

# NONSYNCHRONOUS SPATIAL OVERLAP OF LIZARDS IN PATCHY HABITATS<sup>1</sup>

THOMAS W. SCHOENER

*Biological Laboratories, Harvard University, Cambridge, Massachusetts 02138*

**Abstract.** Sympatric native *Anolis* species with similar structural habitats but contrasting climatic habitats are closer in head and body size on species-rich than on depauperate islands.

In two localities, sympatric *Anolis* species with differential occurrences in sun or shade sought lower, more shaded perches during midday, resulting in partly nonsynchronous utilization of the vegetation by the two species.

The second observation may be related to the first in the following way: nonsynchronous spatial overlap could dictate relatively great resource overlap for species coinhabiting patchy or edge areas, requiring great differences between the species in prey size in addition to those in climatic habitat. The extent of such overlap on small depauperate islands could be greater if these contained a greater proportion of patchy or edge habitats (with respect to insolation), or if climatic preferences were broader and more overlapping than on large, species-rich islands.

In each locality, the relatively more shade-inhabiting species occurred more often on larger perches and on lower perches than did the other species. In both species of the Bermudan pair, adult males occupied higher and larger perches, and in *grahami*, shadier perches, than did female-sized individuals. The statistical significance of these and other differences was evaluated using several unweighted  $\chi^2$  procedures, Cochran's weighted  $\chi^2$  test and a partitioning technique for analyzing interactions among variables in complex contingency tables. The last method is described in detail in the paper by Fienberg, immediately following this one.

The ways in which closely related species differ in their utilization of resources have long been of interest in ecology. Implicit in this work is sometimes the notion that species which differ markedly in one major niche dimension, for example, a feature of the climatic habitat, need not differ in another major dimension, for example, food size, in order to co-exist. Associations of species such as those described below which at first seem to contradict this idea require a quantitative evaluation of niche differences in order to rank these differences according to their relative importance in resource segregation. Of special value in the latter type of analyses are the particularization and measurement of the kinds of resource overlap (Kohn 1966, Horn 1966, MacArthur and Levins 1967).

Certain lizard species of the genus *Anolis* in the West Indies furnish an example of sympatric congeners whose patterns of resource utilization differ in two major ways. On Grenada, Schoener and Gorman (1968) found that its two *Anolis* species, *aeneus* and *richardi*, so markedly unlike in head and body size, could be characterized in the same area by very different body and ambient air temperatures. Insolation preferences of the two species contrast throughout Grenada. In the same species, the larger the head and body size, the larger the average prey size and proportion of large prey (for an elaboration see Schoener and Gorman 1968). Despite highly significant statistical differences between the prey size distribu-

tions of the two species, common utilization of certain prey sizes was considerable.

A clear difference in climatic habitat between lizards on a two-species island is apparently not restricted to those on Grenada, but has been found for every species pair in the Lesser Antilles that has been carefully observed (G. C. Gorman, R. Ruibal, R. Thomas, pers. comm.). In some of the pairs involving *wattsii*, definite differences in perch height have been noted as well (R. Ruibal, G. C. Gorman, R. Thomas, J. D. Lazell, pers. comm.). Yet in all cases, the species differ markedly in size and by a factor considerably greater than most of those observed by Hutchinson (1959) and Schoener (1965) among sympatric birds (Table 1).

On the larger islands of Jamaica and Puerto Rico, pairs of species whose habitats differ primarily with regard to climatic characteristics are never more different in size than pairs of species on the Lesser Antilles and are often a good deal more similar. Table 1 lists associations from these islands whose species have structural habitats (as defined by Rand 1964, and primarily involving perch height and diameter) known to be very similar where they are allopatric, but whose modal climatic habitats are known to be very distinct (Rand 1964, 1967b, Williams and Rand in prep., Schoener in prep.). All such associations are included.

When the same kind of associations are considered on the two largest islands of the West Indies, Cuba and Hispaniola, with 23 and 21 species of *Anolis* respectively, an even more consistent

<sup>1</sup> Received February 7, 1969; accepted October 9, 1969.

size similarity appears, though the average number of species in the associations is larger than on the smaller islands (Table 1). All such associations whose species are widespread are included

TABLE 1. Sets of native *Anolis* species with similar structural habitats but with partially or entirely opposing climatic preferences. Species in each set are arranged in order of decreasing tendency to inhabit shaded and/or closed habitats. Sets involving *wattsi* also show a fairly marked difference in structural habitat

Island	No. <i>Anolis</i> species on island	Species	Mean male head length (mm) <sup>a</sup>	Sample size <sup>b</sup>	Head length larger/head length smaller
Grenada	2	<i>richardi</i>	30.8	16	1.70
		<i>aeneus</i>	18.1	16	
St. Vincent	2	<i>richardi</i>	31.1	13	1.82
		<i>trinitatis</i>	17.1	16	
Antigua	2	<i>wattsi</i>	14.9	23	1.93
		<i>leachi</i>	28.8	20	
Nevis	2	<i>wattsi</i>	14.2	4	1.91
		<i>bimaculatus</i>	27.1	29	
St. Eustatius	2	<i>wattsi</i>	14.3	24	1.65
		<i>bimaculatus</i>	23.6	20	
St. Kitts	2	<i>wattsi</i>	14.3	7	1.95
		<i>bimaculatus</i>	27.9	21	
St. Martin	2	<i>wattsi</i>	13.5	8	1.45
		<i>gingivinus</i>	19.6	31	
Jamaica	7	<i>grahami</i>	19.4	77	1.38
		<i>opalinus</i>	14.1	84	
		<i>lineatopus</i>	19.0	45	1.39
		<i>sagrei</i>	13.7	31	
Puerto Rico	10	<i>gundlachi</i>	19.3	17	1.01
		<i>cristatellus</i>	19.2	147	
		<i>evermanni</i>	19.8	27	1.46
		<i>stratulus</i>	13.6	45	
		<i>krugi</i>	14.9	24	1.01
		<i>pulchellus</i>	14.8	48	
Hispaniola	21	<i>poncensis</i>	13.2	18	1.12
		<i>christophe</i>	13.4	11	1.01
		<i>distichus</i>	13.6	238	
		<i>brevirostris</i>	12.7	46	1.07
		<i>cybotes</i>	20.8	86	1.09
		<i>whitemani</i>	19.1	6	
Cuba	23	<i>semilineatus</i>	12.4	25	1.01
		<i>cochranae</i>	12.6	12	
		<i>olsoni</i>	11.8	47	1.07
		<i>allogus</i>	15.9	87	1.09
		<i>homolechis</i>	14.6	124	
		<i>sagrei</i>	14.4	142	1.01
		<i>alutaceus</i>	10.6	40	1.09
		<i>ophiopsis</i>	9.7	26	
		<i>argenteolus</i>	14.3	25	1.14
		<i>argillaceus</i>	12.5	18	

<sup>a</sup>Specimens measured from collections of Museum of Comparative Zoology, American Museum of Natural History, Albert Schwartz private collection, United States National Museum, Field Museum of Natural History, Carnegie Museum, University of Michigan Museum of Zoology and Florida State Museum.  
<sup>b</sup>Means are of the largest third of the entire collection; justification of this sampling technique is given in Schoener (1969). The truncated samples are slightly skewed, but medians only different from means by 0-0.3 mm.

in Table 1; those with very localized geographic ranges are left out but in general agree with the trend. The habitats of these species have been described by Collette (1961), Ruibal (1961, 1964), Rand (1962, 1964), Thomas and Schwartz (1967), Williams (1961), and Williams and Rand (1961, in prep.).

To summarize, species which differ markedly in climatic habitat tend to be much more dissimilar in size on islands of low *Anolis* species diversity than on islands of high diversity, even though the latter species have been chosen for minimal structural habitat differences. Thus an interesting problem emerges: why is it necessary for species on islands of low diversity to differ strikingly in size when those on islands of high diversity seem to be able to coexist without a great size difference? The most obvious general hypothesis is that the average degree of spatial overlap differs on the two kinds of islands. That hypothesis would gain credence if there were a mechanism which resulted in spatial overlap for species with contrasting climatic preferences on islands of low diversity.

This paper reports a study of two pairs of *Anolis* species previously noted as being different in climatic habitat (Rand 1967b, Wingate 1965). Both sets were observed in vegetation that was patchy with respect to insolation and, hence, presumably with respect to temperature and relative humidity. The comparative structural habitats of the members of these pairs do suggest a mechanism of spatial overlap and in addition suggest why that mechanism should be more common on small than on large islands. These results, while far from conclusive, thus provide hypotheses applicable to the size patterns described above and suggest a new direction for more intensive studies of spatial overlap.

SUBJECTS AND METHODS

The first pair studied, *Anolis grahami* and *A. opalinus*, are found in the same general area at many localities throughout Jamaica. In both the mesic and drier lowlands, *opalinus* occupies more shaded places than does *grahami*; Rand (1967b) has documented this difference (and an associated one in average body temperature) for a seasonally dry area near Kingston, and it has been observed in many other vegetation types as well (Rand 1967b, Schoener in prep., Williams, pers. comm.). In the subtropical regions of higher altitude (> 800 m) *grahami* becomes rare or absent (Underwood and Williams 1959), and there *opalinus* is often found in opener, sunny habitats. Both species are considered "trunk-crown" according to the habitat classification of Williams and Rand (in

prep.). They are very similar in structural habitat where allopatric, but in the same vegetation their structured habitats can be quite different (see below). The plot selected for study was located ca. 1.5 km west of Whitehouse, Westmorland Parish. It consisted of groups of trees and shrubs which remained after clearing for grazing. A section of this area closest to the coast had been partially planted in limes and pimentos. The study plot was bordered by extremely open tracts, inhabited mostly by *grahami* or by a third species, *Anolis sagrei*, and by thickly wooded slopes, inhabited mostly by *opalinus*. The study area was, according to the classification of Asprey and Robbins (1953), "cultivated pasture and second-growth scrub" and was bordered by remnants of "dry limestone scrub forest," or by forest transitional between that and "wet limestone forest." The diurnal weather cycle was consistent during the study period (July 21–27): sunny during the morning and partly cloudy during the early and midafternoon, the clouds sometimes producing heavy downpours.

The second pair studied, *grahami* and *Anolis roquet extremus*, are sympatric at various localities in Somerset Parish, Bermuda. Wingate (1965) has noted that *extremus* inhabits darker, more shaded places than does *grahami*. Both species occurred abundantly and evenly throughout the study plot: a filled mangrove area where the patchy vegetation consisted of similarly sized trees overlaying a moderate-to-dense understory. Most of these trees were *Avicennia nitida*, and there were scattered *Rhizophora mangle* and *Juniperus bermudiana*. The average height of the trees was greater and the understory more herbaceous than near Whitehouse, but in general the two localities were quite similar. Weather during the study period (August 15–19) was similar to that near Whitehouse, but the maximum temperature was lower and the amount of precipitation slight.

The method of data acquisition was similar to that developed first by Rand (1964). Each lizard seen in the study plot was noted as to its size and sex (if possible), its species, the height and diameter of its perch, the time of observation, and whether it was in the sun or shade. The latter judgment, of course, could not be made when clouds blurred the sharp shadows produced under full sun. Data were recorded for each individual only once per "census" and only the position where first spotted was used; if the lizard was obviously disturbed by the observer, no data were taken. Study areas were repeatedly censused during the day, and the census route was varied considerably from one observation period to the next. These data are sufficient to describe a particular species

or size class of lizard with respect to the volume of foliage occupied within a given small area.

## RESULTS

Table 2 presents frequency grids of structural habitat and insolation for each of seven time periods and for each species and size class.<sup>2</sup> The single most striking feature of these data is the tendency for the species in each pair to cycle with respect to perch height and insolation, being more often high and in the sun during early morning and evening than at midday. This cycling results in adult male *extremus* or *opalinus* occupying much the same perches early and late in the day that adult male *grahami* do during midday. The chief residual difference is in perch diameter. The same is true to a lesser degree for female-sized lizards on Bermuda.

In order to see these patterns more clearly, per cent overlap,  $100(1 - \frac{1}{2} \sum_i |p_{x,i} - p_{y,i}|)$ , where  $p_{x,i}$  and  $p_{y,i}$  are the frequencies of species  $x$  and  $y$  respectively in category  $i$ , was computed for several classes of the lizards in each study area. The figures in Table 3 represent per cent overlap of the habitat observations of a given species or intra-specific class during each time period with those observations from each of the seven time periods for the other lizard species or class. Frequency values used to compute per cent overlap are those listed in Table 2, plus the frequencies for the few observations on the ground and on leaves in the three height intervals of Table 2. With very few exceptions, observations of *extremus* or *opalinus* during early or late time periods overlap more with midday observations of *grahami* than with those during early or late periods. In addition, midday observations of the former two species overlap more with midday observations of *grahami* than with those of any other time period.

For *grahami* males versus *extremus* males, the greatest values of overlap are always during the fourth or fifth time period (1130–1629); if the probability of the greatest overlap value being in a given time period is assumed identical for each time period (i.e.,  $1/7$ ), then the probability that the greatest overlap value should always occur during the fourth or fifth period is  $P = 0.0002$ . The lowest of the per cent overlap values occurs always in the sixth or seventh period ( $P = 0.0002$ , considered independently of the greatest overlap values). Female-sized *grahami* versus *extremus* always

<sup>2</sup> Adult males of both species on Bermuda are considerably larger than females. It is very difficult to accurately distinguish small males from females in the field. Hence the two classes "adult males" and "female-sized individuals" are used in the comparisons. Only a single class of the less dimorphic *opalinus* of Jamaica was used.

TABLE 2. Frequency grids for perch height-diameter categories. Perch diameter decreases from left to right; column headings are  $\geq 2$  in., 0.75–1.75 in.,  $< 0.75$  in.<sup>a</sup> Perch height decreases from top to bottom; row headings are  $> 8.75$  ft, 5–8.75 ft,  $< 5$  ft. Figures are the per cent of the total number of observations for a single lizard class during a single time interval. Observations of lizards on ground or leaves are included in totals but were very few

Bermuda							
Time period	1 (0830–0929)	2 (0930–1029)	3 (1030–1129)	4 (1130–1345)	5 (1430–1629)	6 (1630–1729)	7 (1730–1830)
Adult male <i>grahami</i>							
SUN	N=40 8 13 3 3 8 3 3 5 8	N=38 8 5 3 8 5 8 0 0 5	N=41 2 0 5 2 0 2 12 2 5	N=88 2 3 2 6 5 3 3 1 10	N=72 7 4 1 3 10 3 3 1 0	N=33 6 3 12 6 9 6 3 9 0	N=40 10 15 5 8 3 5 13 5 8
SHADE	8 8 0 8 13 3 5 5 3	5 16 5 8 11 3 3 5 3	12 12 0 17 10 7 5 2 0	10 6 1 15 13 3 6 6 3	8 10 0 14 15 7 14 0 0	0 15 6 9 12 3 0 0 0	8 0 0 8 3 3 5 3 3
Female-sized <i>grahami</i>							
SUN	N=74 0 11 10 3 11 15 11 1 5	N=62 2 5 8 2 13 16 0 3 7	N=56 4 5 5 5 2 11 4 11 7	N=98 2 5 2 1 9 15 2 1 9	N=71 1 6 3 7 11 13 1 1 6	N=39 3 5 0 8 10 13 3 0 10	N=48 6 6 8 8 10 10 8 8 2
SHADE	3 3 0 7 3 3 3 3 4	3 3 2 2 7 16 3 2 8	4 2 0 5 4 9 6 7 4	1 5 2 9 7 13 4 2 5	1 7 0 4 10 10 6 7 3	3 8 5 0 10 8 5 3 5	4 0 0 8 0 4 10 0 0
Adult male <i>extremus</i>							
SUN	N=44 2 2 2 5 5 2 5 0 2	N=33 0 0 0 0 0 6 0 0 0	N=22 0 5 0 0 0 0 0 0 5	N=44 0 0 0 2 7 0 2 0 0	N=41 0 7 0 2 5 0 0 0 0	N=17 6 0 0 6 6 0 6 6 0	N=26 8 4 0 23 4 0 0 4 0
SHADE	9 11 2 14 0 2 23 5 10	9 3 0 18 15 12 21 12 3	9 0 0 27 18 5 27 5 0	9 7 0 16 21 5 23 7 2	5 7 2 20 17 2 20 7 5	6 6 0 12 6 6 29 6 0	8 4 0 15 8 0 15 4 4
Female-sized <i>extremus</i>							
SUN	N=19 0 5 0 5 0 5 5 0 0	N=23 0 0 0 9 9 0 4 0 0	N=16 0 0 0 0 6 0 6 0 0	N=22 0 0 0 5 0 0 0 5 0	N=20 0 0 0 0 0 0 5 0 0	N=19 0 5 0 5 0 5 5 11 5	N=13 0 0 0 15 0 0 8 0 8
SHADE	0 11 0 11 16 5 21 5 5	0 0 4 9 17 0 30 17 0	0 13 6 13 6 6 19 6 13	5 0 5 18 0 9 23 18 14	10 20 0 10 15 15 25 0 0	0 5 5 21 11 5 11 5 0	0 0 0 15 8 0 31 15 0
Jamaica							
Time period	1 (0730–0829)	2 (0830–0929)	3 (0930–1029)	4 (1030–1129)	5 (1130–1529)	6 (1530–1729)	7 (1730–1830)
Adult male <i>grahami</i>							
SUN	N=28 4 4 4 11 7 4 11 7 0	N=32 0 0 0 3 3 0 0 0 3	N=29 0 0 0 0 0 3 0 0 0	N=23 0 0 0 0 0 0 4 0 4	N=49 0 0 0 0 0 0 0 0 2	N=18 0 0 0 0 6 0 6 0 0	N=11 0 0 9 9 9 0 9 0 9
SHADE	4 0 0 11 7 7 11 7 0	9 6 0 6 19 0 16 28 3	10 3 0 7 17 3 48 3 3	4 0 0 9 4 4 52 13 0	4 6 2 18 10 2 25 22 8	6 6 0 11 6 11 11 11 17	0 0 0 0 18 0 18 9 0
Female-sized <i>grahami</i>							
SUN	N=36 0 0 0 0 6 3 6 8 19	N=55 2 0 0 0 4 4 6 7 6	N=42 0 0 0 0 5 0 5 2 2	N=42 0 0 0 0 0 5 0 0 5	N=56 0 0 4 0 0 2 2 0 4	N=25 0 0 0 0 12 16 0 0 0	N=17 0 0 0 0 6 6 0 6 12
SHADE	0 3 0 6 8 14 0 11 11	0 0 0 2 6 13 16 7 18	0 0 3 0 7 7 26 19 14	0 0 0 0 10 19 10 17 14	0 2 2 4 5 21 14 16 23	0 0 0 4 4 8 8 0 34	0 0 0 0 18 6 18 18 6



TABLE 2.—Continued

Jamaica							
Time period	1 (0730–0829)	2 (0830–0929)	3 (0930–1029)	4 (1030–1129)	5 (1130–1529)	6 (1530–1729)	7 (1730–1830)
Male and female <i>opalinus</i>	N=14	N=24	N=21	N=18	N=24	N=23	N=11
SUN	0 0 0 0 0 0 14 0 7	0 0 0 0 0 0 4 4 0	0 0 0 0 0 0 5 0 5	0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 9 4 9	0 0 0 9 0 0 9 9 0
SHADE	0 0 0 0 0 14 49 14 0	0 0 0 4 8 4 33 21 17	0 0 0 5 5 0 43 33 5	0 0 0 17 0 0 39 33 11	0 0 0 4 13 0 67 17 0	9 0 0 0 0 0 35 30 4	9 0 0 9 27 0 0 9 9

\*The class,  $\geq 2$  in., was originally divided into  $> 4$  in. and  $\leq 4$  in., but was lumped here. That division, however, was used in comparison 7 of the text.

have their highest overlap values in the third through fifth time periods (1030–1729) ( $P = 0.0027$ ). All of the lowest values are in periods 1, 2 or 7 ( $P = 0.0027$ ). Turning to *grahami* adult males versus *opalinus*, six of the seven highest values are in the fourth or fifth time periods (1030–1529) ( $P = 0.003$ ); six of the seven lowest values are in the first, second or last time period (730–929, 1730–1830) ( $P = 0.027$ ). In both cases the single exception is the last *opalinus* time period, the one with the fewest observations. For female-sized *grahami* versus *opalinus*, all but one (the last time period again) of the highest overlap values are in the third time period (930–1029) ( $P = 5.2 \times 10^{-5}$ ) and all of the lowest values fall in the sixth time period ( $P = 1.2 \times 10^{-6}$ ).

In other words, during the earliest part of the day, the relatively sun-seeking *grahami* are on sunnier and to a certain degree smaller (more exterior) perches compared with the relatively shade-preferring species. As the day warms up, *grahami* find it necessary to seek shadier perches, much the same as those formerly occupied by *extremus* or *opalinus*. Meanwhile, the latter two species seek still shadier perches, which are of course more similar to perches of *grahami* during midday than to those of that species during early or late periods. As the sun sets and the temperature drops, all species move out into the sun, but differentially as before, so as to reproduce in a crude way the situation at the start of the cycle. Inger (1959) has found similar nonsynchronous spatial overlap for two skinks, *Sphenomorphus sabanus* and *Mabuya rudis*, along edges in Bornean rain forest.

Adult male versus female-sized lizards of *grahami* show a different and less consistent pattern of overlap. At the Bermudan locality, overlap of observations of female-sized lizards with those of adult males is greatest most often during the second or last time period ( $P = 0.003$ ) and in five

cases is least during midday ( $P = 0.023$ ). At the Jamaican locality, overlap is greatest most often with those taken during the sixth or seventh period ( $P = 0.003$ ) and least most often with those taken during the third or fourth period ( $P = 0.003$ ). Synchronous spatial overlap on Bermuda shows no clear association with time of day, being least during periods transitional between early and midday when many more females than males are in the sun (see below and Table 2). On Jamaica, where the maximum daily temperature is greater, synchronous overlap is least during midday and greatest during the latest times.

Contrary to *grahami*, observations of female-sized *extremus* overlap least with those of adult males taken during the last time period (six of the seven lowest values fall here;  $P = 5.2 \times 10^{-5}$ ). No regularity for greatest overlap values is evident. But also unlike the same classes of *grahami*, there is no significant difference in sun-shade occurrence between *extremus* classes at the locality studied (see below).

The measure of overlap used above is more or less sensitive to sample size, depending upon properties of the distributions being sampled. While it is possible that certain comparisons (e.g., male *grahami* versus *extremus*) show relatively high overlap partially because of higher sample size, such an artifact is not coincident with most of the differences.

During cloudy weather (observations not tabulated) *extremus* takes positions similar to those occupied when the sun is relatively low. For most time intervals, the cloudy weather distributions of perch height and diameter for adult males of both species, as measured by per cent overlap, are more similar to those in shade than to those in sun during clear weather. However, for female-sized *grahami*, cloudy weather perches during early and late times show a greater similarity to perches recorded in the sun.

Next, it is of interest to analyze in some detail the habitat differences between the species and classes at each locality and to compare these dif-

TABLE 3. Per cent spatial overlap<sup>a</sup> of species or intra-specific classes in various time periods. Headings 1 to 7 are time periods as expressed in Table 2

	Time period							Period with greatest overlap	Period with least overlap
	1	2	3	4	5	6	7		
Adult male <i>extremus</i>	Adult male <i>grahami</i>								
1.....	58	59	60	69	66	46	50	4	6
2.....	48	46	56	61	64	33	35	5	6
3.....	49	43	52	58	60	27	37	5	6
4.....	61	51	58	68	74	42	37	5	7
5.....	62	59	51	67	69	44	40	5	7
6.....	59	53	56	61	68	50	51	5	6
7.....	59	57	49	63	66	44	53	5	6
Female-sized <i>extremus</i>	Female-sized <i>grahami</i>								
1.....	43	38	50	51	57	54	44	5	2
2.....	31	25	32	36	44	41	40	5	2
3.....	37	38	38	48	46	47	35	4	7
4.....	26	33	43	35	36	32	36	3	1
5.....	25	33	32	42	39	36	32	4	1
6.....	45	43	62	55	59	57	54	3	2
7.....	39	32	34	41	43	36	39	5	2
Female-sized <i>grahami</i>	Adult male <i>grahami</i> (Bermuda)								
1.....	60	55	50	54	45	50	66	7	5
2.....	55	55	45	52	47	48	47	2	3
3.....	62	59	52	62	47	51	66	7	5
4.....	63	62	51	66	57	53	50	4	7
5.....	68	71	54	68	60	55	54	2	7
6.....	63	70	49	66	57	56	50	2	3
7.....	56	55	49	50	58	61	67	7	3
Female-sized <i>extremus</i>	Adult male <i>extremus</i>								
1.....	68	69	61	71	73	64	54	5	7
2.....	52	57	58	67	62	66	48	4	7
3.....	70	56	47	66	66	66	50	1	3
4.....	64	68	55	59	62	60	51	2	7
5.....	60	71	64	71	59	64	45	4	7
6.....	54	58	60	56	64	60	54	5	7
7.....	52	56	59	62	55	65	46	6	7
<i>opalinus</i>	Adult male <i>grahami</i>								
1.....	36	33	55	76	43	39	44	4	2
2.....	42	52	56	63	68	57	40	5	7
3.....	32	60	59	74	63	41	42	4	1
4.....	29	53	53	61	72	44	27	5	7
5.....	29	49	68	74	56	32	40	4	1
6.....	35	59	50	61	57	38	45	4	1
7.....	53	49	40	31	41	44	46	1	4
<i>opalinus</i>	Female-sized <i>grahami</i>								
1.....	38	47	55	43	48	16	45	3	6
2.....	50	60	80	53	62	37	58	3	6
3.....	35	45	62	41	49	21	50	3	6
4.....	28	37	56	37	45	23	41	3	6
5.....	24	31	50	36	39	16	47	3	6
6.....	34	43	59	35	40	12	53	3	6
7.....	49	36	35	33	29	17	39	1	6
Female-sized <i>grahami</i>	Adult male <i>grahami</i> (Jamaica)								
1.....	48	37	30	34	40	58	38	6	3
2.....	54	43	37	47	43	68	44	6	3
3.....	44	54	44	59	65	64	46	5	1
4.....	38	45	33	40	48	56	40	6	3
5.....	43	47	37	45	55	63	39	6	3
6.....	37	25	26	25	26	57	25	6	4
7.....	50	61	49	44	56	45	65	7	4

<sup>a</sup>Computed on the basis of the categories in Table 2, plus three categories for leaves at different heights and one for the ground.

ferences with those found among other *Anolis* groups elsewhere. If data are lumped, the following general trends emerge:

(1) *grahami* occur in the sun rather than shade more often than do individuals of the other species ( $P < 0.001$  for Bermuda in a one-tailed  $\chi^2$  test, following the procedure of Siegel 1956;  $P < 0.05$  for Jamaica).

(2) *grahami* occur higher than do individuals of the other species ( $P < 0.001$  in both cases, using the intervals  $\geq 5$  ft or  $< 5$  ft).

(3) *grahami* occur on thinner perches than do individuals of the other species ( $P < 0.001$  in both cases, using the intervals  $\geq 2$  in. or  $< 2$  in.).

(4) Adult male *grahami* occur on higher perches than do female-sized *grahami* ( $P < 0.001$  in both cases, using the intervals  $\geq 9$  in. and  $< 9$  in.).

(5) Adult male *grahami* occupy thicker perches than do female-sized *grahami* ( $P < 0.001$  in both cases, using the intervals  $\geq 0.75$  in. and  $< 0.75$  in.).

(6) Adult male *extremus* occur on higher perches than do female-sized *extremus* ( $P < 0.05$ , using the intervals  $\geq 5$  ft and  $< 5$  ft).

(7) Adult male *extremus* occupy thicker perches than do female-sized *extremus* ( $P < 0.05$ , using the intervals  $> 4.25$  in. and  $\leq 4.25$  in.).

(8) Adult male *grahami* occur less often in the sun than do female-sized *grahami* ( $P < 0.001$  on Bermuda and  $P < 0.05$  on Jamaica).

Results (1) and (3) bear out some of Rand's (1967b) and Wingate's (1965) observations. Results (4) and (6) agree with tendencies found for *porcatus* (Collette 1961), *lineatopus* (Rand 1967b), *conspersus* (Schoener 1967), *sagrei* (Schoener 1968), *richardi* (Schoener and Gorman 1968), and *opalinus* near Kingston (Rand 1967b), but they differ from patterns in species such as *distichus* and possibly *angusticeps* on Bimini (Schoener 1968). Results (5) and (7) agree with patterns found in nearly all classes of *Anolis* of very different size for which sufficient data were sampled (Schoener 1967, 1968, but see Rand and Rand 1967 for a possible exception). Intraspecific differences in structural habitat have been described for other genera of lizards as well (Blair 1960, Tinkle, McGregor and Dana 1962, Hirth 1963a,b, Rand 1967a).

The procedure of lumping all the data together in order to construct a single  $2 \times 2$  contingency table for each of the above comparisons may be objected to on the grounds that some of the environmental variables used in the separate comparisons might be highly associated (for example, sunny perches and small perches). This could easily result in the probabilities that the observa-

tions fall into one or the other level of a particular environmental variable being different for different combinations of the other environmental variable or variables. If that is suspected to be the case, it is not recommended that the data all be lumped (Cochran 1954). One method for taking into account this possibility, suggested by Simpson, Roe and Lewontin (1960, p. 326 ff), is to break down the data in such a way as to construct a series of  $2 \times 2$  tables for each of the two variables being compared (for example, *grahami* perch diameters versus *extremus* perch diameters). Each table of this series holds all the other variables being tested constant (for example, perch height, insolation, and time period), and there are as many tables in such a series as there are different combinations of levels of those other variables.  $\chi^2$  and  $\chi$  values are computed for each table separately, and the latter are assigned a sign depending on whether the difference between the classes being compared is in the expected or opposite direction. The quantity  $\Sigma\chi/\sqrt{n}$  is distributed as a standard normal deviate, where  $n$  is the number of separate tables in the comparison. Using the 12 contingency tables formed by combining the 2 levels for perch height, 2 for perch diameter, 3 for time [early (periods 1 and 2), midday (periods 3–5) and late (periods 6 and 7)] and 2 for insolation (sun, shade), each of the above intra- or interspecific comparisons was repeated, and the new probabilities ( $P_1$ ) are given in Table 4.

Probabilities of no association of certain habitat variables are also given there.

Inspection of this table reveals that nearly all of the above numbered comparisons are still significant; only that between Jamaican adult male and female-sized *grahami* with respect to insolation is not (8).

This more complicated analysis, while superior to the simpler one, still contains several disadvantages, among them being the fact that a large fraction of the quantity  $\Sigma\chi$  may be contributed by tables involving a relatively small number of observations, in which, however, association between the variables is very high (Simpson, Roe and Lewontin 1960). More specifically, if the totals of the number of observations in the individual tables are different by a ratio of more than 2 to 1, or the proportions of the observations in the two categories being compared fall outside the range 0.20–0.80, the method is not very suitable (Cochran 1954). Cochran has proposed a weighted  $\chi^2$  test which compensates for these problems (see also Bliss 1967 for a discussion of this test). New probabilities from this more complicated test were computed and are listed under  $P_2$  in Table 4. In all cases but one, the presence or absence of statistical significance remains the same, though the probabilities of no association are usually lower by Cochran's test. The one exception is the association between perch insolation, and perch diameter on Jamaica, clearly not significant if a weighted  $\chi^2$  is used.

TABLE 4. Probability of no association for several habitat variables and classes of lizards in study plots on Bermuda (B) or Jamaica (J)

Groups being compared	Group vs. perch height		Group vs. perch diameter		Group vs. insolation	
	$P_1^a$	$P_2^b$	$P_1$	$P_2$	$P_1$	$P_2$
<i>grahami</i> : <i>extremus</i>	0.013	0.0014	<0.0002	<0.0002	<0.0002	<0.0002
<i>grahami</i> adult males: female-sized <i>grahami</i> (B)	0.0006	0.003	<0.0002	<0.0002	0.010	0.0012
<i>extremus</i> adult males: female-sized <i>extremus</i>	0.015	0.013	0.038	0.011	0.84	0.70
<i>grahami</i> : <i>opalinus</i>	<0.0002	<0.0002	0.0004	0.0002	0.032	0.026
<i>grahami</i> adult males: female-sized <i>grahami</i> (J)	0.002	0.0002	<0.0002	<0.0002	0.093	0.093
Groups being compared	perch height vs. perch diameter		perch height vs. insolation		perch diameter vs. insolation	
	$P_1$	$P_2$	$P_1$	$P_2$	$P_1$	$P_2$
<i>grahami</i> : <i>extremus</i>	<0.0002	<0.0002	0.52	0.86	0.0046	0.0004
<i>grahami</i> adult males: female-sized <i>grahami</i> (B)	0.0004	0.0002	0.060	0.061	<0.0002	0.0002
<i>extremus</i> adult males: female-sized <i>extremus</i>	<0.0002	<0.0002	0.19	0.12	0.51	0.41
<i>grahami</i> : <i>opalinus</i>	0.035	0.0046	0.41	0.94	0.35	0.23
<i>grahami</i> adult males: female-sized <i>grahami</i> (J)	0.55	0.47	0.37	0.48	0.025	0.14

<sup>a</sup> $P_1$ =unweighted combined  $\chi^2$  probability  
<sup>b</sup> $P_2$ =Cochran's weighted  $\chi^2$  probability

Cochran's method and the unweighted procedure attempt to look at the interaction between a pair of variables in a multidimensional table. However, it is preferable to examine several interactions between pairs of variables *simultaneously* and incorporate all of these into some model whereby the expected numbers of observations in its cells can be compared with the observed. A method in which the iterative procedure of Deming and Stephan (1940) is linked to such models was recently presented by Bishop (1969). It has been used to handle complex contingency tables similar to the ones found here (Mosteller 1968, 1969). The reader should consult the paper by Fienberg (1970) immediately following this one, for a more detailed exposition and a justification of the method.

Briefly, the procedure was as follows. For each of the five sets of data listed in Table 4, a model was first set up containing all possible two-factor or pairwise interactions between the five variables. Thus there are 10 two-factor interactions for each model. Then observed marginal totals were computed for each pair of variables by adding the observed counts over the remaining variables. These marginal totals are summary two-way tables, and the number of cells in such a table is equal to the product of the number of levels in one variable and the number of levels in the other. For example, the height versus time margin contains six cells, and each observation belongs to one of these. Considering these observed marginal totals as targets for the table of expected values, the iterative procedure was used to adjust a set of equal initial values so that they combine to produce the target marginal totals within a preassigned degree of accuracy, in this case 0.5 observations. Usually four iterations were required. The cell values so computed are considered the expected values, and both the standard  $\chi^2$  measure of goodness of fit and the log-likelihood ratio  $\chi^2$  (Kullback 1959) were computed. Both these statistics have the same  $\chi^2$  distribution for sample sizes large enough, where the degrees of freedom are computed in the way described by Ku and Kullback (1968) or by Fienberg in the article immediately following this one. In four of the five sets of data, the models containing all two-factor interactions gave satisfactory fits at the 5% level or better as judged by both these criteria (Table 5).

Next, simpler models were formed by dropping certain of the interactions, to test whether models with fewer parameters could be constructed which still gave satisfactory fits. By inspection of the data and Table 4, it was possible to eliminate interactions roughly in the order in which their deletion would least affect goodness of fit. After

TABLE 5. Values of standard  $\chi^2$  and log-likelihood ratio  $\chi^2$  for models of 5-way contingency tables<sup>a</sup>

Interactions fitted	Standard $\chi^2$	Log-likelihood ratio $\chi^2$	df
<i>grahami: extremus</i>			
[SH] [SD] [SI] [HD] [HI] [DI] [IT]	56.4	53.2	33
difference between models		20.7+	3
[SH] [SD] [SI] [ST] [HD] [DI] [IT]	43.8*	42.7*	32
difference between models		10.2+	2
[SH] [SD] [SI] [ST] [HD] [DI] [DT] [IT]	33.0*	32.5*	30
difference between models		0.3	3
All 2-factor interactions	32.7*	32.2*	27
<i>grahami</i> adult males: female-sized <i>grahami</i> (Bermuda)			
[SH] [SD] [HD]	110.0	102.2	38
difference between models		19.3+	1
[SH] [SD] [HD] [DI]	86.4	82.9	37
difference between models		25.9+	2
[SH] [SD] [HD] [DI] [IT]	56.1	57.0	35
difference between models		10.4+	1
[SH] [SD] [SI] [HD] [DI] [IT]	46.6*	46.6*	34
difference between models		4.8+	1
[SH] [SD] [SI] [HD] [HI] [DI] [IT]	41.8*	41.8*	33
difference between models		10.7	6
All 2-factor interactions	29.7*	30.1*	27
<i>extremus</i> adult males: female-sized <i>extremus</i>			
[SH] [SD] [HD]	46.5*	49.9*	38
difference between models		13.5+	2
[SH] [SD] [HD] [IT]	29.0*	36.4*	36
difference between models		0	1
[SH] [SD] [SI] [HD] [IT]	29.0*	36.4*	35
difference between models		10.5	8
All 2-factor interactions	23.9*	25.9*	27
<i>grahami: opalinus</i>			
[SH] [SD] [SI] [HD]	94.9	95.5	37
difference between models		53.5+	2
[SH] [SD] [SI] [HD] [IT]	41.4*	42.0*	35
difference between models		8.7+	2
[SH] [SD] [SI] [ST] [HD] [IT]	29.7*	33.3*	33
difference between models		5.6	3
[SH] [SD] [SI] [ST] [HD] [DI] [DT] [IT]	23.8*	27.7*	30
difference between models		2.6	3
All 2-factor interactions	20.9*	25.1*	27
<i>grahami</i> adult males: female-sized <i>grahami</i> (Jamaica)			
[SH] [SD] [SI] [ST] [DI] [DT] [IT]	48.9	48.7	31
difference between models		3.4	4
All 2-factor interactions	42.0	45.3	27
[SH] [SD] [SI] [ST] [DI] [DT] [IT] [DIT]	44.3	43.9	29
difference between models		4.1	4
All 2-factor interactions plus [DIT]	37.1*	39.8	25

<sup>a</sup>Interactions are between five variables: sex or species (S), height (H), diameter (D), insulation (I) and time (T).  
\*Model provides satisfactory fit at 5% level.  
+Difference significant at 5% level.

each elimination, the difference between models was evaluated for significance according to the method of partitioning expounded in Kullback (1959) and Ku and Kullback (1968). In this approach, the difference between the log-likelihood ratio chi-squares for the two models can be used to test the hypothesis that the difference between expected values for the two models is due to random variation. The degrees of freedom for this difference are equal to the difference in degrees of



freedom of the two models. Interactions were eliminated, one or two at a time, until such elimination produced a model giving a fit significantly poor at the 5% level, and/or until the difference between models was judged significant. In cases where the new fit was poor but the difference between models was not significant, both models are reported (Table 5), since neither is clearly superior. The interactions remaining for each set of data after its model is sufficiently simplified can be considered non-zero.

For the intraspecific comparison of *grahami* on Jamaica, whose five-way table gives an unsatisfactory fit even when all first-order interactions are included, two kinds of improvements were tried. The first was to eliminate interaction pairs as was done for the other four sets in the hope that the increase in degrees of freedom would proceed sufficiently more rapidly than the increase in  $\chi^2$ , so that a satisfactory model would eventually be obtained. Although at least three interactions could be removed without giving a significant difference between models, the fit was still not satisfactory by the 5% criterion. By comparison of the observed with the expected values for each cell, it was decided that the three-factor interaction [diameter  $\times$  insolation  $\times$  time] might be non-zero. Therefore, a model was tested in which this interaction was included along with all two-factor interactions. That model provided a satisfactory fit according to the standard  $\chi^2$  criterion but not according to the log-likelihood ratio  $\chi^2$  criterion. The same three two-factor interactions were then dropped, and although the difference between models was not significant, the simpler model no longer quite fit by the 5% criterion for either measure. Inclusion of other three-factor interactions would most likely result in an improved fit.

When an interaction or association is said to be significant, what is meant is that variability in the data cannot account for the non-zero interaction at a particular significance level. It is therefore interesting that all associations listed as significant in Table 4 by either test are contained in the preferred model or models for each of the five sets of data. In addition, some interactions not tested by the simpler methods were also found to be important (Table 5). First, there is a significant association between species and time for both study areas: the shade-preferring species was seen relatively less often during midday, probably because on its then mostly shady perches it is often concealed. Second, the insolation-time interaction is important in all cases; as discussed above, lizards of all species are more likely to be found in the sun during early morning or late afternoon than during midday.

Associations between the habitat variables are most interesting and confirm the general impression given by the vegetation structure.

For the intraspecific comparisons in the Bermuda study plot, perches of *grahami* are smaller at lower heights than at greater heights, but the reverse is the case for perches of *extremus*. This is to be expected, since *grahami* are often found in the herbaceous understory, whereas *extremus* are nearly always found on the trees; the habitat of the former thus has many small diameter perches at low heights whereas most small perches in trees are relatively high. The combined totals for the two species, using the same height intervals as were used in the *extremus* comparison, parallel the result for the latter. On Jamaica, intraspecific comparisons between classes of *grahami* show no significant relation between perch height and diameter, but if observations of both species are combined, small perches are found significantly higher than are large perches. However, the probability of no association is greater. These results are probably due to the vegetation on the Jamaican study plot comprising a greater variety of species and hence of shapes and sizes of plants, so that a tendency for trees to individually have smaller branches at greater heights is partially obscured when observations from all trees and shrubs are combined.

For two of the three Bermudan comparisons, there is a strong tendency for sunnier perches to be thinner. Thinner perches are more likely to be found at sunny exteriors of plants than within. The association is also significant for the intraspecific comparison on Jamaica but only by the unweighted test, and the probability is much higher. However, data for *grahami* on Jamaica give some evidence, as pointed out above, for a three-way interaction between diameter, insolation and time (Table 5).

None of the "preferred" models included the height-insolation interaction, implying that that interaction is small considered in terms of the variability of the data and the other interactions. That result should be much more likely true within very patchy vegetation such as that of the study plots than within continuous forest.

Despite the above tests, the problem remains that it is not possible to separate entirely the effects of climatic preference upon structural habitat in these data. For example, the individual tests show that for both sunny and shady perches taken separately, *grahami* occur on significantly smaller perches than do *extremus*. But the lizards may not be responding to the "instantaneous" insolation of the perch at the time of the observation but rather to the temperature or relative humidity

of the air surrounding that perch. These latter quantities are less correlated with present conditions than with some measure of cumulative insolation, wind conditions or other variables over some time period prior to the observation. Thus while we can state that there are significant differences in the distributions of perch heights, diameters and sun-shade observations, we cannot yet state which of these is purely a consequence of preferences for different states of another variable. Controlled experimental work would seem best for answering the latter kind of question (e.g., Sexton and Heatwole 1968).

#### IMPLICATIONS

The kind of nonsynchronous spatial overlap documented in the last section must of course be restricted to edges where the preferred vegetation of the two species is abutting. Since the proportion of such areas is greatest in patchy habitats like those of the two study plots, overlap should be especially common there. Now while some of the insect prey of these lizards will cycle synchronously with their predators, others certainly will not; hence it is possible that in patchy areas resource overlap would be considerable between species of the same size, considerable enough to favor the evolution and/or maintenance of size differences between the species enabling them to select differently sized foods.

If differences in the degree of spatial overlap are to produce the size pattern discussed in the introduction, it would be necessary that either or both of the following be true: the proportion of patchy or edge habitats is greater the smaller the island, or the relative degree of generality or similarity in requirements is such that even in areas with exactly the same vegetation structure, species on small islands overlap more than on larger islands (see below). While the second phenomenon may seem likely, the first could be sufficient by itself to favor the difference in the sizes of sympatric species. It seems likely that small islands contain a greater proportion of edge habitats if for no other reason than that the circumference of an island and associated coastal vegetation should increase roughly as the square root of that island's area. Of course, on very small islands, the vegetation can be quite uniform, but there climatically distinct *Anolis* species should not and do not usually occur (Schoener 1969).

The two hypotheses posed as alternatives may in fact be causally related. If the proportion of continuous habitat does increase with island size, then the probability that a given individual on a large island has patchy vegetation in its home range is less than that probability for an individual

on a small island. Hence individuals on small islands would be likely to evolve a greater degree of behavioral generality with respect to climatic factors than on larger islands. While it could be argued that individuals may simply avoid occupying such composite home ranges, they might then be too scattered to breed successfully. Studies on the sets of species in Table 1 in comparable habitats on the different islands are needed to test these hypotheses.

The species association investigated on Jamaica is a natural one, both species having apparently evolved in situ (Williams and Rand in prep.). The two can be found in adjacent and interdigitating vegetation types throughout the island, and they are intermediate in their size difference (Table 1). To what degree their present-day contiguity is an artifact of man's interference is unknown.

In contrast to Jamaica, the species on Bermuda have overlapped for only about 14 years: *grahami* formerly enjoyed solitary status in western Bermuda from about 1935, and it did not occur on Bermuda at all before its purposeful introduction from Jamaica in 1905 (Wingate 1965); *extremus*, introduced from Barbados, is and probably always was the only species of *Anolis* on that island. Although rigorous proof is lacking, casual observation suggests that while *grahami* is restricted to open or edge areas on Jamaica (Rand 1967b, Williams and Rand in prep., Schoener in prep.), *extremus* is not at least now found merely in closed or edge areas on Barbados (G. C. Gorman, pers. comm.). The species are very alike in size, both on their islands of origin and on Bermuda. Thus species interaction on Bermuda was observed soon after its inception, and the existing pattern of resource partitioning may be taken as an example of one of the first stages of the fusing of species' ranges. As such, it supports the "compression" hypothesis of MacArthur and Pianka (1966), elaborated in MacArthur and Wilson (1967), that an early consequence of the coming together of two species should be that "the variety of occupied habitats (or more correctly the space searched) should shrink, or at least be altered, but the range of foods within the occupied habitats should not (MacArthur and Wilson 1967, p.107)." It will be interesting to see to what extent the two species have yet to change and whether situations such as that in Somerset will prove stable.

#### ACKNOWLEDGMENTS

I thank S. E. Fienberg, A. S. Rand, R. Ruibal, A. Schoener, P. Vanzolini, E. E. Williams, and E. O. Wilson for a critical reading of the manuscript, and the following curators for assistance with their collections: E. E. Williams, C. M. Bogert and R. Zweifel, A. Schwartz and

R. Thomas, D. Cochran and J. A. Peters, R. F. Inger, N. Richmond, C. Walker and W. Auffenburg. I am grateful to S. E. Fienberg and R. C. Lewontin for advice on statistical aspects. I also thank D. B. Wingate on Bermuda and C. B. Lewis, T. Farr, and I. Goodbody on Jamaica for assistance in the field and those individuals mentioned above who have allowed me to see unpublished data. Data analysis and write-up were supported by National Science Foundation grants GB-6944 to E. E. Williams and GS-2044X to the Department of Statistics, Harvard University. The study was carried out while the author held National Science Foundation Graduate Fellowships (1966-67; 1968-69) and a General Biological Supply House Scholarship (1967-68).

## LITERATURE CITED

- Asprey, G. F., and R. C. Robbins. 1953. The vegetation of Jamaica. Ecol. Monogr. 23: 359-412.
- Bishop, Y. M. M. 1969. Full contingency tables, logits, and split contingency tables. Biometrics 25: 383-400.
- Blair, W. F. 1960. The rusty lizard: A population study. U. of Texas Press, Austin.
- Bliss, C. I. 1967. Statistics in biology. Vol. 1. McGraw-Hill, New York.
- Cochran, W. G. 1954. Some methods for strengthening the common  $\chi^2$  tests. Biometrics 10: 417-451.
- Collette, B. B. 1961. Correlations between ecology and morphology in anoline lizards from Havana, Cuba and southern Florida. Bull. Mus. Comp. Zool. Harv. 125: 137-162.
- Deming, W. E., and F. F. Stephan. 1940. On a least squares adjustment of a sampled frequency table when the expected marginal totals are known. Ann. Math. Statist. 11: 427-444.
- Fienberg, S. E. 1970. The analysis of multidimensional contingency tables. Ecology 51: 419-433.
- Hirth, H. F. 1963a. The ecology of two lizards on a tropical beach. Ecol. Monogr. 33: 83-112.
- . 1963b. Some aspects of the natural history of *Iguana iguana* on a tropical strand. Ecology 44: 613-615.
- Horn, H. S. 1966. Measurement of "overlap" in comparative ecological studies. Amer. Naturalist 100: 419-424.
- Hutchinson, G. E. 1959. Homage to Santa Rosalia, or Why are there so many kinds of animals? Amer. Naturalist 93: 145-159.
- Inger, R. F. 1959. Temperature responses and ecological relations of two Bornean lizards. Ecology 40: 127-136.
- Kohn, A. J. 1966. Food specialization in *Conus* in Hawaii and California. Ecology 47: 1041-1043.
- Ku, H. H., and S. Kullback. 1968. Interactions in multidimensional contingency tables: an information theoretic approach. J. Res. Nat. Bur. Stand. Math. Sci. 728: 159-199.
- Kullback, S. 1959. Information theory and statistics. Dover Publications, New York.
- MacArthur, R. H., and E. Pianka. 1966. On optimal use of a patchy environment. Amer. Naturalist 100: 603-609.
- MacArthur, R. H., and R. Levins. 1967. The limiting similarity of coexisting species. Amer. Naturalist 101: 387-400.
- MacArthur, R. H., and E. O. Wilson. 1967. The theory of island biogeography. Princeton U. Press, Princeton.
- Mosteller, F. 1968. Association and estimation in contingency tables. J. Amer. Statist. Assoc. 63: 1-28.
- . 1969. Statistical comparisons of anesthetics: the national halothane study. Bull. International Statist. Inst.
- Rand, A. S. 1962. Notes on Hispaniolan herpetology: 5. The natural history of three sympatric species of *Anolis*. Breviora 154: 1-15.
- . 1964. Ecological distribution in anoline lizards of Puerto Rico. Ecology 45: 745-752.
- . 1967a. Ecology and social organization in the iguanid lizard *Anolis lineatopus*. Proc. U. S. Nat. Mus. 122: 1-79.
- . 1967b. The ecological distribution of the anoline lizards around Kingston, Jamaica. Breviora 272: 1-18.
- Rand, A. S., and P. J. Rand. 1967. Field notes on *Anolis lineatus* in Curaçao. Stud. Fauna Curaçao 93: 112-117.
- Ruibal, R. 1961. Thermal relations of five species of tropical lizards. Evolution 15: 98-111.
- . 1964. An annotated checklist and key to the anoline lizards of Cuba. Bull. Mus. Comp. Zool. Harv. 130: 476-520.
- Schoener, T. W. 1965. The evolution of bill size differences among sympatric congeneric species of birds. Evolution 19: 189-213.
- . 1967. The ecological significance of sexual dimorphism in size in the lizard *Anolis conspersus*. Science 155: 474-477.
- . 1968. The *Anolis* lizards of Bimini: resource partitioning in a complex fauna. Ecology 49: 704-726.
- . 1969. Size patterns in West Indian *Anolis* lizards: I. Size and species diversity. Syst. Zool. 18: 386-401.
- Schoener, T. W., and G. C. Gorman. 1968. Some niche differences among three species of Lesser Antillean anoles. Ecology 49: 819-830.
- Sexton, O. J., and H. E. Heatwole. 1968. An experimental investigation of habitat selection and water loss in some anoline lizards. Ecology 49: 762-768.
- Siegel, S. 1956. Nonparametric statistics. McGraw-Hill, New York.
- Simpson, G. G., A. Roe, and R. C. Lewontin. 1960. Quantitative zoology. Harcourt and Brace, New York.
- Thomas, R., and A. Schwartz. 1967. The *monticola* group of the lizard genus *Anolis* in Hispaniola. Breviora 261: 1-27.
- Tinkle, D. W., D. McGregor, and S. Dana. 1962. Home range ecology of *Uta stansburiana stejnegeri*. Ecology 43: 223-229.
- Underwood, G., and E. E. Williams. 1959. The anoline lizards of Jamaica. Bull. Inst. Jamaica Sci. Ser. 9: 5-48.
- Williams, E. E. 1961. Notes on Hispaniolan herpetology: 3. The evolution and relationships of the *Anolis semilineatus* group. Breviora 136: 1-8.
- Williams, E. E., and A. S. Rand. 1961. Notes on Hispaniolan herpetology: 2. A review of the *Anolis semilineatus* group with the description of *Anolis cochraniae*, new species. Breviora 135: 1-11.
- Wingate, D. W. 1965. Terrestrial herpetofauna of Bermuda. Herpetologica 21: 202-218.