.

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APPENDIX A

TABLE A1

DEFINITION OF TERMS

Term	Definition
α	Competition coefficient reflecting dietary overlap between two size-sex classes
ASVL	Asymptotic snout-vent length for the individuals in a population
M	Body mass
RMR	Resting metabolic rate
SDEN	Square root of female population density
SSD	Sexual size dimorphism
SSDas	Sexual size dimorphism based on asymptotic size
SVL	Snout-vent length

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