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THE *ANOLIS* LIZARDS OF BIMINI: RESOURCE PARTITIONING IN A COMPLEX FAUNA

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Abstract. The tiny island of South Bimini contains 4 species of lizards of the genus *Anolis*, a number surpassed only on the 4 largest islands of the Greater Antilles and on 2 very large and nearby satellite islands. These species are syntopic with respect to a two-dimensional area of the ground but divide the habitat according to perch height and perch diameter: *sagrei* is partly terrestrial but occurs more often on small and large low perches; *distichus* prefers the trunks and large branches of medium to large trees; *angusticeps* inhabits small twigs, especially at great heights; and *carolinensis* is found mostly on leaves or on the adjacent twigs and branches. The size classes of the species are staggered in such a way that the inter-specific classes which overlap most in habitat overlap least in prey size. Similarities in prey size and prey taxa for classes of the same species are somewhat greater than those expected on the basis of habitat and morphology alone. The distribution of the species among the vegetation communities of Bimini can be explained on the basis of perch height and diameter preference. Within the same species, the larger lizards usually eat larger food, fewer items, and in *sagrei* more fruit; and they have a greater average range of food size per digestive tract. One species (*distichus*) is extremely myrmecophagous: about 75–90% of its food items are ants. In 3 of the 4 species, subadult males take more food and average smaller prey than females of the same head length. That species (*distichus*) which takes the smallest food items and whose classes overlap the most in habitat preference with those of other species is least dimorphic in size between the sexes. It is suggested that such small, non-dimorphic species are best suited for insinuation into complex faunas, whereas larger, dimorphic forms are best for the colonization of empty areas. The usefulness of various measures of "overlap" and "specialization" is evaluated for this lizard association.

Less than 60 miles from the Florida shore lies the circular archipelago of Bimini, a tiny outpost of the West Indies fauna in general and the Bahaman fauna in particular. A scant 5 square miles in extent, it supports going populations of 4 species of anoline lizards, a number unrivaled on any other island of its size class in the West Indies and surpassed only on the much larger islands of the Greater Antilles: Hispaniola, Cuba, Jamaica, Puerto Rico, Gonave and the Isla de Piños. Far from containing a complicated array of mountains and valleys with concomitant areas of xeric and mesic vegetation, each with unique or nearly unique faunas, Bimini is almost totally flat and was covered in its natural condition with a fairly uniform "blackland" forest and with several types of beach, marsh or mangrove associations (Howard 1950). Not only do the anoles fail to be completely separable on the basis of vegetation types, but all 4 species are relatively common in the blackland forest or transitional regions, essentially "syntopic" with respect to a two-dimensional area of the ground. Part of the anomaly can be explained historically: Bimini is attached to the vast shelf known as the Grand Bahama Bank, an area of hundreds of square miles which almost certainly was largely exposed when the northern Bahamas were invaded by anoline lizards (Rand in prep., Williams in prep.). While thus being able to account for what would otherwise be a series of very improbable colonizations, the fact remains that the 4 species of Bimini are apparently organized into a stable and co-adjusted complex, and that the existing diversity, barring interference by man, appears to be far from ephemeral. Indeed, with respect to anoline lizards, the island of Bimini probably approaches as well or better than any other area the condition designated by MacArthur and Wilson (1963) as species "saturation."

The object of this study is to describe and document those characteristics of the 4 species, *Anolis sagrei, distichus, angusticeps* and *carolinensis,*

which apparently allow them to coexist on Bimini. The situation is complicated by the addition of a second series of variables, differences within the same species, not only between the age classes but between the sexes as well. The latter differences range from very striking to practically absent with respect to both morphology and behavior, a fact which makes the lizards of Bimini ideal for studying the possible ecological effects of potentially or actually competing species on sexual differences. The notions of "specialization" and "overlap" are evaluated in terms of the Bimini anoles. Finally, a comparison is made of modes of niche partitioning on Bimini with modes on islands whose anoline faunas are both richer and poorer.

HABITAT DIFFERENCES

One of the ways in which ecologists can often illustrate interspecific spatial differences is to list the animals which were seen in various "habitats" as defined by vegetation types, in the hope that at least partial two-dimensional allopatry of the species can be demonstrated. If this is done for 8 of the 9 vegetation types (the ninth, "whiteland," is only found over an extremely small area) which Howard[1] (1950) recognizes for South Bimini, a clear pattern of overlap results (Table 1). *Angusticeps,* the species seen in the fewest vegetation types (2), is always found with the 3 more widespread species. Likewise, *distichus,* inhabiting one more vegetation type, always coexists with the 2 more widespread species. *Carolinensis,* seen in 5 vegetation types, always occurs with the most widespread species, *sagrei,* found in 7 of the 8 communities. Thus the problem of the coexistence of 4 anole species on the Bimini archipelago, despite all its islands and vegetation types, simplifies to the problem of coexistence in the blackland and incipient blackland forest on South Bimini. The additional problem, that of explaining the degree of restriction of each species within the range of available vegetation types, does develop, however. It is clear that both questions can be most satisfactorily analyzed if a detailed study is made of microhabitat preferences within that vegetation type where the 4 species are most abundant, namely, the blackland forest.

Rand (1964) has pointed out that it is often the case that the habitat preferences of anoline lizards living in the same area are readily separated if perch height and perch diameter, his "structural habitat," are considered, either singly or especially in combination. Areas of blackland forest, including both interior and edges, were repeatedly censused during the period November 18 to 30,

[1] His mangrove community was split into *Rhizophora* and *Avicennia* dominated areas.

TABLE 1. *Anolis* species seen in the vegetation types of South Bimini as classified by Howard (1950). A = abundant relative to other areas where the species was seen. R = present but rarely seen. O = not observed.

Habitat	Species			
	angusticeps	*carolinensis*	*distichus*	*sagrei*
Blackland (interior)	A	R	A	A
Coccothrinax shrub	O	A	R-A	A
Mangrove (*Rhizophora*)	O	O	O	R
Mangrove (*Avicennia*)	O	R	O	R
Salicornia tide flats	O	O	O	R
Uniola strand	O	R	O	R
Coastal rock	O	O	O	O
Incipient blackland	A	A	A	A
Total habitats where seen	2	5	3	7

1966, between 9:00 A.M. and 4:30 P.M. (the time of greatest activity of the lizards for this part of the year), and the perch height and diameter of each lizard seen were recorded. Weather was sunny during nearly the entire observation period. In addition, the presence of the lizard on leaves or on the ground rather than on branches was noted when appropriate. If the lizard was moving, its position when first sighted only was used. If the movement was obvious escape behavior with reference to the observer, the observation was not counted. The observations gathered in this manner are catalogued by sex and age class in Tables 2–3.

Sagrei was the only species in which males could be distinguished from females at all ages (by the sharpness of the middorsal stripe); this resulted in 4 classes being recognized: adult males, females, subadult males (males the same size as females) and juveniles, arbitrarily designated as those individuals with head lengths less than 9 mm. (This is slightly lower than the size at which females contain oviducal or maturing ovarian eggs during periods of reproductive activity.) Females and subadult males could not be told apart in *angusticeps* and *carolinensis,* so had to be lumped. In the latter species, juveniles were considered to range up to 10 mm head length because of the much larger absolute size which this species attains. In *distichus,* the smallest of the species and the one with the least size dimorphism between the sexes, only two classes were recognized: adults-subadults and juveniles.

Table 4 lists the probability of difference in perch height and diameter for all combinations of intraspecific size and sex classes which could be distinguished in the field. Because sample sizes were sometimes less than 40 for at least 1 of the 2 classes being compared or were unequal, Kolmogorov-Smirnov tests could not be used (Siegel 1956). Instead, 2 × 2 chi-square tables were set

TABLE 2. Habitat observations for Bimini anoles.

	sagrei				distichus		angusticeps			carolinensis		
	adult males	sub-adult males	females	juveniles	adults sub-adults	juveniles	adult males	sub-adults females	juveniles	adult males	subadults females	juveniles
Number on branches	164	122	112	51	245	71	24	12	4	8	7	13
Number on leaves	3	5	10	3	0	0	2	0	0	5	22	23
Number on ground	10	44	35	78	1	1	0	0	0	0	0	0
Percent on greyer bark	80.3	80.0	75.3	84.6	84.8	79.1	92.3	84.6	100.0			
Percent on redder bark	17.7	20.0	22.6	10.3	14.4	17.9	7.7	15.4				
Percent on green bark	2.0		2.1	5.1	0.8	3.0						

TABLE 3. Frequency of structural habitat categories for various classes of Bimini anoles.

Perch height (feet)	Perch diameter (inches)									
	$>4\frac{1}{4}$	$2\text{-}4\frac{1}{4}$	$\frac{3}{4}\text{-}1\frac{3}{4}$	$\frac{1}{8}\text{-}\frac{5}{8}$	leaves	$>4\frac{1}{4}$	$2\text{-}4\frac{1}{4}$	$\frac{3}{4}\text{-}1\frac{3}{4}$	$\frac{1}{8}\text{-}\frac{5}{8}$	leaves
	sagrei adult males					*sagrei* subadult males				
>8.5	1	0	1	0	0	0	0	0	0	0
5.5–8.5	4	8	4	0	<1	0	1	0	0	0
3–5.25	10	26	7	0	1	2	10	11	4	2
<3	10	14	6	2	0	9	15	15	5	<1
ground	6	0	0	0	0	26	0	0	0	0
	distichus adults-subadults					*distichus* juveniles				
>8.5	3	4	0	0	0	0	0	14	0	0
5.5–8.5	9	17	1	0	0	3	21	7	0	0
3–5.25	17	19	2	0	0	13	15	10	0	0
<3	13	13	0	0	0	0	13	4	0	0
ground	<1	0	0	0	0	<1	0	0	0	0
	angusticeps juveniles					*carolinensis* adult males				
>8.5	0	0	25	25	0	0	0	9	0	0
5.5–8.5	0	0	0	25	0	9	9	18	0	9
3–5.25	0	0	0	25	0	0	9	0	0	27
<3	0	0	0	0	0	9	0	0	0	0
ground	0	0	0	0	0	0	0	0	0	0
	sagrei females					*sagrei* juveniles				
>8.5	0	0	0	0	0	0	0	0	0	0
5.5–8.5	0	2	3	0	0	0	0	0	0	0
3–5.25	2	9	11	1	2	0	1	2	1	1
<3	10	18	10	6	4	6	7	17	5	2
ground	22	0	0	0	0	60	0	0	0	0
	angusticeps adult males					*angusticeps* females-subadults				
>8.5	0	11	14	11	0	0	0	42	17	0
5.5–8.5	4	7	21	4	0	0	0	25	8	0
3–5.25	4	4	7	0	7	0	0	0	8	0
<3	4	0	4	0	0	0	0	0	0	0
ground	0	0	0	0	0	0	0	0	0	0
	carolinensis females-subadults					*carolinensis* juveniles				
>8.5	0	4	0	0	4	0	0	0	0	5
5.5–8.5	0	4	8	4	23	0	0	5	5	22
3–5.25	0	0	4	0	42	0	0	0	5	41
<3	0	0	0	0	8	0	0	3	0	14
ground	0	0	0	0	0	0	0	0	0	0

up in which the intervals were determined by noting the point of greatest difference in the cumulative frequencies. When the expected value of the observations in 1 or more of the 4 boxes was below 5, binomial tests were performed to determine the exact probability of differences as great or greater than those observed. Table 5 lists the significance of difference in occurrence on leaves for certain class combinations between and within the 4 species, as determined by the same tests.

A verbal summary of the differences documented in these tables for each of the 4 species as well as a description of escape behavior is given below. With the exception of those for *angusticeps*, my observations are extensions of those made by Oliver (1948) for the same species on Bimini.

A. sagrei.—This is by far the most terrestrial of the anoline lizards of Bimini. 167 out of 637 observations for this species were of lizards on the ground or on low rocks, as compared to only 2 such observations (both *distichus*) for all the other species combined. All classes of this lizard occurred at significantly lower heights than did any class of each of the other species. Within the species, adult males occurred significantly

TABLE 4. Significance level of differences in perch height (top right) and diameter (bottom left) for classes of the 4 species found on Bimini. $O = > 0.05$; $1 = < 0.05$; $2 = < 0.01$; $3 = < 0.001$. ( ) = class heading column has greater values. * = exact test used

Height / Diameter	sagrei adult males	sagrei subadult males	sagrei females	sagrei juveniles	distichus adults and subadults	distichus juveniles	angusticeps adult males	angusticeps females and subadult males	angusticeps juveniles	carolinensis adult males	carolinensis females and subadult males	carolinensis juveniles
sagrei adult males		3	3	3	(3)	(3)	(3)	(3)	(2)*	(3)	(3)	(2)
sagrei subadult males	(3)		0	3	(3)	(3)	(3)	(3)	(3)*	(3)	(3)	(3)
sagrei females	(3)	0		3	(3)	(3)	(3)	(3)	(3)*	(3)	(3)	(3)
sagrei juveniles	(3)	(1)	(2)		(3)	(3)	(3)	(3)	(3)*	(3)	(3)	(3)
distichus adults and subadults	2	3	3	3		(3)	(3)	(3)	(1)*	(1)	(1)	(0)
distichus juveniles	(1)	2	3	3	(3)		(2)	(1)*	(0)*	(0)*	0	3
angusticeps adult males	(3)	(2)	(2)	(1)	(3)	(3)		(0)*	0*	1*	2	3
angusticeps females and subadults	(3)	(2)	(2)*	(1)	(3)	(3)	(0)		0*	2*	3	3
angusticeps juveniles	(3)*	(2)*	(2)*	(1)*	(3)*	(3)*	(2)*	(0)*		0*	0*	1*
carolinensis adult males	(2)*	(0)*	(0)*	(0)*	(3)*	(3)*	0*	0*	0*		0*	3
carolinensis subadult males and females	(3)*	(1)*	(1)*	(0)*	(3)*	(2)*	(0)*	0*	0*	(0)*		0
carolinensis juveniles	(3)*	(3)	(3)	(3)	(3)	(3)	(1)*	(0)*	0*	(0)*	(1)*	

TABLE 5. Significance level for difference in occurrence on leaves. S = *sagrei;* D = *distichus;* A = *angusticeps;* C = *carolinensis;* sa = subadult males; ♂ = adult males; ♀ = females; juv = juveniles. Significance levels as in Table 4.

greatest % on leaves	smallest % on leaves	significance level
♀ S	♂ S	0
♀ S	sa S	0
♀ S	juv S	0
juv C	♂ C	0
juv C	♀ C	0
♀ C	♂ C	0
C	S	3
S	D	2
A	S	0
C	D	3
C	A	3
A	D	2

higher than did any of the other classes. Subadult males and females had nearly identical height distributions, but both occurred significantly higher than did juveniles.

Sagrei individuals occupied a wide variety of perch diameters, being found on both tall and short plants. Adult males occupied perches of significantly greater diameter than did any other class of lizard except adult-subadult *distichus.* Females and subadult males again had nearly identical distributions, and were surpassed in diameter by both classes of *distichus.* They did, however, perch on significantly larger diameters than all other classes but adult male *carolinensis.* Juveniles occurred on the smallest perches of all. About 3.3% of all individuals seen were perched on leaves, significantly greater than the value for *distichus* but about the same as that for *angusti-*

ceps; no significant intraspecific differences in this regard were found.

The escape behavior of this species was usually to jump onto the ground rather than ᴛo up the tree. The latter is seldom possible anyway, since low plants so often serve as perches.

A. distichus.—This species occurred usually at medium heights nearly always on the trunks of fairly large trees. The category of adults-subadults was seen at significantly lower heights than all classes of the 2 remaining species except *carolinensis* juveniles. Juveniles of *distichus* occurred significantly higher than did larger individuals of the same species and significantly lower than only the 2 classes of larger *angusticeps.*

Adult-subadult *distichus* perched on significantly larger diameters than did any other class of lizard. Juvenile *distichus* were on significantly larger diameters than all classes but *sagrei* males and, of course, adult-subadult *distichus.* Out of 329 observations, none were of individuals on leaves.

Escape behavior of this species was usually to run rapidly around the back of the tree and then up (most often) or down; they could hardly ever be forced onto the ground. Rand (1962) makes the same observations for this species in Hispaniola. Both *distichus* and *sagrei* have proportionately long legs, clearly an adaptation for running rapidly over relatively flat, broad surfaces.

A. angusticeps.—This species usually occurred fairly high in the crown on branches of quite small diameter. Less often, individuals were seen at medium to low heights but nearly always on small perches. The classes of adult males and subadults-females were seen at significantly greater heights than any class of each of the other species; the number of juveniles seen (4) was too low to

achieve statistical significance in most of the comparisons.

The perch diameters of each of the 3 classes of *angusticeps* were significantly smaller than any class of *sagrei* and *distichus* but very similar to those for *carolinensis*. Only adult males had significantly larger perches than did juveniles. No significant differences in either perch height or diameter could be detected between males and subadults-females with a sample of this size.

In contrast to the rapid escape behavior of the other three species, *angusticeps* relied on stealth and deception to avoid possible threats. At the approach of the observer, individuals often squirrelled carefully around the back of the twig until completely hidden from view. Short-legged and narrow-headed, the species is admirably suited for its "tightrope walking" existence and surreptitious behavior. The crypticity of this species undoubtedly made it appear much rarer than it actually was.

A. carolinensis.—In perch height this species seems intermediate between *distichus* and *angusticeps*. Adult males were recorded at significantly greater heights than were juveniles; this trend may be partially an artifact of observation, since small green lizards are especially difficult to pick out from the foliage at great heights, although the difficulty applies to a lesser degree to larger individuals as well.

In diameter, perches of *carolinensis* juveniles were significantly smaller than those of any class of *sagrei* or *distichus;* diameters of females-subadults were smaller than all those classes but *sagrei* juveniles. The diameters of males were significantly exceeded only by those of *sagrei* adult males and the 2 classes of *distichus*. Only *carolinensis* females-subadults had significantly greater diameters than did juveniles of the same species.

Although very similar to *angusticeps* in perch diameter and height, this species differs strikingly from the former in its occurrence on leaves. Over 2/3 of the *carolinensis* seen were in foliage, either perched on a very large leaf, particularly those of *Coccothrinax* or other Palmae, or straddling a cluster of small ones. In contrast, 4.4% of the *angusticeps* were recorded on leaves. *Carolinensis* thus occurs on leaves a significantly greater proportion of the time than does any other species (Table 5). No significant intraspecific differences in this regard could be demonstrated. The bright green color of all classes of this species serves as very effective cryptic coloration.

When frightened, large *carolinensis* usually rapidly climb higher into the leafy portion of the canopy or sometimes plunge into the central, darker cores of the crown. Juveniles more often

were seen in twisted tangles or clumps of vines, particularly those of *Ipomoea*. These lizards attempt escape most often by scurrying into such clumps and were sometimes observed changing color to a very dark brown shortly thereafter.

Because the body color of *carolinensis* is so indicative of the color of its substrate, it was thought that the slightly different body colors of the other species might be correlated with their backgrounds. *Sagrei* is the brownest of the three and so might be expected to prefer trees with browner or redder bark than would the "mouse-grey" (Oliver 1948) *distichus* or the grey-white *angusticeps*. On all but the first 2 days of field study, the bark color of the perches of each individual was recorded. Because of the tremendous amount of intergradation of color and the often blotchy nature of the perches, it was thought realistic to divide the color observations into only 2 groups, one ranging from white through various shades of grey-brown, and the other ranging from reddish brown to red. Nearly all trees found on Bimini fall under the first category, with *Bursera simaruba* being the most common tree by far in the second. The frequencies of observations in the white to grey-brown class range from 0.753 to 1.0 (Table 2). The class occurring the most often on reddish-brown bark was female *sagrei*. However, juvenile *distichus* was next in frequency on this color bark. *Angusticeps* were seen most on grey-brown to grey-white bark. However, the differences are so slight that none can be proven statistically significant with this sample size (Table 6).

One final way in which the habitats of Bimini anoles might be expected to differ is in microclimatic characteristics. These were not recorded in this study because they seemed both slight and ancillary to structural habitat differences. It is not surprising that climatic differences should be small, since most vegetation types on Bimini are quite open and rather dry. *Sagrei* was seen almost with equal frequency in very open situations and in the forest interior. *Distichus* likewise was found in both situations but seemed to become active at a slightly later part of the morning than did *sagrei*. *Angusticeps* was more often seen in edge situations and when located in the forest interior, was usually high in the canopy. *Carolinensis* was seen usually along edges or in the open but possibly this was an artifact, since lizards on the surface of leaves in the forest canopy usually escape detection from below. However, it should be remembered that insolation and the concomitant production of new growth and insect prey is greatest along edges, and thus species which feed in or near the leafy crown are more

TABLE 6. Significance level for difference in occurrence on greyish as opposed to reddish bark. Abbreviations as in Table 5.

Greatest % on greyish bark	Greatest % on reddish bark	Significance level
♂, ♀, sa D	♂ S	0
♂ S	juv D	0
♂, ♀, sa D	sa S	0
sa S	juv D	0
♂, ♀, sa D	♀ S	0
juv D	♀ S	0
♂, ♀, sa D	juv S	0
juv D	juv S	0
♂, ♀, sa D	juv D	0
♂ A	♂ S	0
♂ A	sa S	0
♂ A	♀ S	0
♂ A	juv S	0
♂ A	♀ A	0
♂ A	♂, ♀, sa D	0
♂ A	juv D	0
D	S	0
A	S	0
A	D	0

likely to occur along edges than in bushy understory. It is quite possible that there are average temperature differences between the species at a given time in particular situations, but these would appear to be predictable from a knowledge of their respective structural niches.

As has been shown, it is in properties of the structural habitat that the species and intraspecific classes of Bimini anoles can be best separated. With that information, it is now useful to go back to the vegetation types of Table 1, to see how the preferences of the four species can best be explained. *Angusticeps* occurs only in blackland and incipient blackland; it is there and there alone that large, continuous volumes of its preferred structural habitat, relatively high twigs, are found. *Distichus* prefers the trunks of large trees; these are found mostly in the blackland communities, but the rather good-sized trunks of *Coccothrinax*, dominating the *Coccothrinax*-shrub zone, are also highly preferred perches. *Carolinensis* seems to occur wherever there are large amounts of leafy growth: only in the *Salicornia* tide flats or the *Rhizophora* mangrove has the species not been seen; these areas are low in the production of new leafy material. Finally, *sagrei* has been seen in all but the coastal rock zone. That area is nearly devoid of even moderately high vegetation. It is possible that *sagrei* occurs as a spillover into the *Salicornia* and *Rhizophora* areas; certainly it is not at all common there. Likewise, it appears possible that some of the other species could be found occasionally in areas outside those listed in Table 1, were the observation period sufficiently long. Pianka (1966) has found that a measure of

"plant volume diversity," a measure of vertical foliage diversity similar to those used by MacArthur and his colleagues (see MacArthur, Recher and Cody 1966 for the relevant literature), is well correlated with lizard species numbers in the deserts of North America. He was able to relate this correlation, at least in part, to the differing microhabitat preferences of the species. From the foregoing, it is easy to see that the anoline lizards of Bimini should also probably fit such a relationship. The variety and evenness in abundance of plant forms are greatest in the blackland forest and transition and least in the *Salicornia* and beach vegetation types.

Preference for a certain structural habitat and thus vegetation type can also be invoked to explain the distribution of the 4 species on other islands of the Bimini group. Two of the 4 species, *sagrei* and *carolinensis,* occur in abundance on North Bimini; *angusticeps* was reported as collected there at least once (in the 1940's, MCZ 46066) but was not seen there during this study and is not represented in any of the other large collections of *Anolis* which I examined. *Angusticeps* and *distichus* have not been reported anywhere else in the Bimini group. None of the vegetation types in which *angusticeps* or *distichus* occur on South Bimini is present anywhere else but on that island (Table 1; Howard 1950). *Sagrei* has also been seen and collected on East Bimini by myself and several others; other records are from South Cay (Carnegie 34168–9) and Tokas Cay (Carnegie 32451). Vegetation on these islands is, with the exception of planted *Casuarina* trees, low and shrubby.

FOOD DIFFERENCES

Prey size. While partially non-overlapping in structural habitat, classes of the 4 species could utilize still more discrete resources if those which overlap most in structural habitat were somehow selecting different foods. Since the head and body sizes of the different classes vary considerably and are often especially unlike among the pairs most overlapping in foraging habitat (see below), it is reasonable to expect important differences in the size and taxonomic affinity of the food taken. The diets of the 4 species were analyzed by collecting specimens in the observation area and cataloguing all items found in the digestive tracts by size and taxon. Only a few of the agile adult male *carolinensis* could be captured; hence, these are not included in the discussion to follow. Likewise, 3 of the 4 classes of *angusticeps* were undercollected: results from these classes (all but adult males) are included with reservations. The significance of differences in prey size distributions

TABLE 7. Significance level of differences in prey size. Abbreviations as in Table 5.

Greatest % large prey	Smallest % large prey	Significance level
♂ D	sa D	3
♂ D	♀ D	3
♂ D	juv D	3
♀ D	sa D	3
sa D	juv D	3
♀ D	juv D	3
♀ C	sa C	0
juv C	sa C	0
♀ C	juv C	1
sa A	♂ A	3
♂ A	♀ A	1
♂ A	juv A	2
sa A	♀ A	3
sa A	juv A	3
♀ A	juv A	0
♂ S	sa S	3
♂ S	♀ S	3
♂ S	juv S	3
♀ S	sa S	3
sa S	juv S	0
♀ S	juv S	3
sa S	♂, ♀, sa D	3
♀ S	♂, ♀, sa D	3
juv S	juv D	0
♂ S	♂ A	3

was determined by use of the Kolmogorov-Smirnov one-tailed test (Table 7).

Intraspecific differences. Within all 4 species there is the unsurprising trend that larger individuals ate larger food than did smaller lizards (Figs. 1–4). This tendency is significant for adult male *sagrei* and adult male *distichus* versus all other intraspecific classes. Subadult male *angusticeps,* on the other hand, took significantly larger food than did adult males; however, as mentioned, the number of lizards examined was very low. Similarly, it was usually possible to show that juveniles took significantly smaller food than did all other intraspecific classes; scattered exceptions are probably the result of small sample size. If the proportions of the various prey size classes are plotted by volume instead of by individual prey items, differences in the distributions are accentuated (Figs. 1–4).

More interestingly, in 3 of the 4 species (all but *angusticeps*), subadult males, defined as those males with head sizes ranging over the same values as do the head sizes of females, took more small food items than did females (Figs. 1–4). In the case of *carolinensis,* the difference is not significant, but it is highly significant for *sagrei* and *distichus,* those species with greatest sample sizes (Fig. 5). This result is all the more surprising because it is the opposite of most of those obtained in previous studies on similar comparisons (Schoener 1967, Schoener and Gorman 1968). In the study on *A. richardi* and *aeneus* of Grenada,
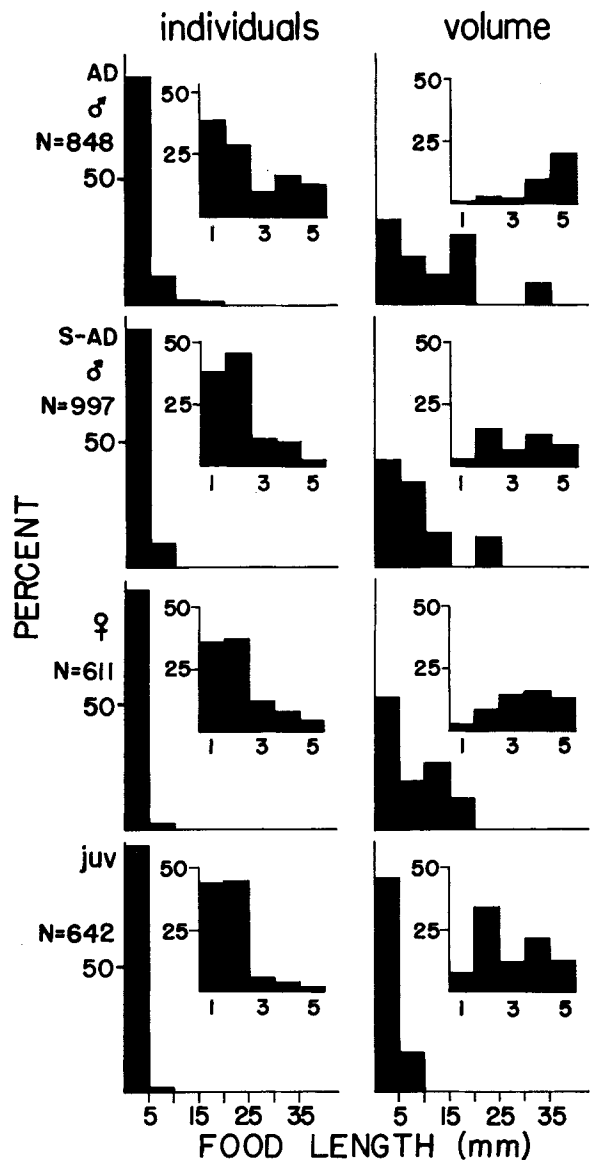

FIG. 1. Distribution of prey by frequency and volume according to prey length for classes of *sagrei.*

4 hypotheses were suggested to account for the greater number of small prey in the diets of females than in subadult males. The first, that it is somehow associated with the slightly different habitat preferences of the sexes, must be ruled out, for subadult males and females of *sagrei* are practically indistinguishable in their habitat preferences. The second, that one sex has a preference for larger prey, or the third, that one sex might have a greater probability of overcoming large prey, are both unlikely because the mechanisms involved in the establishing of such differences favor the male taking the larger prey. By far the most likely hypothesis is the fourth, namely, that individuals of one sex have a greater
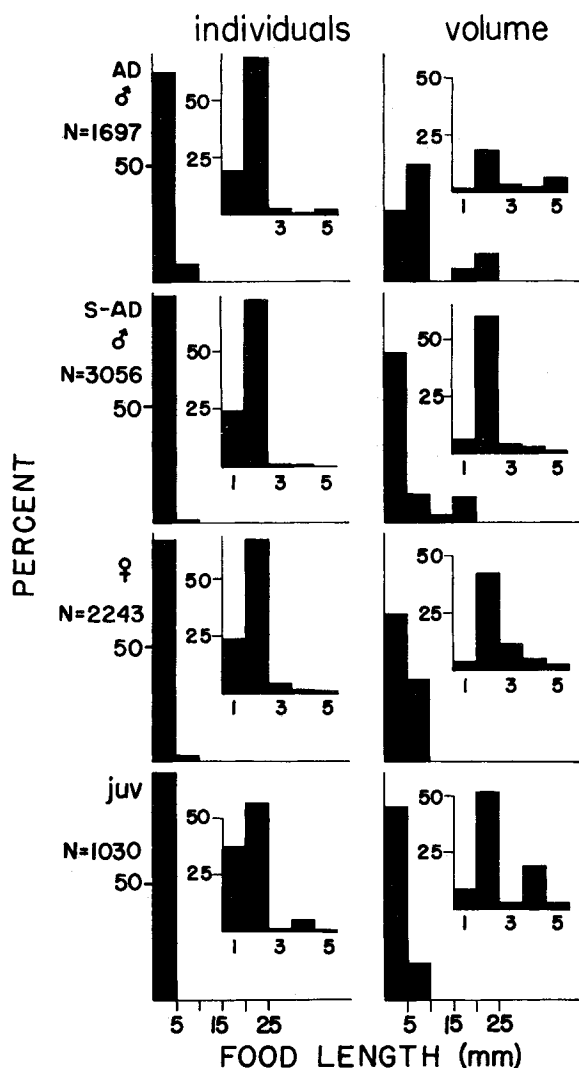
FIG. 2. Distribution of prey by frequency and volume according to prey length for classes of *distichus*.

FIG. 3. Distribution of prey by frequency and volume according to prey length for classes of *angusticeps*.

energy requirement per unit time than do those of the other sex which have the same head size. Depending on the relative abundance of small and large food, that sex might find it necessary to take more items from classes of food whose net yield in energy/unit time is less than from other items of preferred food. It was pointed out for *richardi* and *aeneus* that males of the same head length as females tended to have slightly smaller snout-vent lengths, and on that basis alone, would be expected to have slightly smaller energy requirements. If regressions of head length on snout-vent length for the 4 Bimini species are examined (Figs. 6–9), it can be seen that in all cases, intersexual comparisons parallel those in the Grenada species, being most striking in *angusticeps* and least so in *carolinensis*. Yet the tendency in prey size is
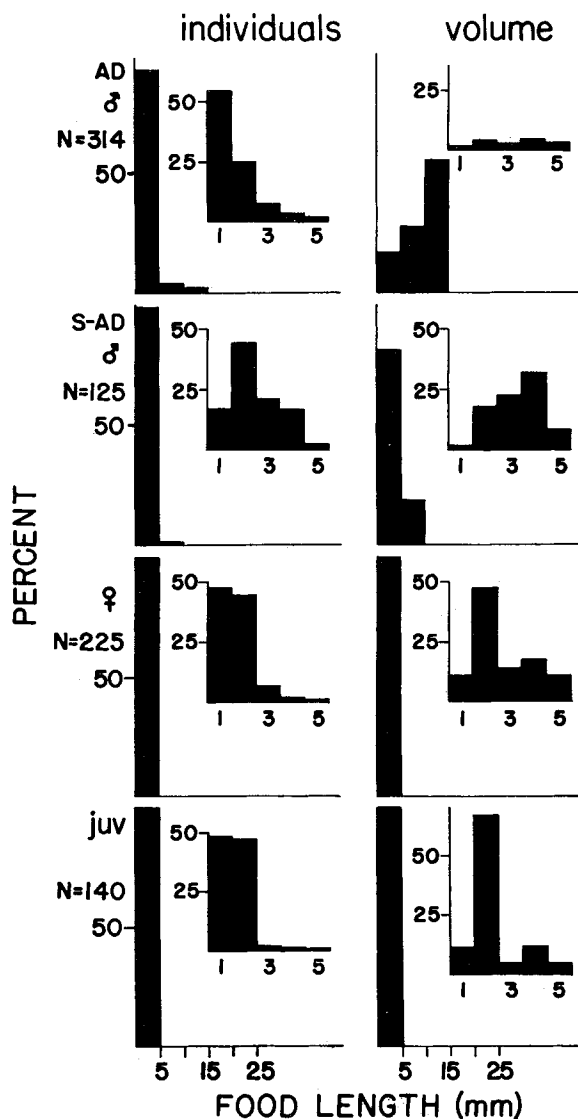
reversed. Either there are differences in the relative frequency of small and large prey between Grenada and Bimini, and/or subadult males on Bimini are taking more food per unit time despite their slightly smaller size. Indeed the latter possibility is exactly what is happening: the volume of food per digestive tract of the females averages about 2/3 the volume for the subadult males for *sagrei* and *distichus* and about 1/3 the volume for *carolinensis* (Table 8). In *angusticeps*, the values are very similar, but sample size is probably too small to be conclusive. Furthermore, the volume trend is the reverse of the situation on Grenada. However, in the latter species, as well as *conspersus* of Grand Cayman, females contained oviducal or maturing ovarian eggs, and hence, prob-
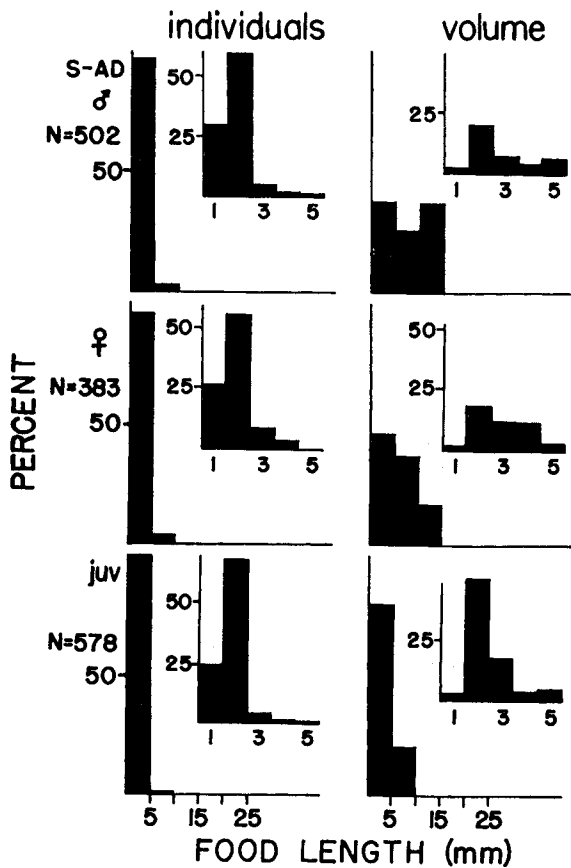
individuals   volume

FIG. 4. Distribution of prey by frequency and volume according to prey length for classes of *carolinensis*.
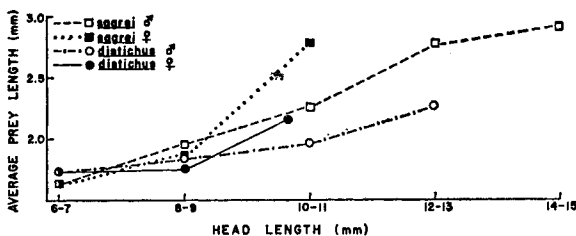

FIG. 5. . Relationship of average prey length to predator head length for *distichus* and *sagrei*.

ably needed to take in large amounts of food for reproduction.   On Bimini, on the other hand, females did not contain eggs in this condition, and in fact gonads are inactive in *sagrei* and *distichus* on Bimini during the time of year (November) when the lizards were collected (G. Gorman, personal communication).   Since subadult males are far from their maximum size, they undoubtedly need larger amounts of food for growth than do females, and hence, during the non-breeding season, should require more food per unit time than females.   In summary, if we assume that greater

energy requirements per unit time entails taking more small prey in most situations, then the opposing results on Bimini and Grenada can be explained by a single hypothesis.

Interspecific differences.   It is expected that the greater the differences in head length or in head volume, the greater the differences in distributions of prey size between species.   The anoles of South Bimini differ in the maximum head length attained: male *carolinensis* reaches a maximum head length of about 19.7 mm, and the largest third of the males of several museum collections (Museum of Comparative Zoology, Carnegie Museum, American Museum of Natural History, A. Schwartz) average 18.0 mm in head length; *sagrei* and *angusticeps* males are very similar in head length, with maxima of about 15.5 mm and 16.4 mm, respectively, and with the largest third averaging 14.4 mm and 15.7 mm, respectively; male *distichus* have the smallest head lengths, reaching a maximum of about 13.5 mm with largest third averaging 12.6 mm.   Adult females and other smaller classes are more overlapping in their head length distributions.   These facts in themselves are not very interesting.   For example, it is of little importance that juvenile *sagrei* and juvenile *distichus* have similar head lengths, since their structural niches are almost discrete.   We need to ask: What are the differences in head lengths and corresponding prey size distributions for those interspecific combinations of classes whose habitats overlap the most?   Or conversely, are the intraspecific habitat differences of the age and sex classes arranged in such a way as to minimize competition between those lizards which have similar distributions of prey size?

In order to answer these questions quantitatively, it is necessary to define what is meant by overlap, or, more operationally, how it is to be measured.   In choosing a measure for a given niche dimension, 2 sources of arbitrariness arise. First, a particular equation has to be constructed which compares the relative or absolute number of observations for 2 or more species over a series of categories into which the dimension in question has been divided.   Thus we may (and will) use the simple measure

$$D = 1 - \frac{1}{2} \sum_{i=1}^{n} |p_{x,i} - p_{y,i}|$$

where $p_{x,i}$ and $p_{y,i}$ are the frequencies for species x and y, respectively, for the ith category.   Alternatively, we may try a more complicated measure such as Horn's (1966) R_o or Morisita's C_λ (1959, discussed by Horn 1966).   The choice from these measures is not totally arbitrary of course, but it is guided by a combination of mean-
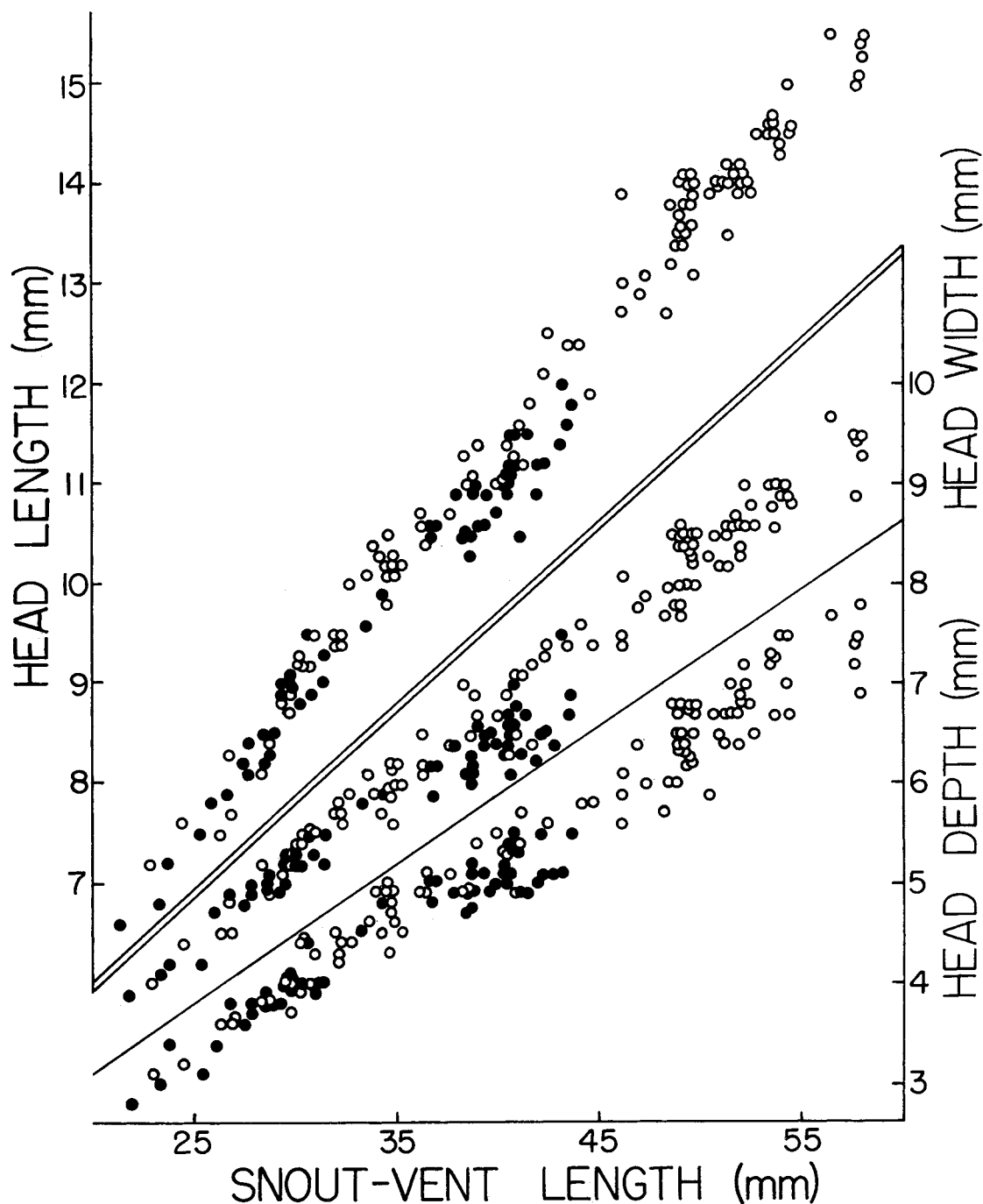
FIG. 6. Regressions of head length, width, and depth on snout-vent length for specimens of *sagrei* used in this study. Head length was taken as the distance from the anterior edge of the ear opening to the tip of the snout. Head width was taken as the horizontal line joining the angles of the jaw. Head depth was measured from the center of the vertical plane whose upper edge is marked by the posterior margin of the frontal bones as indicated by a ridge in the preserved animal.
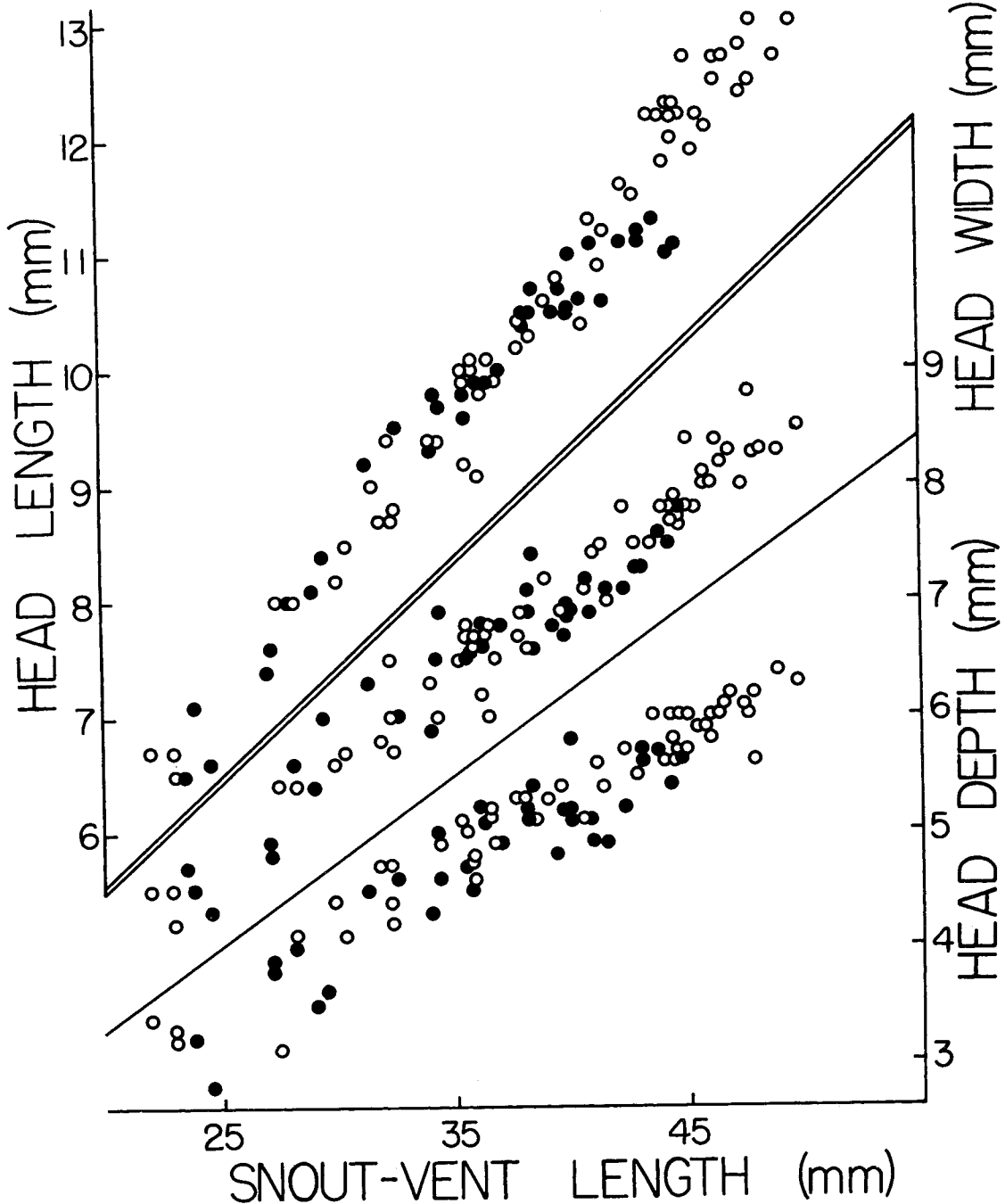
FIG. 7. Regressions of head length, width, and depth on snout-vent length for specimens of *distichus* used in this study. Measurements as in Fig. 6.

ing and practicality. For example, Morisita's measure,

$$C_\lambda = \frac{2 \sum\limits_{i=1}^{n} x_i y_i}{(\lambda_x + \lambda_y)\, XY}$$

where x_i is the number of observations for species x and y_i the number of observations for species y in category i, X and Y are the total number of observations for species x and y, respectively, and

$$\lambda_x = \frac{\sum\limits_{i=1}^{n} x_i (x_i - 1)}{X(X-1)} \quad \lambda_y = \frac{\sum\limits_{i=1}^{n} y_i (y_i - 1)}{Y(Y-1)},$$

can be interpreted as the probability that 2 observations drawn randomly from populations X and
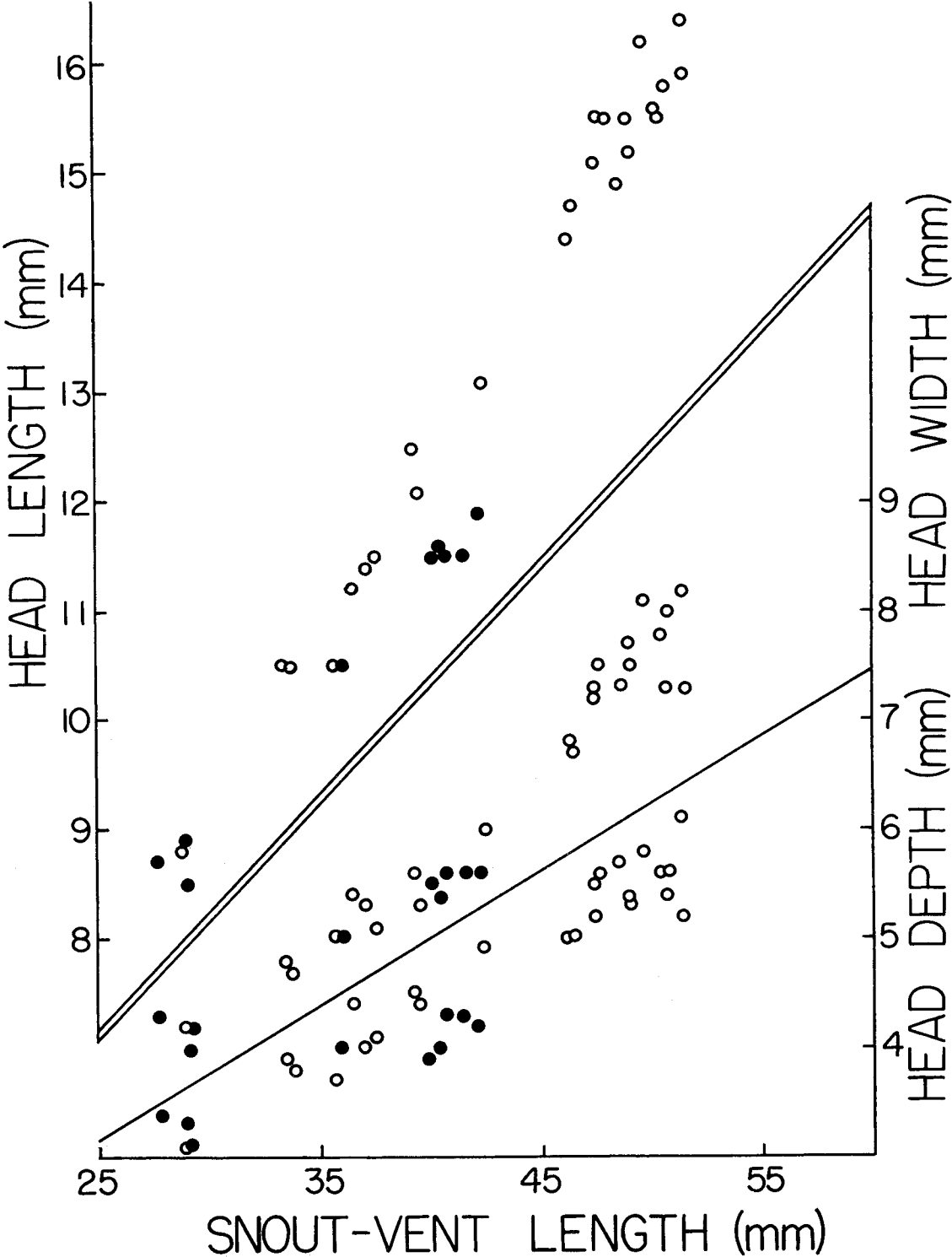
FIG. 8. Regressions of head length, width, and depth on snout-vent length for specimens of *angusticeps* used in this study. Measurements as in Fig. 6.
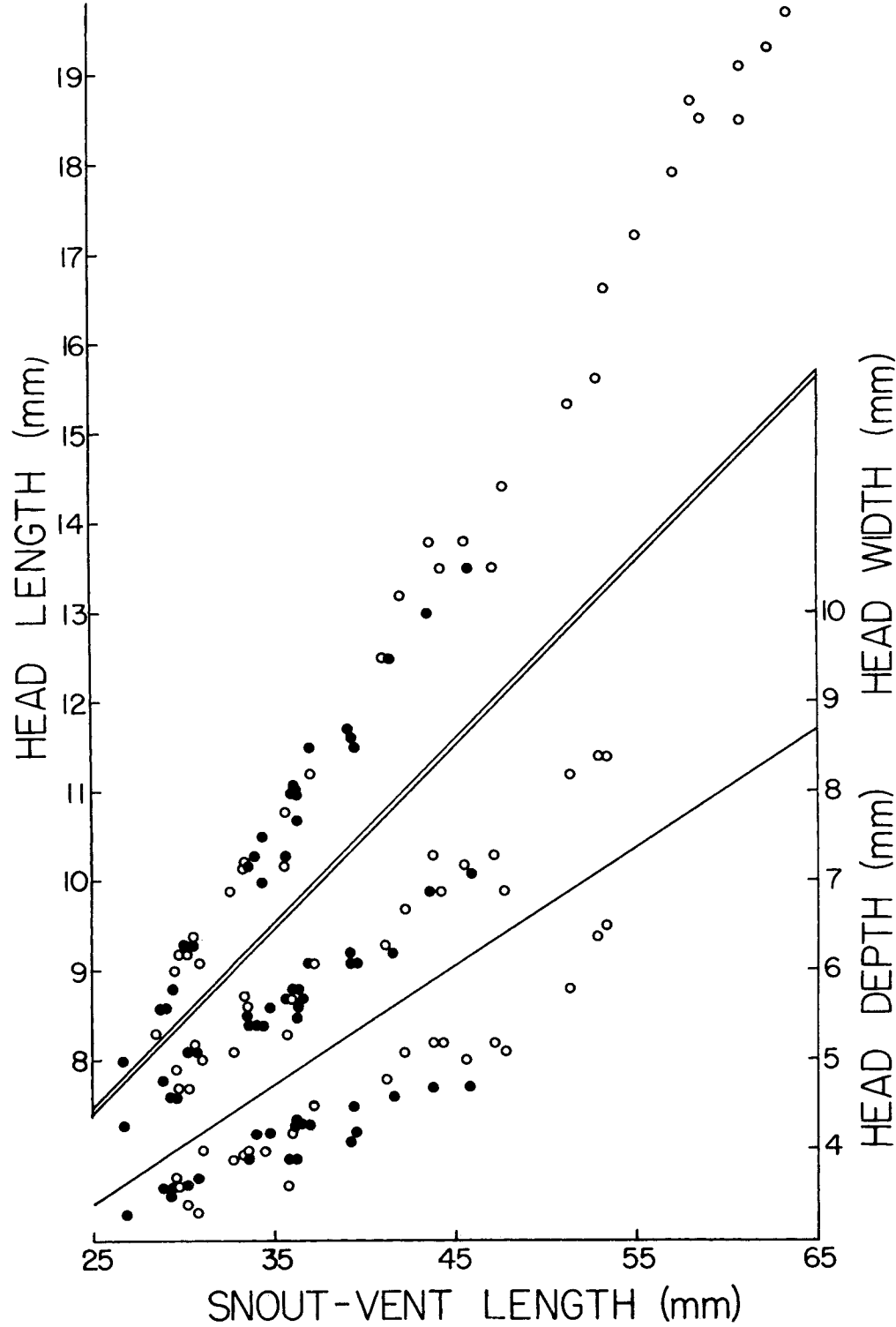
FIG. 9. Regressions of head length, width, and depth on snout-vent length for specimens of *carolinensis* used in this study. Points above 17 mm taken from museum specimens. Measurements as in Fig. 6.

TABLE 8. Diet characteristics of classes of Bimini anoles. Abbreviations as in Table 5. σ = standard deviation.

Class	Number examined	Head length range (mm)	Mean volume food per tract (mm)³	H"	Food size range (mm)		Number food items	
					mean	σ	mean	σ
S ♂	60	>11.9		3.1866	8.2	6.6	14.4	19.1
S sa	37	9–11.9	52.5	3.0719	6.5	3.9	26.9	19.6
S ♀	40	9–11.9	37.3	3.2853	5.1	3.3	15.4	11.9
S juv	27	6– 8.9		3.1213	3.3	1.8	24.6	10.8
D ♂	23	>11.3	106.8	0.9589	7.2	4.4	69.4	50.5
D sa	22	9–11.3	61.9	0.6787	4.8	3.1	138.2	110.1
D ♀	29	9–11.3	47.4	0.9408	5.0	1.7	79.5	73.5
D juv	18	6– 8.9		1.4414	3.4	2.0	60.1	34.3
A ♂	16	>11.9	78.1	2.5221	5.5	3.5	18.5	31.1
A sa	6	9–11.9	26.8	2.4559	3.2	1.3	20.8	24.5
A ♀	6	9–11.9	22.7	2.1082	2.7	0.8	37.5	41.1
A juv	4	6– 8.9		1.0827	2.0	1.4	35.0	44.1
C sa	8	10–13.5	104.7	1.9048	5.5	2.4	62.5	89.1
C ♀	18	10–13.5	36.1	2.4321	3.9	8.2	22.9	15.3
C juv	13	8– 9.9		2.3145	3.3	2.0	46.6	31.0

Y will both belong to the same category, relative to the probability of randomly drawing two observations of the same category from X or Y alone (Horn 1966); a disadvantage is that for 2 sample distributions of the same shape and position, C_λ is dependent on sample size, particularly when X, Y, or both are very small.

A more serious source of arbitrariness can arise in the choosing of categories. Depending on the number and boundaries of these categories, overlap between the same 2 distributions could range from zero to very nearly one. For example, if the subdivisions are too gross, the entire frequency distribution of both species might be incorporated into one category; thus even if the distributions were entirely discrete, overlap would be considered equal to one. On the other hand, if the subdivisions are too fine, and if measurements can be made very precise relative to the number of measurements taken, there could be so little overlap in any of the categories as to make overlap values very close or equal to zero, regardless of the distributions. Ideally, if the dimension under consideration is continuous or is finely subdivided, the frequency distributions might be approximated by functions and the area of overlap calculated by an integration technique after suitable normalization. Very often, however, as in this study, practical considerations preclude the use of this procedure: functions may not be continuous or niche characteristics might not be able to be linearly ordered, a suitable distribution function may not be obtainable or could result in the masking of significant differences if it is too approximate, and the functions, if found, might not be integrable analytically.

More often than not, the problem is partially solved for the ecologist in that boundaries are set up by the precision of the measuring system being used, the latter, in turn, usually being determined by practical considerations having nothing to do with setting up an overlap measure. This is true for 2 of the 3 niche characteristics being considered in this study, namely, prey taxa and prey length. In the case of the first, prey were subdivided into a number of taxa, mostly on the ordinal level, chosen because they were easily recognizable even in nearly digested material. Twenty-two such categories were used (Table 10). Similarly, the available prey length intervals were limited partially by the degree of accuracy possible for estimates of the lengths of items in the digestive tract. Thus small prey could not be placed into length intervals less than a millimeter, and the estimates for longer prey ought to be even less accurate. Furthermore, the number of large prey (> 5 mm) is relatively so low that excessive subdivision is pointless. The intervals finally decided upon were 1, 2, 3, 4, 5, 6–10, 11–15, 16–20, 21–25, 26–30, and 31–35 mm. This procedure is nearly equivalent to the technique of partitioning the area under a frequency curve in order to approximate the integral of its function; larger intervals are needed at the long right tail to compensate for the fact that, with this sample size, the distribution is not smooth over high values.

The intervals for the "structural niche" were more difficult to select, since perch height and diameter could be measured with great accuracy relative to the number of observations that were taken. Originally it was thought desirable to measure overlap with regard to height and diameter separately. Intervals were chosen by beginning at the greatest value of the particular dimension and proceeding toward smaller values,

TABLE 9. Overlap values for classes of Bimini anoles. Abbreviations as in Table 5.

Overlap pair		Prey size by item (D)	Prey size by item (Cλ)	Prey size by volume (D)	Prey taxa (D)	Structural habitat (D)	Structural habitat (Cλ)
♂ S	sa S	.835	.946	.539	.766	.573	.686
♂ S	♀ S	.848	.973	.668	.739	.608	.729
♂ S	juv S	.795	.944	.407	.668	.304	.251
♂ S	♂, ♀, sa D	.590	.735	.360	.440	.687	.899
♂ S	juv D	.674	.831	.328	.544	.659	.826
♂ S	♂ A	.802	.943	.436	.513	.384	.416
♂ S	♀, sa A	.775	.935	.343	.486	.051	.088
♂ S	♀, sa C	.689	.835	.476	.419	.134	.088
♂ S	juv A	.715	.917	.189	.290	.011	.047
♂ S	juv C	.600	.749	.329	.306	.095	.060
sa S	♀ S	.879	.983	.659	.787	.871	1.009
sa S	juv S	.943	.996	.575	.833	.634	.753
sa S	♂, ♀, sa D	.754	.904	.646	.372	.370	.415
sa S	juv D	.838	.961	.493	.494	.396	.420
sa S	♂ A	.782	.902	.580	.528	.231	.211
sa S	♀, sa A	.919	.995	.528	.481	.041	.019
sa S	♀, sa C	.853	.965	.782	.452	.079	.083
sa S	juv A	.871	.986	.375	.323	.041	.146
sa S	juv C	.764	.914	.519	.353	.097	.092
♀ S	juv S	.846	.975	.613	.823	.562	.685
♀ S	♂, ♀, sa D	.673	.836	.446	.250	.391	.481
♀ S	juv D	.759	.905	.445	.362	.421	.480
♀ S	♂ A	.769	.911	.577	.614	.262	.265
♀ S	♀, sa A	.918	.992	.557	.562	.032	.041
♀ S	♀, sa C	.785	.921	.711	.514	.147	.107
♀ S	juv A	.766	.948	.319	.363	.006	.026
♀ S	juv C	.685	.851	.481	.405	.123	.106
juv S	♂, ♀, sa D	.725	.881	.669	.286	.162	.081
juv S	juv D	.821	.950	.810	.412	.141	.075
juv S	♂ A	.804	.932	.318	.630	.110	.045
juv S	♀, sa, A	.901	.988	.889	.589	.008	.002
juv S	♀, sa C	.821	.946	.565	.551	.046	.017
juv S	juv A	.920	.999	.640	.415	.008	.010
juv S	juv C	.756	.895	.727	.460	.058	.033
♂, ♀, sa D	juv D	.871	.983	.669	.861	.644	.832
♂, ♀, sa D	♂ A	.550	.657	.451	.148	.283	.380
♂, ♀, sa D	♀, sa A	.726	.902	.590	.127	.012	.017
♂, ♀, sa D	♀, sa C	.887	.983	.666	.117	.108	.055
♂, ♀, sa D	juv A	.738	.884	.548	.118	.000	.000
♂, ♀, sa D	juv C	.965	1.000	.751	.111	.012	.004
juv D	♂ A	.624	.773	.316	.263	.489	.682
juv D	♀, sa A	.836	.956	.717	.236	.211	.452
juv D	♀, sa C	.913	.994	.492	.227	.147	.100
juv D	juv A	.821	.952	.785	.219	.141	.561
juv D	juv C	.889	.988	.782	.205	.135	.073
♂ A	♀, sa A	.720	.884	.272	.720	.500	.919
♂ A	♀, sa C	.661	.764	.721	.598	.299	.383
♂ A	juv A	.774	.933	.169	.400	.286	1.800
♂ A	juv C	.560	.677	.365	.512	.242	.341
♀, sa A	♀, sa C	.835	.966	.518	.659	.115	.103
♀, sa A	juv A	.848	.971	.593	.522	.583	1.768
♀, sa A	juv C	.761	.916	.710	.492	.216	.208
♀, sa C	juv A	.795	.940	.374	.727	.038	.087
♀, sa C	juv C	.900	.988	.585	.545	.791	1.076
uv A	juv C	.756	.898	.664	.401	.162	.367
♂ C	♂ S					.369	.564
♂ C	sa S					.213	.229
♂ C	♀ S					.245	.289
♂ C	juv S					.076	.036
♂ C	♂, ♀, sa D					.376	.530
♂ C	juv D					.371	.620
♂ C	♂ A					.523	1.153
♂ C	♀, sa A					.273	.585
♂ C	juv A					.479	1.046
♂ C	♀, sa C					.091	.625
♂ C	juv C					.472	.988

enlarging the interval until the number of ob-
servations of any one of the lizard classes being
considered exceeded 10%. At that point a new
category was begun and the procedure was re-
peated until the smallest value was reached. This
convention avoids loss of information by lumping
too many observations under one category and
results in 16 categories each for the height and
diameter observations. If, however, the dimen-
sions are combined so that each category is charac-
terized by both a height and diameter interval,
the resulting grid has far too many categories in
proportion to the number of observations. There-
fore, in order to produce 16 categories, intervals
were lumped by fours, resulting in the arrange-
ment shown in Table 3. In addition 4 categories
for leaves (one for each of the height intervals)
and the category "ground" were added.

For each of the measures of overlap, C_λ and
D, overlap values in structural habitat were plotted
against overlap values in prey length using fre-
quency by the individual items in the case of D
(Table 9, Fig. 10). In addition, D values were
also computed for prey length overlap using fre-
quency by volume and plotted against overlap in
structural habitat; the latter is a more adequate
reflection of the relative sources of energy from
prey of different length.

The principal generalizations that can be made
from these plots are the following:

1. Most intraspecific comparisons show higher
overlap values in both dimensions combined than
do any interspecific comparisons. Two of the 3
exceptions are of juveniles versus adult males, the
classes with the greatest size differences (*angusti-
ceps* and *sagrei*).

2. With respect to interspecific comparisons,
the greater the overlap values in habitat, the lower
the maximum overlap value in prey size. In
other words, taking similarly sized prey is avoided
if spatial overlap is great, but may or may not
occur if spatial overlap is slight.

3. The use of prey volume instead of prey indi-
viduals accentuates the tendency noted under (2).

4. Using C_λ instead of D masks the tendency
noted under (2). Comparisons with small num-
bers of observations tend to have overlap values
much greater than those of any of the other com-
parisons, regardless of the positions of the dis-
tributions.

Now that the general tendency has been de-
scribed, it is of interest to examine in more detail
the prey size preferences of some of the classes at
the boundaries of the species distributions, i.e.,
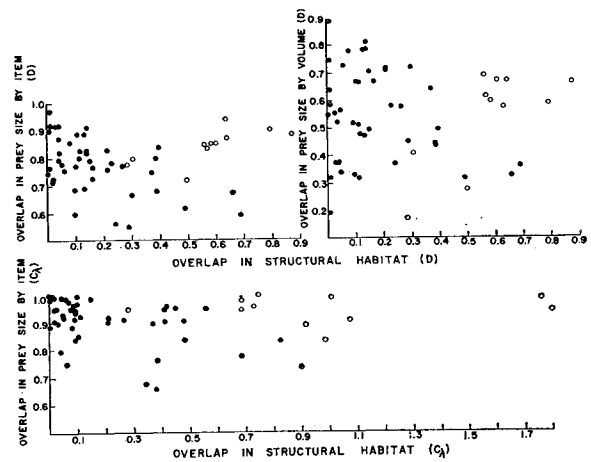those classes which overlap most in habitat with
classes of other species.

FIG. 10. The relationship of overlap in structural habi-
tat to overlap in prey size by item (2 measures) and to
overlap in prey size by volume (1 measure). Clear cir-
cles are intraspecific comparisons; solid circles are inter-
specific comparisons.

a. *Distichus* vs. *sagrei*. The interspecific pair
which overlaps the most in structural habitat con-
sists of *distichus* adults-subadults and *sagrei* males.
The next most overlapping interspecific combina-
tion is the pair, *distichus* juveniles and *sagrei*
males. Both pairs consist of individuals rather
different in head length and general body size
(Figs. 6, 7). Other possible combinations of the
two species, such as *sagrei* females versus *distichus*
juveniles, *sagrei* subadult males versus *distichus*
juveniles and especially *sagrei* females versus adult
distichus, are of classes much more similar in size,
yet show relatively high overlap values for struc-
tural habitat. In all cases, overlap in prey size
is relatively low. Even *sagrei* subadult males and
adult-subadult *distichus,* with slightly less habitat
overlap, show less overlap in their prey size dis-
tributions than might be expected from their
nearly identical head lengths.

If the prey size distributions are examined more
closely, it is found that adult-subadult *distichus*
take significantly smaller prey than do *sagrei* of
the same head length (Figs. 5, 6, 7; Table 7).
This result is similar to that obtained with another
sympatric pair, *A. richardi* and *A. aeneus* of
Grenada (Schoener and Gorman 1968). In that
case too, individuals of the larger species which
were of the same head length as adults of the
smaller species were found to prefer larger prey.
Correlated with this was a slight tendency for the
heads of the larger species, even when immature,
to be proportionately wider and deeper than those
of the smaller. However, if regressions are com-
pared for *distichus* and *sagrei,* different results are
obtained (Figs. 6, 7): Although there is little
difference in head depth, *distichus* heads are pro-

portionately wider than those of *sagrei* of the same size, yet they take smaller food.

From the ratio of head length to snout-vent length (the latter being a good indicator of body size), it would be expected that *distichus* would require more food per unit time than *sagrei* of the same head length. In fact, volumes of food found in *distichus* average higher than those in *sagrei* of the same head length, although there probably were slightly more *sagrei* caught during the earliest part of the day due to *sagrei* being more active at that time (Table 8). Thus the same correlation of greater food requirements with smaller prey for lizards of the same head length occurs in this interspecific comparison as was the case for intraspecific classes. However, it should be mentioned that, although the perching habitats of the 2 species overlap considerably, the feeding habitats may not be so coincidental, *sagrei* taking a good deal of food on the ground. Not only does this present *sagrei* with a larger potential hunting ground, but food on the ground might average larger than that on trunks. As will be discussed below, most of the food of *distichus* consists of ants.

Finally, note that the prey size distributions of *sagrei* juveniles and *distichus* juveniles are very similar; these comprise the interspecific pair which overlaps least in structural habitat.

b. *Angusticeps* vs. *distichus*. Another interspecific pair which overlaps widely in habitat are *distichus* juveniles and *angusticeps* adult males. These are the smallest and the largest lizards, respectively, in the 2 species and overlap very slightly in prey size.

c. *Angusticeps* vs. *carolinensis*. The adult males of these species overlap rather much in habitat. Although food size data were not available for adult male *carolinensis*, it should be noted that the head length ratio for the largest third of the males of the 2 species is about 1.15 (1.21 if only the maximum sized individuals are used), *carolinensis* adult males being much larger than any of the other species.

d. *Sagrei* vs. *angusticeps*. The adult males in these species overlap in habitat to a moderate degree. Their prey size preferences are not very similar, however, despite the fact that their head lengths are nearly the same. *Angusticeps* males take a significantly greater number of small prey items (Table 7). This fact can be anticipated from the other dimensions of the head. *Sagrei* have far wider and deeper heads than do *angusticeps* of the same head length (Figs. 6, 8).

Prey size range and prey number. Within each of the 4 species there is a general tendency for larger individuals to average larger ranges of their prey items per digestive tract (Table 8). The same tendency has been noted for *A. conspersus* (Schoener 1967), *richardi, aeneus* and *roquet* (Schoener and Gorman 1968). In 3 of the 4 Bimini species, subadult males took prey over a greater average range than did females, *distichus* being the exception. Average prey number per digestive tract is least for adult males in all cases but *distichus*, where juveniles averaged slightly smaller number of prey items. In the latter species, all classes took considerable proportions of small prey items. The trend in average prey number is again in agreement with the diet studies cited above. Variances for both distributions of prey size range and number were quite large and were usually greatest for the largest means.

Prey taxa. Most species of *Anolis* studied so far are general arthropod predators, taking small numbers of other animals and varying quantities of fruit as well (Rand 1967, Schoener 1967, Schoener and Gorman 1968). The four species vary greatly in the proportion of their diets drawn from different taxa (Table 10).

Perhaps the most striking case of concentration on a single prey taxon is that of *distichus*. From 75.5% (juveniles) to 91.3% (subadults) of the individual prey items of this species are ants (Formicidae). The only other taxon which is at all important is the Diptera. When percent contribution by volume is considered, the relative importance of ants drops slightly, but it is still by far the most important group: The large Lepidoptera larvae which *distichus* adult males sometimes eat also serve as major food items by bulk.

Sagrei have a much more diverse diet. Ants are still important, but considerably less so, especially by volume. By item, dipterans, aphids, beetles, termites and psocids are all important, the latter particularly in juveniles. By volume, Lepidoptera (larvae and adults) are most important in adult males, followed by plant food and beetles.

The tendency for plant food to be most important for the animals within an assemblage that take the largest food has been noted for lizards of other areas (Schoener and Gorman 1968). Lepidoptera are also most important for subadult males and females, but the proportion by volume of other groups, such as Diptera, Coleoptera, Isoptera and Psocoptera, is much greater. Juveniles depend largely on dipterans, psocids, termites and ants.

Angusticeps also clearly have a more diverse diet than *distichus*, with aphids and dipterans contributing the most items. The rather great differences in frequencies between subadult males and females are probably an artifact of small sample size. By volume, Diptera and Homoptera (mostly leafhoppers) are the major components

TABLE 10. Percentage of total individuals (I) and total volume (V) of various prey taxa.

TAXON	sagrei adult males		sagrei subadult males		sagrei females		sagrei juveniles		distichus adult males		distichus subadult males		distichus females		distichus juveniles		angusticeps adult males		angusticeps subadult males		angusticeps females		angusticeps juveniles		carolinensis subadult males		carolinensis females		carolinensis juveniles	
	I	V	I	V	I	V	I	V	I	V	I	V	I	V	I	V	I	V	I	V	I	V	I	V	I	V	I	V	I	V
Formicidae	32.7	5.6	25.8	8.0	13.6	4.7	17.2	8.3	85.9	61.9	91.3	74.1	86.9	78.5	75.5	67.7	3.8	0.2	4.9	1.7	0.9	0.4	4.3	4.3	0.2	0.2	2.5	0.7	0.3	0.1
Homoptera: Aphids	17.1	0.4	11.9	1.4	15.9	1.1	13.8	2.7	0.6	0.1	2.8	0.9	0.6	0.1	4.0	1.6	42.9	2.4	3.3	0.3	39.1	14.9	2.9	0.3	15.1	2.2	6.3	0.6	2.3	0.4
Diptera	15.8	3.4	18.0	13.9	21.8	9.8	26.9	34.1	5.7	2.1	2.3	3.2	5.2	4.5	10.9	14.2	25.0	63.4	32.8	22.7	40.9	49.6	83.5	82.6	64.5	66.7	54.3	52.7	29.3	26.4
Hymenoptera (excluding ants)	3.0	2.1	4.0	1.7	4.8	0.4	6.0	1.1	1.9	0.3	0.6	0.0	1.0	0.5	1.6	0.8	7.7	2.7	5.7	0.8	4.9	2.6	2.9	0.4	4.8	1.0	12.4	1.4	12.8	3.8
Thysanoptera			0.7	0.0	0.5	0.0	4.2	0.2	0.1	0.0	0.0	0.0	0.0	0.0	1.2	0.1	0.6	0.0			2.2	0.1	1.4	0.1	0.2	0.0	0.8	0.0	1.0	0.0
Coleoptera: adults	6.1	9.1	7.8	13.8	6.4	4.9	5.7	5.4	2.1	12.5	0.7	2.5	1.1	4.2	2.0	3.5	2.9	2.7	1.6	1.8	0.4	1.5			2.0	4.6	3.0	3.2	1.6	1.3
Homoptera (excluding aphids)	1.0	1.1	1.5	0.7	2.1	1.8	1.2	2.5	0.4	0.3	0.3	0.5	0.2	0.4	0.3	1.2	6.4	22.1	6.6	10.6	2.7	5.8	2.9	11.1	3.8	4.3	9.1	9.1	39.9	41.4
Psocoptera	2.9	17.0	17.0	6.1	12.7	3.4	15.7	11.6	2.1	0.9	0.9	0.8	2.3	1.5	1.4	0.8	5.4	0.9	1.6	1.0	4.4	4.3			2.6	1.5	3.0	1.5	4.0	3.2
Lepidoptera: larvae	2.0	12.9	2.5	1.9	1.9	1.4	1.4	2.8	0.4	18.6	0.2	11.6	0.3	2.1	0.2	4.2	1.0	0.3	38.5	34.0					1.4	1.5	1.8	5.2	0.3	0.2
Acarina	0.4	0.0	1.6	0.0	0.8	0.0	1.5	0.2	0.1	0.0	0.2	0.0	0.4	0.0	2.0	0.2	0.6	0.0									1.0	0.3		
unidentified	1.1	4.0	0.7	0.1	1.0	0.2	0.6	0.2	0.3	0.0	0.1	0.5	0.3	0.3	0.3	0.1	0.6	0.3	1.6	1.1	1.8	0.8	0.7	0.1	0.2	0.1	1.0	0.3	0.7	0.8
Coleoptera: larvae	0.6	0.1	1.0	0.7	0.6	0.8	0.8	0.4			0.1	0.0	0.0	0.0															0.3	5.2
Lepidoptera: adults	2.7	27.8	1.2	16.5	1.8	17.7	0.5	7.3	0.1	0.0	0.2	3.9	0.2	0.2	0.2	4.4	0.3	0.6	0.8	0.8					1.8	6.4	1.8	9.9	0.1	2.1
Hemiptera	0.4	0.0	0.3	0.9	0.8	1.8	0.5	1.0			0.1	0.0	0.0	0.0			0.3	0.3			0.9	13.1			2.2	3.7	2.0	1.6	1.2	11.9
Plant matter	4.2	16.3	0.5	4.9	0.2	2.4			0.1	0.6	0.0	0.7					0.1	3.9									0.8	5.3		
Isoptera	7.7	6.6	2.6	7.4	12.5	23.1	1.7	11.2			0.2	0.7	0.8	5.2	0.1	0.3														
Araneida	1.4	2.0	2.0	3.4	1.1	2.4	1.2	4.9	0.2	0.8	0.1	0.1	0.4	1.1	0.4	0.9	1.3	0.2	1.6	24.4	1.3	6.4	1.4	1.1	0.8	6.0	5.1	5.1	0.7	1.2
Orthoptera	0.5	8.0	0.3	2.3	1.0	8.9	0.5	3.8	0.1	1.7			0.0	1.3											0.3		3.7	3.7	0.2	0.8
Neuroptera	0.2	0.0	0.0										0.0	0.1			0.8	0.8	0.8	0.9	0.4	0.6								
Mollusca																											0.2			
Miscellaneous arthropods[1]	0.2	0.3	0.8	0.6	0.5	0.1	0.6	2.3	0.2	0.3															0.2	1.7			0.2	1.3
Dermaptera					0.2	2.1																								

[1] Isopoda, Pseudoscorpionida and Chilopoda

of adult male diets. Ants are only a very minor prey item in this twig-dwelling species. Diptera, Homoptera other than aphids, and winged Hymenoptera other than ants comprise the bulk of the prey items ingested by *carolinensis*. The former 2 groups and adult Lepidoptera contribute the greatest volume, with Diptera being by far the most important group in subadult males and females. Ants are once again of little importance.

Thus the habitat and prey size differences discussed above have apparently contributed to the striking differences in frequency of different taxa in the diets. Even with as gross categories as these, the diets of some of the species and classes, such as *distichus* and *carolinensis,* can be seen to be almost non-overlapping, and therefore must be at least as discrete with respect to prey species.

The question might then be asked, to what extent is it possible to predict the frequencies of the various prey taxa from a knowledge of structural habitat? This question can be posed for both species and classes within species.

In regard to species, gross differences in the frequency of prey items are easily correlated with structural habitat differences. Ants are most important in the trunk-dwelling *distichus* whose habitat they dominate in relative abundance; they are next most important for the trunk and ground foraging *sagrei*. They are scarcely found at all in the diets of the twig and crown species, *angusticeps* and *carolinensis,* the twig-inhabiting *Pseudomyrmex* constituting a large portion of the exceptions. In the case of the 2 latter lizard species, flying insects such as dipterans and winged Hymenoptera are very important, as well as homopterans such as aphids and leafhoppers.

In regard to classes within species, the question can be asked in a slightly different manner. Do those classes which show great overlap in structural habitat also show great overlap in prey taxa, and vice versa? As before, D values for habitat overlap and prey taxa overlap were plotted against one another for interspecific and intraspecific pairs of classes (Fig. 11). Notice that pairs which overlap most in habitat tend to be quite similar in prey taxa as well. However, pairs which overlap least in habitat can also be quite similar in prey taxa, although are more often different. This latter result would probably not have occurred if prey taxa were split into species. What is more interesting is that for the same degree of overlap in structural habitat, intraspecific pairs, with one exception, have greater similarity in their prey taxa than do interspecific pairs. Previously, it was pointed out that for the same overlap in structural habitat, intraspecific pairs showed greater similarity in prey size than did interspecific pairs.
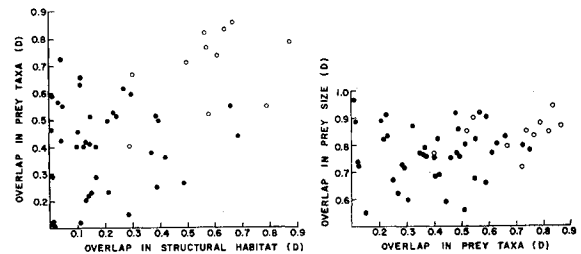

Figure 11

FIG. 11. Relationship of overlap in prey taxa to overlap in structural habitat and to overlap in prey size by item. Clear and solid circles as in Fig. 10.

Why are intraspecific pairs more similar in prey size and taxa than pairs from different species with the same structural habitat overlap? One possible explanation, already mentioned in the case of *sagrei* and *distichus,* is that structural habitats are not equivalent to foraging habitats. There is no way to test this alternative other than to extend the field study over a much longer period of time. Observations of what appeared to be ingestion of food were made for *sagrei* and *distichus* over nearly the whole range of their structural habitat; however, the distribution of observations over that range might be different. If the 2 kinds of habitats do coincide fairly well, then we must interpret this prey difference as a predisposition for conspecific classes to select either more similarly sized prey or prey with greater taxonomic affinity, or both, from the same available prey than do classes of different species. Note that, although intraspecific combinations tend, on the average, to be more similar in head size than interspecific combinations, this is not the sole explanation, for as we have seen, intraspecific pairs are even more similar in prey size than expected from their head sizes. For a particular habitat, preference for a certain prey size distribution would usually necessarily imply preference for a certain taxonomic distribution and vice versa. Therefore, without doing experiments such as subjecting the lizards to similarly sized insects of totally different taxonomic affinity than those encountered in their natural habitat, it is impossible to say how much of size or of taxonomic preference or of both is involved in these similarities.

If overlap in prey taxa is plotted against overlap in prey size (Fig. 11), it is seen that great taxonomic overlap invariably implies great size similarity, but great size similarity can also be found for pairs whose prey taxa are very different. As necessarily would be the case, intraspecific combinations are usually those with both high prey size overlap and high prey taxa overlap.

SPECIALIZATION

In this study, the niches of the 4 species on Bimini have been characterized in several ways: vegetation type, structural habitat, bark color, frequency on leaves, prey size and prey taxa. The species have had varying success as colonists throughout the West Indies, *carolinensis* and *sagrei* being particularly good colonizers, *distichus* and *angusticeps* being relatively poor (Williams, in prep.). It is possible that, even on a multispecies island such as Bimini, the species differ in specialization with respect to the niche characteristics investigated and so will throw light on the differences in colonizing ability which they so dramatically demonstrate.

There are a variety of meanings that have been ascribed to the term "specialization." Perhaps the most frequent is in regard to the relative magnitude of the arithmetic range of a particular kind of resource which the species is found to utilize. Interpreted in this way, the following patterns of specialization emerge:

1. Vegetation type: *sagrei* is the most generalized, followed closely by *carolinensis; angusticeps* and *distichus* are the most specialized.

2. Perch diameter: *sagrei* and *distichus* are the most generalized, *angusticeps* and *carolinensis* the most specialized.

3. Perch height: *sagrei* and *distichus* are the most generalized, followed closely by *angusticeps; carolinensis* is the most specialized.

4. Occurrence on leaves as well as bark: *carolinensis, sagrei* and *angusticeps* are the most generalized; *distichus* is the most specialized.

5. Bark color: none of the species differs in specialization.

6. Prey size: *sagrei* and *distichus* are the most generalized; *carolinensis* and *angusticeps* the most specialized.

7. Prey taxa: *sagrei* is the most generalized followed closely by *distichus* and *carolinensis; angusticeps* is the most specialized.

Counting up, we find that *angusticeps* is relatively more specialized 4 times, *carolinensis* 3 times, *distichus* 2 times and *sagrei* 0 times. Except for *sagrei,* the species are distributed irregularly with respect to specialization. What has happened? The ranking from *angusticeps* to *sagrei* also happens to be the order of increasing frequency of observations. In other words, range, and hence specialization interpreted in this way, are a function of sample size. Even if sample size were to be increased immensely, range would not be a very good measure of specialization: for most of the above characteristics, the species ranges

would probably expand over all natural values or categories, giving identical and maximum specialization values.

A second class of measures takes into account the evenness of resource utilization over a given continuous or discontinuous dimension.

If dimensions are composed of discrete parts, or if they are continuous but are artificially broken up, a measure such as $H'' = - \sum_{i=1}^{n} p_i \log_2 p_i$ can be used, where p_i is the frequency of utilization of the ith category. All measures which depend on categories have the same disadvantages which were pointed out for overlap measures, that is, depending on the number and position of categories, values can be radically shifted around in relation to one another. Again, as in overlap, whenever there is a fairly obvious set of categories available, the choices with respect to number and kind of categories are often quite limited. In Table 8, H'' values are given for the set of prey taxa listed in Table 10. Measured in this way, *sagrei* is the least specialized and *distichus* the most specialized with respect to prey taxa (the latter takes enormous quantities of ants). Within the species, there seems to be no particular trend of specialization, unlike the case of the lizards of Grenada, where males were usually found to be more specialized in this regard (Schoener and Gorman 1968). If, however, taxa were lumped into, say, winged versus apterous forms (a perfectly reasonable property when considering specialization), rather different results would undoubtedly be obtained.

Another measure which can be used if values of the dimension are quantifiable is the variance. This measure also involves categories, but if automatic computing methods are available, there are as many categories as there are distinguishable values of the variable. While thus having the number of categories determined by the precision of the measuring system, the relative variances of different distributions might be scale dependent. This is best illustrated with an example. *Sagrei* adult males occur on perches of a great range in diameters, and observations of that class are rather evenly distributed over medium to thick perches. Adult males of *angusticeps,* on the other hand, are restricted, for the most part, to perches under an inch. Our natural tendency, because we tend to think of dimensions such as diameters on an arithmetic scale, is to assert that *angusticeps* is more specialized with respect to perch diameter. Indeed, if the standard deviations (in inches) for the 2 classes are computed, *sagrei* is found to have a value of 4.11 and *angusticeps* a value of 1.85.

However, if a logarithmic scale of perch diameters is used instead of an arithmetic one (and, incidentally, perch diameter preference is found to be almost perfectly lognormally distributed for many classes of lizards), the opposite result is obtained: the standard deviation (in $\log_e$ inches) for *sagrei* adult males is 0.786 and for *angusticeps* is 0.829. What has happened, of course, is that the logarithmic transformation has in effect "spread out" the range of small diameters relative to larger values. The logarithmic transformation is far from being biologically absurd: in fact, the perch world of a lizard may be closer to a logarithmic or some similar scale than to the arithmetic with respect to the evolutionary or short-term changes the lizard has to undergo in order to move a given interval along the diameter scale. Put another way, a change in value from a quarter to a half inch (or the reverse) may be far more important in terms of necessary adaptations or behavioral flexibility than a change from 16.25 to 16.5 inches. The variance also has the disadvantage that as skewness increases, it becomes relatively poorer in describing the distribution of the individual observations.

These dilemmas are partially solved if we ask why it is desirable to measure specialization. Oftentimes, we somehow hope to relate the measure to the success an animal has had in utilizing the distribution of available resources or to predict its success in an area where the distribution of resources is known. Sometimes it has been argued that specialization involves a greater probability of extinction; if by specialization is meant any of the measures discussed above, this may or may not be true, depending on the relative amounts of energy extractable from the categories of resources and their fluctuation in time. It is possible to measure the relative availability of different categories of resources and the relative frequency of their utilization by different species over a short interval of time. Then by comparing the two distributions using the overlap measures or by other means, a kind of specialization measure which might be called "density specialization" can be computed. This would measure how much of an available resource was being used by a species during that time interval relative to other species and could serve to predict its success given other distributions of that resource. Projects of this sort are now being carried out.

Interpreted in this way, it might be guessed that *sagrei* is least specialized with respect to the range of vegetation types on South Bimini because it is able to exist in areas where all vegetation is low and bushy as well as in areas where there is a good deal of tall vegetation such as trees. Thus

it is a matter of resource availability relative to its structural habitat which has enabled *sagrei* to become so widespread on Bimini and perhaps on other islands as well.

SEXUAL DIMORPHISM AND THE CONSTRUCTION OF AN ARBOREAL LIZARD FAUNA

Of the 4 species of Bimini anoles, 3 (*sagrei, angusticeps,* and *carolinensis*) are quite highly dimorphic in size between the sexes, whereas in the fourth (*distichus*) the sexes are so similar in size and other respects that it is usually impossible to distinguish them in the field without capture except in the most favorable of situations (Figs. 6–9).

If the D values for overlap in structural habitat of interspecific pairs are classified according to magnitude, it is found that classes of *distichus* have much higher values than do classes of any of the other 3 species (Table 11). In other words,

TABLE 11. Percent interspecific overlap values in structural habitat (D) falling within various size intervals.

overlap interval	sagrei	distichus	angusticeps	carolinensis
0–.099	41.9	15.0	44.4	33.3
.100–.199	19.4	30.0	14.8	29.6
.200–.299	12.9	10.0	29.6	22.2
.300–.399	16.1	25.0	3.7	11.1
.400–.499	3.2	10.0	3.7	0
.500–.599	0	0	3.7	3.7
.600–.699	6.5	10.0	0	0

that species whose classes collectively overlap the most in structural habitat with classes of other species shows the least sexual dimorphism in size. For species which occupy their habitats more or less exclusively, sexual dimorphism in size would enable the species as a whole to exploit the available range of food sizes or perches more efficiently by reducing intraspecific competition and thus allowing more individuals per unit volume of habitat. This advantage has been pointed out for solitary species on small islands (Selander 1966, and included references, Schoener 1967) and for species on larger islands as well (Rand 1967). *Carolinensis* and *angusticeps* do in fact occupy fairly discrete habitats. *Sagrei* dominates the ground almost exclusively in many areas, although *Ameiva* and *Leiocephalus* act as partial competitors, and it overlaps with *distichus* on low trunks. Therefore, for *carolinensis, angusticeps* and *sagrei,* sexual dimorphism can be seen at least partially as a consequence of habitat exclusiveness. *Distichus* is "boxed in" by other larger species: it could not increase sexual dimorphism in size by increasing the size of the adult male without coming into considerable competition with male *sagrei*

and to a much lesser extent with male *carolinensis* and *angusticeps*. The only other way *distichus* could increase its sexual dimorphism is by decreasing the size of the female. But the smaller the lizard, the smaller the size and for very small species the total biomass of available prey, and the greater the likelihood of predation; hence, the possible advantage of competing less with males for food is counterbalanced by other selective disadvantages for the female. In fact, for *Anolis* generally, mature females rarely are smaller than those of *distichus;* only in special habitats, such as grass or very small twigs, are adults very small (Williams and Rand in prep., Schoener in prep.).

Looked at another way, the fact that two similarly sized sexes of the same species are able to survive with almost completely overlapping habitat preferences must mean that the small food which they feed upon is quite abundant. Lizards which eat mostly larger food, such as *sagrei,* ought to be more different in the prey size preferences of the sexes: such species should ordinarily have to space themselves out more with respect to food size due to a decreasing biomass of food per unit area with increasing food size over most of the range of food size. The models explaining this prediction are given for interspecific comparisons in Schoener (1965) and evidence for the decline in biomass with large food size for insects in Janzen and Schoener (1968); Selander (1966) has suggested its application to size dimorphism between the sexes as well. As is the case with the two sympatric species on Grenada (Schoener and Gorman 1968), the rate of increase of average prey size with predator size is greater for the larger species (the one that feeds on larger food) than for the smaller species (Fig. 5).

Since on Bimini anoline lizards which are small are also the ones which overlap most in structural habitat, it is impossible to separate the effects of small size and overlap. However, it is probable that the 2 factors are interrelated: animals which are small can support similarly sized sexes on the same food in the same habitat, and this in turn allows greater interspecific overlap. Small, non-dimorphic species might be best for insinuation into complex faunas, whereas larger, more dimorphic species might be best for the colonization of depauperate or empty areas. Such rules as these provide constraints on the number of possible faunas an area can support. While the first few species to arrive or evolve in an area might be due to colonizing ability combined with geography and historical accident (see Williams in prep.), the number of degrees of freedom in the construction of a saturated fauna rapidly vanish as more and more species are evolved.

The question may now be asked if it is possible to fit another species into the Bimini anole fauna.

One way in which the lizards of both large and small islands sometimes divide the habitat is by microclimatic differences. These have been documented for certain species on Cuba by Ruibal (1961), for species on Puerto Rico by Rand (1964), and for the 2 species on Grenada by Schoener and Gorman (1968). These islands are topographically diverse, and particularly the larger ones have extensive regions of closed forest and open, drier areas. The opportunity for climatic segregation without considerable loss of population continuity is present in such islands. The Bahamas, in contrast, are, as mentioned above, topographically uniform and thus vegetatively more uniform as well; segregation has to occur syntopically, either in regard to microhabitat or to prey selection.

A larger ground species might seem appropriate, but both *Ameiva* and *Leiocephalus,* the former fairly common in part of the study area, are occupying that position already. A very small species could fit in almost anywhere, but this would compete with juveniles of the already existing species no matter what its structural habitat. A very large species would also fit in almost anywhere, but it is possible that large food items are not as common on Bimini, at least on a year-round basis, as is smaller food. Large anoles have been found to be very frugivorous (Schoener and Gorman 1968, Schoener in prep.); it is possible that fruit on this seasonally dry island is also seasonal in availability. Furthermore, if there is such seasonality, both lizards and their animal food would not be expected to be able to reach as large a maximum size as when food was available in abundance throughout the year.

Of course, hypothetical species can always be inserted between existing ones: there might, for example, be a species which spends more time on twigs than *carolinensis* and more time on leaves than *angusticeps.* Aside from the danger of being outspecialized or conversely, of being so restricted that not enough food is available per unit time, the situation in lizards is complicated by the fact that there are so many size classes, some differing in structural niche, within the same species. The relative survival of these classes might be different from year to year and be partially a function of the other species present, making it difficult to consider each species as a whole.

It has been empirically determined that no more than 5 species of *Anolis* are ever found together syntopically over a large uniform area; at least one of these species must be very large (Williams and Rand in prep.). Therefore, it is likely that

Bimini is at or near saturation, although the theory of saturation in anoline faunas remains to be worked out.

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SURFACE ACTIVITIES OF SOME NORTH AMERICAN SCORPIONS IN RELATION TO FEEDING

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Abstract. Field and laboratory studies were conducted on the nocturnal surface activities and feeding behavior of scorpions, using ultraviolet light. Two species, *Vejovis confusus* and *V. mesaensis*, showed a decrease in surface occurrence as the evening progressed, while *Centruroides sculpturatus* showed a random occupation throughout the night. Increased intensity of moonlight resulted in a significant decrease in surface occurrence in *V. confusus* and *V. mesaensis;* *C. sculpturatus* showed no significant response to increased illumination. Species differences in the amount of surface activity and feeding behavior were noted. Potential prey, food preferences, and mechanisms used in prey detection are also discussed.