tion that these globular subunits within the wall are hexagonally and uniformly distributed upon a mucopeptide substrate and may be composed of protein or lipoprotein.

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The Ecological Significance of Sexual Dimorphism in Size in the Lizard Anolis conspersus

Abstract. *Adult males of* Anolis conspersus *capture prey of significantly larger size and occupy perches of significantly greater diameter and height than do adult females; similarly, these three dimensions of the niche are significantly larger for adult females than for juveniles. Adult males on the average eat a smaller number of prey, and the range in size of prey is larger. The relationship between the average length of the prey and that of the predator is linear when the predator size is above 36 millimeters, but becomes asymptotic when it is below that value. Subadult males as long as adult females eat significantly larger food than do the latter, but only in the larger lizards is this correlated with a relatively larger head.* Anolis conspersus *selects prey from a wide range of taxa and shows no obvious intraspecific specialization not connected to differences in microhabitat and prey size. The efficiency of this system for solitary species is pointed out.*

Anoline lizards make up the most conspicuous and diversified vertebrate genus in the West Indies. There are many very small islands with at least one species, and the greatest numbers occur on the large islands of Cuba, with 22 species, and Hispaniola, with 20 species. Most species of *Anolis* which occur without congeners are about the same absolute size from island to island, the heads of adult males measuring 17 to 21 mm and the snout-vent lengths being 65 to 75 mm. Furthermore, the sexes are highly dimorphic in size, the head length of adult males averaging 1.3 to 1.5 times that of females (*1*). This striking convergence from at least seven different stocks (*1*) implies that on islands where an anoline lizard occurs without congeners, natural selection has favored an optimum size and sexual dimorphism, either because unsuitably proportioned colonists are eliminated, or because later there is an increase in size dimorphism between the sexes. Presumably this latter process, at least, is a reflection of the phenomenon of "ecological release," in which one species, in the absence of closely related species, increases the breadth of certain critical dimensions of its ecological niche.

Two nonexclusive hypotheses concerning the adaptive significance of sexual dimorphism in size were tested for one of the convergent solitary species, *Anolis conspersus* of Grand Cayman Island. The first, that size differences might reflect differences in structural habitat (*2*) such as perch size, I tested by noting the height above ground and the diameter of perches of 474 lizards in several habitats. The second, that such differences reflect a difference in the distribution of prey size, I examined by analyzing the stomachs and intestinal contents of 166 lizards collected in the same areas (*3*).

Differences in both prey size and microhabitat have previously been reported for age and sex classes of different sizes within other species of lizards. A greater proportion of large insects were found in larger adult males than in adult females of *Anolis lineatopus* and *Agama agama* (*4, 5*); similarly, juveniles take smaller food than adults (*5–7*). Sexual differences in preferred microhabitat have been found in *Anolis lineatopus, A. cybotes,* and *A. sagrei* (*4, 8*), and juvenile-adult stratification has been observed (*4, 7–9*).

Grand Cayman is a flat, relatively dry island about 32 km long with a maximum width of a little over 6 km. Most of the vegetation consists of several types of mangrove associations or xeric scrub forest, some growing directly on top of bare coral rock.

Table 1. Frequency of perch height and perch diameter combinations for male and female adults, subadult males, and juveniles. Results are percentages observed. Five adult males, 17 adult females, 3 subadult males, and 14 juveniles were found on the ground.

Perch height (feet)	Perch diameter in inches (1 inch = 2.54 cm) for											
	Adult males $N = 133$			Adult females $N = 222$			Subadult males $N = 43$			Juveniles $N = 37$		
	3	3–½	½	3	3–½	½	3	3–½	½	3	3–½	½
>10	5	1	0	0	0	0	2	0	0	0	0	0
6–10	21	8	0	4	6	3	14	0	2	3	0	8
3–5	32	16	2	16	32	2	23	33	0	3	16	10
1–2	10	7	0	15	20	2	9	16	0	10	25	25

Anolis conspersus occurs in nearly all habitats where there is shade but seems most common in moderately shaded areas with a variety of tree sizes and a relatively open forest floor. Lizards were observed and collected in areas including beach vegetation (especially *Rhizophora, Coccoloba,* and *Casuarina*), inland mangrove forests, open scrub forest vegetation (especially *Bursera,* palms, and a variety of leguminous trees and shrubs), or more closed forest vegetation (especially *Bursera, Ficus, Cassia*). Although more females than adult males were collected, the two were sampled in approximately the same proportions in all habitats.

The properties of the structural niche were determined according to the method of Rand (*2*), in which the diameter and height of the perch occupied by each individual is recorded. An area was covered only once, and each observation is of a different individual. To facilitate comparison, I placed the resulting data into frequency tables with intervals identical to those used by Rand (Table 1). Although there is a good deal of overlapping, adult males tended to occupy larger perches and to occur higher than did females; females, in turn, occupied larger perches and occurred at greater heights than did juveniles (lizards with snout-vent length below 33 mm). All these differences are statistically highly significant. The perches of subadult males (males the same sizes as adult females) have distributions of height and diameter intermediate between those of adult males and females (*10*). Therefore, the hypothesis that sexual differences in size are associated with structural differences in habitat is confirmed.

For each prey item the length and volume (length times average width times average depth) was measured or estimated. Prey from the entire length of the digestive tract were included rather than just those contained in the stomach, because the tendency for a large item to be more widely spread over the entire tract than a small one would otherwise result in a disproportionate frequency of large prey. Although both adult males and females take a much greater number of prey that are from 1 to 5 mm long than they do of larger prey, the food items of females are significantly smaller, both within the range of 1 to 5 mm ($P < .001$) and over the whole range of food size ($P < .001$). Nearly all the food items of juveniles are 1 to 5 mm long, and prey taken by subadult males are intermediate in size relative to those taken by males and females (Fig. 1, left). These compilations, in which prey items from all lizards belonging to a given size and sex class are combined, do not indicate if the distributions of prey within an individual lizard are of the same kind as the total distribution for that lizard's class, or if the total distribution is the resultant of radically different individual distributions of prey. To evaluate these alternatives, I tabulated the frequency of lizards containing large (greater than 3 mm) prey items in various percentages for each of the four classes (Fig. 2). While individual females and juveniles usually contain a large proportion of small food, in about half the males over 50 percent of the food items were large. Thus the similarity between adult males and females with respect to frequency distribution of prey is due in part to a small proportion of males containing many small food items. On the average, the tracts of adult males contain a much smaller number of prey (18 items) than do those of females (32 items). Finally, adult males tend to take prey over somewhat greater ranges of size than do adult females, the average range in prey size of 47 males being 12.6 mm and of 84 females 8.2 mm.

A more meaningful measure of the importance of the various classes of prey size in the diets of males and females is obtained if the percentage of the total volume composed by each

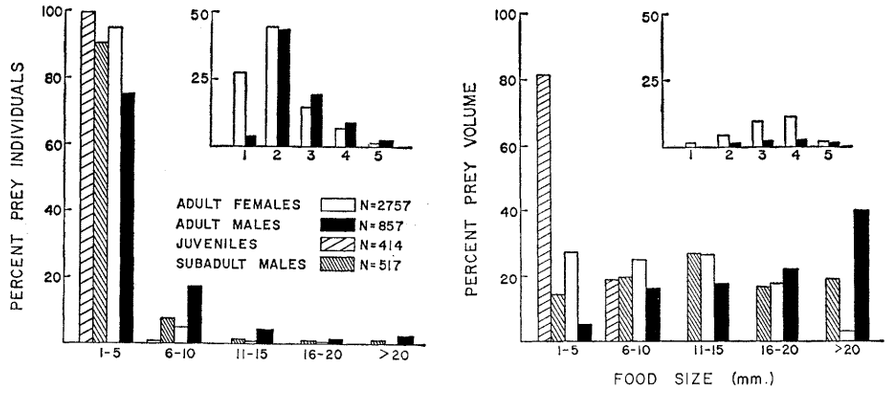

Fig. 1. Percentage of prey individuals (left) and prey volume (right) in five categories of prey size for four age and sex classes of lizards. The breakdown for the first food size category is given in the inserted graphs, which have the same axes as the main graphs.

Table 2. Percentage of total individuals (I) and total volume (V) of various prey taxa.

	Adult males ($N = 857$)		Adult females ($N = 2757$)		Subadult males ($N = 517$)		Juveniles ($N = 414$)	
	I	V	I	V	I	V	I	V
Hymenoptera: Formicidae	64.4	7.1	40.8	10.2	67.1	12.9	63.7	27.9
Other Hymenoptera (winged adults)	1.3	2.8	1.9	0.7	3.0	5.2	2.8	1.1
Diptera	2.5	1.0	10.5	2.8	5.1	0.3	12.3	9.9
Coleoptera (adults)	8.6	4.6	9.0	5.3	5.5	3.8	2.4	6.0
Coleoptera (larvae)	0.1	0.0	0.0	0.0	0.4	0.2		
Psocoptera	1.8	.0	11.0	1.2	2.8	.2	3.5	1.1
Isoptera	4.3	1.3	9.1	12.8	3.0	2.5	1.7	12.8
Homoptera	1.1	0.6	2.5	2.1	1.3	1.7	5.7	3.2
Hemiptera	0.3	.3	0.3	0.4	0.2	0.0	0.2	3.0
Lepidoptera (adults)	.3	.0	.6	1.6	.4	1.8	.5	1.3
Lepidoptera (larvae)	.6	1.4	1.7	0.6	.2	0.3	.5	0.3
Neuroptera (adults)			0.3	.2				
Neuroptera (larvae)	.1	0.0	0.1	.0	0.2	.0		
Thysanoptera	.2	.0	.2	.0	.2	.0	0.9	.1
Orthoptera-Blattaria	4.8	73.6	1.7	52.5	2.3	55.6	.2	7.8
Araneida	1.6	1.7	2.5	4.1	2.4	6.7	2.1	18.5
Pseudoscorpionida	0.1	0.0	0.3	0.3	0.9	0.5	0.9	4.8
Chilopoda	.3	.8	.0	.0				
Acarina	.2	.0	1.2	.0			.5	0.1
Isopoda					.4	.0		
Mollusca			0.0	.0				
Anolis					.2	6.6		
Plant matter	1.6	2.1	.7	.3	.9	0.3	0.2	1.1
Unidentified material	5.4	2.7	5.8	4.7	3.6	1.1	1.9	1.0

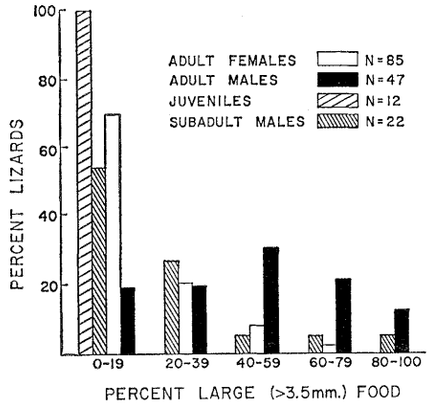

Fig. 2. Percentages of lizards containing various percentages of large food.

of the prey classes is calculated. Relative volumes should be proportional to relative biomass, an indication of relative caloric values. This kind of tabulation results in a much neater separation by food size of the two sexes (Fig. 1, right). Adult males obtain 62 percent of their food by volume from prey over 15 mm, whereas adult females obtain only 21.1 percent from such large prey. Hence, the second hypothesis, that sexual dimorphism in size is correlated with differences in prey size, is also apparently correct.

The relationship between average prey length and predator length appears approximately linear above a certain minimum predator size, the prey length gaining about 0.5 mm for every 5-mm increase in snout-vent length (Fig. 3). Below 36 mm, there is a gradual leveling off of average prey size for females (*11*). This effect might be caused by a decrease in the relative abundance of extremely small prey that are acceptable to *Anolis*. For the three size classes of males whose sizes are identical to adult female classes (subadult males), distributions of prey size tend slightly but significantly toward sizes larger than those of prey taken by females in all cases (Fig. 3; $P < .05$; $P < .005$; $P < .05$). In the larger two

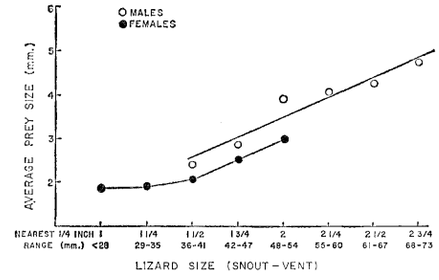

Fig. 3. Relationship of predator size to prey size for male and female lizards.

classes, heads of males are significantly longer than those of females of the same snout-vent length ($P < .001$ by the t test), thus being a better indicator of food size than snout-vent length. But in the smallest size class (36 to 41 mm), head lengths of males and females are almost exactly the same, yet the males' prey distribution was significantly larger (*12*). The most likely hypothesis explaining this finding is that males are genetically predisposed to take relatively larger food sizes, although there could also be differences arising from a mere trial and error mechanism connected with ease of manipulation.

Almost the entire diet of *Anolis conspersus* consists of animal food (Table 2). The small percentage of plant matter may be partially ingested by accident, but in the case of large berries and certain other plant items intentional consumption seems likely. All four classes of anoles eat more ants than members of any other taxon listed in Table 2. Adult females eat considerably fewer ants than do juveniles or either class of males and have their prey items more evenly distributed over the categories of available prey. Some of the major differences in the kinds of food ingested are explainable on the basis of microhabitat and size differences. Males are more likely to encounter ants on the trunks of large trees than are females, which frequent much smaller trees and shrubs and are more likely to encounter insects inhabiting foliage. Juveniles, which spend a large part of their time on the ground, are also relatively likely to encounter ants. The Orthopterans, which are more numerous in the diet of adult males, tend to be larger than other insects. Psocopterans and flies, nearly all minute, are taken much more frequently by females.

In adult females and both classes of males, the Orthoptera form over half the diet by volume. These probably belong to only three or four species, but females tend to eat the smaller nymphs much more often. In addition, other groups such as termites and ants compose a greater proportion of the volume of the food of females than of the food of adult males. Juveniles depend largely on ants, spiders, and termites (*13*).

A. S. Rand (*4*, *14*) first pointed out differences in prey size between the sexes of a dimorphic species of lizard (*Anolis lineatopus* of Jamaica) and stressed the importance of such a system in increasing the efficiency of the total exploitation of its habitat. In *Anolis conspersus*, differences between the sexes with respect to microhabitat combined with differences with respect to prey size are probably largely instrumental in allowing the species to build up the extremely dense populations in which it is sometimes found, especially in areas with varied perch sizes. Such an ability is of particular value to colonizing species and those in other ecologically marginal situations. As has been shown, sexual differences in size are correlated with differences with respect to both microhabitat and prey size. Although perhaps not the only selective pressures operating, the advantage of a more thorough utilization of environmental resources combined with a lack of closely related species is probably the cause of the similar size and dimorphism of the anoles which occur alone on islands.

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10. Chi-square tests were performed for perch height and diameter separately. Using the intervals 1 to 2 feet, 3 to 5 feet, and >6 feet, I found significantly different height distributions for adult males compared with adult females and adult females compared with juveniles ($P < .001$) but not for subadult males compared with adult females or subadult males compared with adult males ($P < .25$; $P < .10$). Using the intervals >3 inches, 3 to ½ inches, and $<½$ inches, I found significantly different perch diameter distributions for the first two categories ($P < .001$) and also for subadult males compared with adult males ($P < .025$) but not for subadult males compared with females ($P < .10$).
11. I did not have enough material available for males of this size to see if a similar asymptote occurs, because five of every six juveniles collected were females.
12. Chi-square values were computed for the intervals 1, 2, and >2 mm, which is the largest combination of intervals in which

at least ten prey items occur in each category for all comparisons.

13. The method of analyzing both stomach and intestinal contents probably resulted in fewer of certain soft-bodied insects, such as some Homopterans, larvae, and spiders, being recognized than actually occurred, but the effect on the total distributions would be slight.
14. A. S. Rand, unpublished.
15. I thank E. E. Williams and E. O. Wilson for their assistance in a variety of ways, including a critical reading of the manuscript, A. S. Rand for allowing me to see unpublished manuscripts, and J. A. Peters for bibliographical information. Supported by NSF grant GB-2444 to E. E. Williams.

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Acetylcholinesterase: Method for Demonstration in Amacrine Cells of Rabbit Retina

Abstract. *The activity of acetylcholinesterase in the inner plexiform layer of the rabbit retina was not affected detectably by prior section of the optic nerve. After the animals were treated with diisopropyl phosphorofluoridate, acetylcholinesterase reappeared in the somata of the amacrine cells and in certain cells of the ganglion cell layer before it reappeared in the inner plexiform fibers. This confirms the normal presence of acetylcholinesterase at the former site. The possible role of acetylcholine in intraretinal transmission is considered.*

The acetylcholinesterase (AChE) of the mammalian retina has been shown by the histochemical method with copper thiocholine (*1*) to be present chiefly in two distinct bands: one extending from the innermost region of the inner nuclear layer to the bordering portion of the inner plexiform layer and the other extending from the inner zone of the inner plexiform layer to the outer portion of the ganglion cell layer. Between these two heavily stained bands the intermediate zone of the inner plexiform layer shows much lighter staining (*2*). This pattern was interpreted originally as representing the amacrine cells and their processes. However, the relatively intense staining of the rich network of fibers renders the visualization of the amacrine cell bodies extremely difficult. On the basis of essentially the same pattern of staining, other investigators have reached the same conclusion (*3*, *4*), or have attributed staining additionally or alternatively to the processes of the bipolar cells (*5*, *6*), the ganglion cells (*4*, *5*), or centrifugal fibers from the optic nerve (*7*).

When a sufficient dose (4.0 mg/kg, given intravenously) of diisopropyl phosphorofluoridate (DFP) is given to produce virtually complete, irreversible inactivation of the AChE of the ciliary ganglion of the cat, the reappearance of newly synthesized enzyme occurs in the somata of the ganglion cells before it is detectable in the surrounding axons or dendrites (*8*). This is consistent with the proposal that neuronal AChE is synthesized in the granular endoplasmic reticulum, then transported to other parts of the neuron (*9*), although quantitative evidence of this sequence is lacking (*10*). We have taken advantage of this observation in staining selectively the AChE of the amacrine-cell bodies of the rabbit retina.

We examined retinas from normal rabbits, rabbits in which the right optic nerve had been sectioned 3 or 6 months previously, and rabbits treated with DFP (4.0 mg/kg, given intravenously, followed by 10.0 mg of atropine sulfate per kilogram, given intramuscularly) ½, 5, 7, and 10 hours before enucleation. The eyes were rapidly removed, either after the animals were killed by an overdose of urethane, or, in the case of animals treated with DFP, while they were under urethane anesthesia. Frozen sections of portions of the retinas were cut at 10 μ as soon as possible; the remaining portions were fixed for 2 hours in cold 10 percent formalin solution, buffered to *p*H 7.4 and made isotonic with sucrose, and were then stored in cold, buffered sucrose solution and sectioned the following day. Immediately after the tissues had been sectioned, we stained them for AChE using the copper thiocholine method (*1*), with incubation periods of 1 to 7 hours.

The architecture of the rabbit retina is shown in Fig. 1A. Figure 1B shows the distribution of AChE in the normal retina; staining is concentrated chiefly in two bands at the borders of the inner plexiform layer; most cells in the ganglion-cell layer are stained, and there is a suggestion of staining of occasional cells along the innermost aspect of the inner nuclear layer, where the amacrine cells are located. The only difference in the retinas from rabbits in which the optic nerve had been sectioned several months previously was the absence of neuronal elements, and consequently of AChE staining, in the ganglion-cell layer (Fig. 1C). This would indicate that centrifugal fibers from the optic nerve could account at most for only a minimal portion of the AChE of the inner plexiform layer. One-half hour after treatment with DFP, there was no evidence of staining for AChE anywhere in the retina, with incubation periods up to 7 hours. In retinas from eyes removed 5 or 7 hours after treatment with DFP, the fibers of the inner plexiform layer remained unstained, but there was distinct staining of the somata of the amacrine cells and of a considerable number of cells in the ganglion-cell layer (Fig. 1D).

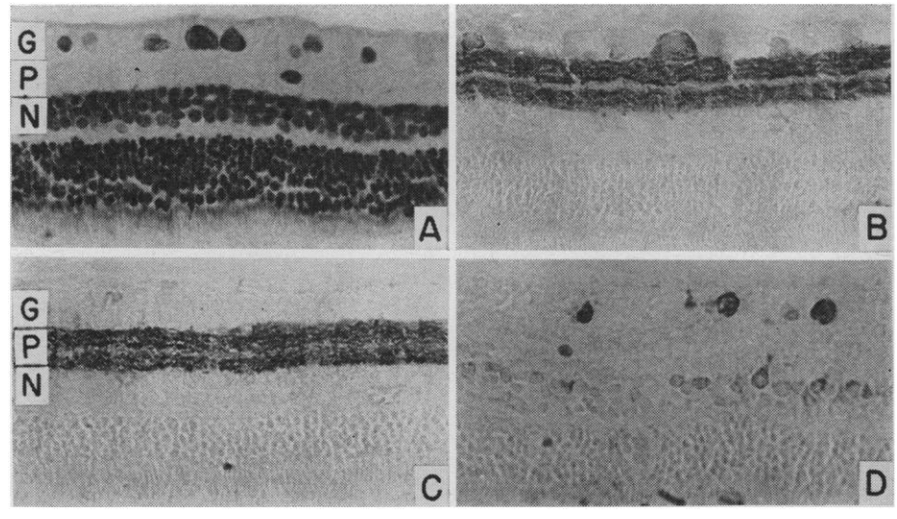

Fig. 1. (A) Normal rabbit retina; cresyl-violet stain. (B) Normal rabbit retina; section incubated 1 hour with acetylthiocholine for localization of AChE. (C) Rabbit retina 6 months after sectioning of optic nerve; stained for AChE as in B. (D) Normal rabbit retina from eye removed 7 hours after 4 mg of DFP per kilogram was given intravenously. The section was incubated 5 hours with acetylthiocholine for localization of AChE. *G*, Ganglion-cell layer; *P*, inner plexiform layer; *N*, inner nuclear layer (× 290).