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ANOLIS NEWSLETTER, 1st, 1972

February 24, 1972

The "First" Anolis Newsletter

Dr. William Sievers
Systematic Biology
National Science Foundation
Washington, D.C. 20550

Dear Dr. Sievers:

The two year report enclosed is lengthy and elaborate, but I feel that this is necessary because of the diversity of approaches which our group working under NSF B 019801X are bringing to bear on a single but complex subject.

I have also, I confess, the objective of summarizing for myself and for our whole group the totality of our effort of which each individual has seen only a small part. Though in the interest of cross-communication and cross-fertilization I have instituted a "Lizard Ecology Discussion Group" at Harvard and we have had rather regular and quite profitable sessions, there has still been insufficient opportunity to fill in the general picture.

I enclose also a budget for the projected third year. It seems unlikely at the time of writing that any funds will be left from our first two years. The budget is therefore much like that originally presented except for those adjustments necessary because of modifications of personnel and plans. Cost sharing will conform to current NSF policy. Overhead has been increased in accordance with Negotiation Agreement A-88 between the Department of Health, Education and Welfare and Harvard University.

Sincerely yours,

Ernest Williams

Ernest Williams

Enclosures

EW/aim

Approved:

A. W. Crompton, Director
Museum of Comparative Zoology

Approved:

M. C. Barstow, Director
Office for Research Contracts

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A Two - Year Report
for NSF B 019801X

The general problem which we have tried to attack under the grant is that of the effects upon and within species of interaction with other species. We have used for this study diurnal New World lizards, especially Anolis. The levels of approach have been quite diverse, descriptive, analytical, theoretical, and the methods any which seemed likely to provide results.

In fact an enumeration of the methods we are using may be a good introduction to the scope of our project.

A. Field Studies

1. censuses: records of sightings or captures as evidence of species distribution, density, activity, perch, etc.

2. continuous observation: Study of single individuals for shorter or longer periods provide a supplement to the preceding where foraging strategies, mating, home range, etc. are concerned.

3. mark and recapture: This, of course, provides the long term evidence on population turnover, persistence, replacement, and longevity.

4. filmed behavior: We have recorded in this way displays either natural or in response to introduced animals of the same or different species. (This is fundamental in the study of communication within and between species.)

5. collection: Specimens have been collected for karyotyping and electrophoresis to provide evidence on genetic difference or similarity, and on genetic heterozygosity and on relationship.

B. Laboratory and experimental studies:

1. studies of display patterns with captured animals
2. choice experiments (See below.)
3. maze experiments (See below.)

C. Computer analysis, including simulation testing of competition equations for goodness of fit to empirical data.

D. Modelling. Verbal models or more elaborate mathematical studies are being used.

The results of these diverse methods are being reported in series of papers, published, in press, and in preparation that deal with individual facts and ideas in a fashion that provides no synthesizing theme. I have found it useful to attempt organization of our apparently amorphous mass of information in two ways:

(1) in *terms of faunas of varying sizes* since these faunas can be thought of as the units in which species interactions occur.

(2) in *terms of general topics or methods* where our activities cannot be satisfactorily summarized in terms of faunas or areas.

I. Faunal studies and comparisons.

One anole faunas:

Old one anole islands. We have recently looked at one anole faunas on Guadeloupe and on Dominica, two of the largest islands of the Lesser Antilles, and those in which Lazell (1962, 1964*) has found very striking geographic variation. It was easy to confirm the sharpness of the changes seen in travelling around these islands; Lazell's subspecific names conform closely to real biological phenomena. Some populations morphologically very remarkable e.g. *setosus* on Guadeloupe have very small ranges (a few miles). Ecological differences are clear for some of the subspecies in Guadeloupe (*girafus* on the arid west coast, *alliaceus* in montane forest. The ecological correlates for others are quite unclear. The dewlap color and display patterns of each of the populations on the main double island of Guadeloupe and on Marie Gallante and also on Dominica have been studied (Rand). Dewlap color and display patterns do not correspond to intra-island variation in morphology or body color in either Guadeloupe or Dominica. Electrophoretic techniques have been used to examine the genetic differentiation of five subspecies on Guadeloupe: *girafus*, *marmoratus*, *setosus*, *inornatus* and *speciosus*. The observed differences are slight; only albumen may differ enough to permit clear separation of the subspecies (Webster). In spite, however, of Webster's result it is hard to avoid a prediction that the very striking external differences which are shown by geographically replacing populations on Guadeloupe do act to limit gene flow and have evolved with that function. Just such sharp differences in body color and pattern are the kinds of external signals that are frequently involved in species recognition and act to limit or prevent gene flow. (Theoretical studies of the concept of "gene flow" are in preparation by Roughgarden.)

Thermoregulation was investigated on Guadeloupe (Webster and Huey) and on Dominica (Rand) because of Ruibal and Philobosian's (1970**) description of eurythermy in *A. oculatus* of Dominica. It was fully confirmed that on both these islands even adjacent individuals might be operating under quite different thermal regimes, and that at quite different body temperatures these solitary anoles performed all ordinary diurnal activities without obvious differences in efficiency. Rand, however, observed on Dominica a social aspect to thermoregulation. Adult males of *A. oculatus* choose perches thermally different from those utilized by subadult anoles. These latter are probably sub-optimum, but social dominance prevents the subadults from using the best perches.

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* Bull. MCZ 127: 466-475; Bull. MCZ *131*: 359-401.

**Copeia 1970: 645-653.

Other Lesser Antillean Islands are old one anole islands also and, as on Guadeloupe and Dominica, these "solitary" anoles have evolved their characters *in situ* but these other "solitary" anoles do not show clear intra-island geographic variation. In other respects, however, study by Rand has shown all Lesser Antilles 'solitary anoles to have very similar features. Not only, as already shown by Schoener (1970*), do they tend to a certain size range (ca 60-70 mm snout-vent length in males) but they all show:

1. strong sexual size dimorphism

2. All have uniform yellow dewlaps.

3. Dewlaps are moderately large in all.

4. Displays may differ between island banks but show no intra-island differentiation.

5. Body color differs sharply on the different island banks, as well as sometimes within islands.

6. There is strong sex dichromatism.

Two anole faunas: old two anole islands:

Again the Lesser Antilles provide the only examples. Work under the current grant has been on dewlaps and displays and on climatic niche (Rand). Again patterns emerge:

1. As previously pointed out by Schoener (1970*) the two species of two anole islands usually differ strikingly in size by a factor of about two. There is sexual dimorphism as well.

2. Dewlaps are yellow in both species on all the two anole islands.

3. Dewlaps may be relatively small in the larger of a species pair.

4. Displays may differ between islands but show no intra-island differentiation.

5. The two species of pairs differ in body coloration but show reduced or absent sexual dichromatism.

6. In northern Lesser Antilles the smaller of the species pair prefers wetter shadier areas, the larger the more exposed sunnier situations. In the southern Lesser Antilles the reverse is true.

Four anole faunas:

There are no old four anole faunas extant. The four-anole fauna of the Great Bahama Bank is the only one available for study, and is young -- derived during the Pleistocene from Cuba and Hispanolia. The cautionary statement must therefore be made that part at least of the ecology and character of each of the four species was acquired in the complex faunas of the source islands.

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* Amer. Nat. 104: 155-174.

In any event the four anoles of South Bimini on the Great Bahama Bank have been subjected to a more thoroughgoing and meticulous study than any other anole fauna or in fact any tropical lizard fauna anywhere. Schoener has used all possible methods: census, individual observation, mark and recapture. A summary of his results follows:

a. *Population density and relative abundance of the species.* The population density of the species on the study areas has not yet been computed exactly, but Schoener is in a position to calculate this as or more accurately than in any previous studies on lizards because he 1) had under observation every lizard that inhabited any part of the area on a long-term basis, and 2) knew with a fair degree of accuracy what fraction of each individual's home range fell within the study area. He tentatively estimates that there were two anoline lizards per square yard in the two major study areas and that the four species had abundances which were roughly geometrically distributed (*sagrei* > *distichus* > *carolinensis* > *angusticeps*).

b. *Foraging behavior.* Much of the fieldwork consisted of watching individual lizards for long periods of time, ranging from 1/2 hour to 4 hours, in half-hour increments. During these observations he was able to obtain a fairly complete description of foraging behavior, even though these lizards take prey much less frequently than birds or other warm-blooded vertebrates.

Each of the species is different in some respects from each of the others, the two most similar being *angusticeps* and *carolinensis*, which also occur in fairly similar vegetation structure. Of particular interest was the difference in foraging technique between *distichus* and *sagrei*, a difference more extreme than could have been surmised from the gut analyses of a previous study. *Distichus* feeds mostly on ants, an aggregated prey which the lizard can capture immediately with little pursuit or searching effort. Because of the small size of their prey, most eat a relatively large number of items and therefore have a relatively great feeding rate per unit time. *Sagrei*, on the other hand, is a specialist on large, non-aggregated prey: adult males especially eat very infrequently (about one item every 1 and 1/2 hours), pursue prey over relatively great distances, and have a relatively long handling and swallowing time per item. Individuals of *sagrei* have often been seen ignoring ants except when the ants are carrying some much larger insect. Then the *sagrei* will dart down to the ant column and try, usually successfully, to rob the ants of their food. Thus both species tend to deplete ant populations, but in a different way.

Schoener will also be able to describe the relationship between several characteristics of the predation process. For example, there is a relation between pursuit distance and swallowing time: the greater the distance travelled, the longer the minimum handling and swallowing time. The shape and position of this relation when calculated will provide data for wild predators against which predictions (e.g., Schoener 1969*) about optimal foraging strategies can be checked. This sort of data has previously been virtually restricted to artificial laboratory situations.

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* Amer. Nat. 103: 277-313.

Home range plots for *sagrei* over a 10-week period show considerable overlap. Unfortunately, some of the changes occurred faster than they could be traced in a statistically significant way. In the other study area where no such temporary food source appeared, territories of *sagrei* were fare more stable.

In addition to the information on spacing patterns, Schoener has made many observations on social behavior *per se*. For example, he recorded the result of all aggressive interactions, so that he would be able to document any relations which may exist between body size, site attachment or other factors and social dominance. Although not yet collated, the data will probably conclusively show that larger individuals win more often in aggressive encounters for all species.

c. *Growth rates and development to maturity*. Even over a 10-week period, Schoener was able to gather clear-cut data on the relative rates of growth of the sexes for the most abundant species. These data showed that males grew more rapidly than females of the same size; males in all four species reach an absolutely greater size, but even in the least dimorphic species (*distichus*) a marked difference in growth rate was evident. He also found that sub-adult males sometimes (perhaps often) tended to eat faster and for more extended periods of time than did females of the same size. Such data, combined with the previously ascertained fact that subadult male stomachs contain more items than do those of similarly sized females, provide an interesting contrast in the energetics of growth to maturity for the sexes.

The same four anoles have had attention even beyond that received from Schoener. T. P. Webster has made collections on South Bimini partly supported by the grant for electrophoretic study in Selander's laboratory in Texas. A paper by Webster and Selander on genetic similarity and variability in these four species has been submitted to *Evolution*. The following is a summary:

Estimates of genetic difference for the four species were about 0.7 on a scale of 1 to 1.0 for any comparison of the four. (Other evidence - osteology, morphology, external characters - is at variance with this: *sagrei* would be very different from the rest, and *angusticeps* and *carolinensis* very close by these other measures). Three populations of *carolinensis* from the continental United States were found to be virtually identical, but Bimini *carolinensis* differed from these by 31%. Difference of 18% was found between Bimini and Jamaican *sagrei*. Webster and Selander conclude that such studies of electrophoretic differences are most useful between close relatives. For more distantly related species the approximation of genetic difference to genetic distance is no longer useful.

Tests of genetic variability (genetic heterozygosity) were made for the four Bimini species also. They were found to differ significantly in the amount of variability detected at 23 loci. These heterozygosities, could not be explained by any taxonomic, zoogeographic or ecological relationship among the species. However, there is a correlation with the extent of morphological differentiation shown by the species both in their source areas and on the islands they have colonized.

A seven anole fauna: Jamaica has been studied by Schoener, by Trivers, and is being studied by Webster and by Rand and Williams.

Schoener's field studies on Jamaica were completed before the current grants. His analysis of data, however, was only completed recently and owes much to a statistical method described by Fienberg. Schoener's most interesting result is the discovery that the four commonest lowland anoles are arranged in the vegetation so that there is a *direct* relationship between perch diameter and body size *within* species but an inverse relationship between species. This arrangement permits maximum interspecific separation of similarly sized animals in the vegetation.

Schoener's statistical analysis also permitted him to detect the maximum differences in perch height and perch diameters (taken separately) between the various lizard classes. This permits a better definition of ecological types of anoles based on perch heights and diameter ("ecomorphs", see below) than has ever before been possible.

Schoener's climatic correlations show female sized individuals of three of the Jamaican species to be more frequently in sunnier (*grahami* and *opalinus*) or shadier perches (*sagrei*) than males of the same species. This clearly requires comparison with Rand's observations on Dominica, where Rand explained parallel results by social interaccions which exiled smaller anoles to sub-optimum situations.

Trivers' work documents some significant aspects of population biology for two of the Jamaican species -- *A. garmani* and *A. valencienni*. *A. garmani* is a strongly sexually dimorphic species in which Trivers has been able to show that the larger the males the more frequently do they copulate and with the larger females, have larger territories with more females in residence. The females of *garmani* show similar but lesser increase in mating success with size. *A. valencienni* in contrast shows little sex dimorphism and only slight territoriality, the female apparently none.

Trivers emphasizes sexual selection in the *garmani* case and has gone on to a theoretical discussion of the parameters and consequences of sexual selection.

Williams has interested himself in the history of the Jamaican fauna, endeavoring to see whether the niches found in this relatively small fauna represent any stage regularly occurring in the evolution of larger faunas such as those of Hispaniola and Cuba. There are several interesting aspects of the Jamaican fauna: there are no grass anoles, an ecological type present on the other Greater Antilles, all of which have larger faunas. There are no geographically replacing species with similar perch preferences, nor any species very similar but with different climatic niches. *A. lineatopus* breaks into climatically differentiated and geographically replacing populations but these are clearly subspecific. *A. valencienni* (snout-vent length ca. 80 mm) is very different from the other Jamaican species in that it is in foraging strategy a searcher and not a sit-and-wait predator and unless *A. darlingtoni*, similar in size and appearance, is similar in ecology, it has no analogues except the *dwarf* twig searchers (ca. 40 mm) of the other Greater Antilles (*A. isolepis*, *A. insolitus*, *A. occultus*). It is tempting to ascribe many of these differences between the other Greater Antilles and Jamaica to the latter's smaller land area and hence smaller fauna, and this is Williams' hypothesis at the moment.

Williams has, however, been unable to define with any confidence the sequence of speciation in the intra-island radiation of anoles in Jamaica. Ecological hypotheses are possible but these cannot be tested by any phylogeny of Jamaican anoles based on non-ecological evidence: no such phylogeny exists. Webster is therefore endeavoring to find electrophoretic evidence on the similarity or difference of the Jamaican species. The results have thus far demonstrated the closeness of relationship of the Jamaican species but not much else. Investigations are still proceeding.

Rand and Williams are interested in the features involved in species recognition. In Jamaica it is evident that there are multiple cues to species identity -- size, body color *and* dewlap -- a step therefore beyond the simpler islands of the Lesser Antilles in which body color and size were the cues and dewlaps identical.

A ten anole fauna: The mainland of Puerto Rico boasts ten species. Our understanding of these is well along.

Here again Schoener and Schoener have provided the most careful analysis of anole niches in terms of the two parameters of structural habitat and climatic habitat. His most interesting result is the discovery that the two crown species - *stratulus* and *evermanni* are far more often syntopic than the trunk-ground species - *cristatellus* and *gundlachi* the striking size difference between *stratulus* and *evermanni* is postulated as necessitated by this strong tendency to syntopy. Schoener and Schoener use here the same careful statistical analysis provided for Jamaica.

Gorman has only just begun his studies on Puerto Rico and neighboring islets. The reproductive data so far collected for this area are interestingly different from those previously collected in Jamaica and Hispaniola. Six species are being studied in detail: *A. cristatellus*, *A. stratulus*, and *A. krugi*, *A. evermanni* and *A. gundlachi* from montane elevations only whereas in Jamaica and Hispaniola females showed high sensitivity to rainfall (100% reproductive in wet periods, non-reproductive in dry periods), on Puerto Rico of the three montane species, the female which had been reproductively active in October showed marked decline in reproductive activity in November and December despite high rainfall and very minor fall in temperature. Lowland *A. cristatellus* on the other hand showed no marked decline in reproductive activity in either upland or lowland localities. *A. stratulus* females in both upland and lowland localities on mainland Puerto Rico virtually ceased producing eggs in December, yet a Virgin Islands sample of the same species in late December showed virtually 100% female activity. *A. pulchellus* is very puzzling. The lowland population declined to about 10% reproductive activity, but at 800 feet where *pulchellus* overlaps *krugi* (altitude 1500 feet it is replaced by *krugi*) the *pulchellus* population was still virtually 100% reproductive in mid-December and early January. These puzzles and similar puzzles in male reproductive behavior in Puerto Rico will doubtless be unraveled with further study.

Gorman is also studying female receptivity (female caught in copulo always have oviducal eggs), mating activity (seen in October and November, not in December or early January) and recruitment of young.

Gorman is collaborating with Michael Soule in electrophoretic studies of A. cristatellus populations from five Puerto Rican localities, Anegada, Virgin Gorda, Tortola, St. Thomas, five small islands near St. Thomas and St. John. About 20 loci will be examined in Soule's laboratory and the attempt will be to determine genetic variation as a function of island size and habitat diversity. It is hoped to extend this study to the other common Puerto Rico bank species.

Simultaneously Gorman hopes to obtain data on "immunological distance" between the several Puerto Rican species, probably with Vincent Sarich of the University of California at Berkeley. Again he is collecting material for study of DNA content per nucleated cell, this analysis in conjunction with Ralph Hinegardner of the University of California at Santa Cruz.

Gorman has obtained incidental information on the extent to which weather and time of day influence the frequency of observations and capture in the Puerto Rican anoles. He is following this lead with especial emphasis on _A. stratulus_.

Williams has found it possible to use the anole fauna of Puerto Rico to test a model of faunal buildup. The model accepts as a first premise the importance of size adaptation in the initial stages of faunal accumulation. An empirical basis for such a premise is found in the striking size difference found in species pairs in the two-anole islands of the Lesser Antilles. Purely as a simplification character displacement in size is treated in the model (1) as if it were the only _initial_ modification by which species secondarily coming into contact coadapt. and (2) the ratio (approximately two times) by which the larger of the species of a two anole island in the Lesser Antilles differs from the smaller is taken to be the necessary ratio by which coexisting anole species will differ _if_ other factors than size are not to be called into play.

When this simplest hypothesis of faunal build-up is carried forward into further stages of complexity, it is found still to work for the next stage - i.e. three coexisting species may differ by the size ratios 1-2-4. Any stage beyond this (i.e. 1-2-4-8, four species with ratios, five species with the ratios 1-2-4-8-16) would take the largest or the smallest species to a size which would require structural, physiological or ecological modifications other than size alone. Such changes would violate the model in its pure form, requiring as it does that no change other than size occur. Empirically there appears to be in any case an upper and lower limit to anole size, and character displacement by size alone would not carry beyond the three species stage.

A look back at the Lesser Antilles (used always as the model for a model) shows that, though less well-documented than the size change, all two anole islands have the two members of a species differing not only in size but also in climatic niche and in perch height. It remains true that size difference is the most obvious feature of the Lesser Antillean species pair; the other two aspects are subtler. However, it will clearly be more realistic to allow changes in the climatic and the perch height axes as well as in a size axis.

There appear to be no grounds for assigning priority to either of these alternative axes and it is probable that they may often be considered essentially simultaneous. Use of these other axes permits completion of an ecological history of the 10 anole fauna of Puerto Rico.

In the case of Puerto Rico - and at present in no other case - it is possible to match this ecological history against a phylogeny of Puerto Rican anoles based on classic morphological and karyotypic characters. The match is quite surprisingly good and hence does provide an example of an ecological analysis of the history of faunas (sequences in faunal build-up) which is more than the mere insertion of ecological stages into dendrograms or faunal histories constructed on wholly non-ecological grounds.

The Larger Islands (Cuba, Hispaniola) --

General remarks:

Williams has attempted to carry the concepts of faunal history which he employed with some success for Puerto Rico to the two largest Greater Antillean islands. As mentioned above, however, there are no sound phylogenies based on non-ecological characters. Some complexities, also, on these islands seem to result solely from island size. There are, for example, geographically replacing forms -- vicariants -- in each of these islands. *A. argenteolus*, *A. lucius* and *A. bartschi* are one such series in Cuba. *A. homolechis* and *A. quadriocellifer* are a pair of such species in Cuba. *A. equestris* is said by Schwartz and Garrido to break into a series of geographically replacing, minimally overlapping species. The so-called races of *A. ricordii* on Hispaniola may be a similar series. The giant anoles of neither Puerto Rico nor Jamaica break up in this way (but Puerto Rico does have *A. roosevelti* as a vicariant of *A. cuvieri* on Culebra). A substantial fraction of the species count on both Hispaniola and Cuba are vicariants.

A second complication, most important for Hispaniola, is the division between montane and lowland faunas. A montane species does occur in Jamaica (*A. reconditus*), one does also in Cuba (*A. clivicolus*), but while something of a division between montane and lowland species is said to be true in Puerto Rico, except for *A. occultus* which seems genuinely montane, the separation is more nearly a matter of wet and dry regions. Hispaniola, however, has whole series of montane endemics, and not one but several montane faunas.

However, all the large islands display a standard series of ecological types, of "ecomorphs" definable by habitat and structure, which Williams calls the "main sequence" - inferring by this that these ecological types are the most readily evolved and most stable adaptive configurations possible to a radiating anole fauna.

These large island "ecomorphs" are specialists peculiar to and characteristic of complex anole faunas. They are very different from the anoles of the one-anole or two-anole islands. The latter are, comparatively speaking, generalists; they too are definable by habitat and structure, but, because he believes they may represent the adaptive type from which the "standard" ecomorphs of the large islands evolved, Williams calls these "central" ecomorphs.

Without naming them Rand described the Puerto Rican representatives of the standard ecomorphs in 1964.* Rand and Williams in 1969** gave them informal names and defined them crudely in terms of their *modal* perches. New data, including those provided by Schoener and Schoener,*** permit more precise definitions in terms of perch frequency determined by actual census. Thus trunk-crown species have more than 60% of their perches above seven feet in the tree crowns *or* below seven feet on trunks more than 2 1/4 inches in diameter. Trunk-ground species have more than 60% of their perches below seven feet on trunks of more than 2 1/4 inches diameter (or on the ground) or on bushes of less than 2 1/4 inches diameter. Grassbush anoles have more than 90% of their perches less than 2 1/4 inches in diameter. The newer definitions are not only better than the old in being quantitative but in admitting that in addition to a modal perch, ecomorphs frequently have a second perch which may be nearly (or quite) as frequent as that we formerly called modal.

The hypothetical Puerto Rican history provided an expected sequence for the evolution of standard ecomorphs and seemed to imply that this would be a simple and regular phenomenon. Consideration of the faunas of the other Greater Antilles forces the admission of some limitations on this idea: (1) in both Cuba and Hispaniola (in Cuba unquestionably, in Hispaniola according to the hypothesis stated in Rand and Williams 1969, p. 13) the anole fauna is not a unit radiation as it is believed to be in Puerto Rico and as six of the seven species of Jamaica are assumed to be. In Cuba the trunk-ground ecomorphs and some derivative ecomorphs are betas while the remainder of the Cuban anoles are alphas of the carolinensis sub section. In Hispaniola *darlingtoni* and *insolitus*, the *monticola* group, the green anoles and *hendersoni* are all one radiation of the carolinensis subsection, but *ricordii*, the *cybotes* species group of the *cristatellus* series, the *distichus* species group of the *bimaculatus* series and the *semilineatus* species group of the *carolinensis* sub section are all separate invasions into Hispaniola.

What this, particularly the Hispaniolan picture, implies is that the "main sequence" is not necessarily a phyletic series stemming from one radiation but is a community that can be fitted together from various sources. If one thinks then of the main sequence as only the most frequent and most stable ecological *fit* of syntopic species, the species, especially prominent in the two largest islands, that lie outside the "main sequence" are no longer anomalous. They are alternative ecomorphs that in the permissive larger space of large islands has persisted alongside the main sequence. The *lucius* series in Cuba (rock walls and complex trees) and the *monticola* group in Hispaniola (rock walls, rock slides and bushes) are merely less probable ecomorphs than the standard series.

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* Ecology *45*: 745-752.

** Breviora No. *327*: 1-19.

***Breviora No. 368: 1-52; Breviora No. *375*: 1-39.

(2) Again such a species as *A. valencienni*, widespread in Jamaica, has no obvious widespread or common species representing it in Cuba or Hispaniola. But (a) there may be uncommon or ill-understood species on those islands that *locally* represent it in Cuba or Hispaniola (*darlingtoni*?, *vermiculatus*?), (b) the type that it represents may be one that has evolved more than once, but which rarely persists.

As we shall see below the montane faunas of Hispaniola are peculiar and do not fit the main sequence as do the lowland faunas. They frequently lack one ecological component or in another case have too many. May they not possibly represent or model for us the kinds of local faunas from which the widespread closely co-adapted lowland faunas have arisen. Whether faunas arise by radiation or accumulation, the end result derives from the secondary contact of local faunas in which the individual species with their special adaptations took shape. Very frequently when local faunas met and merged secondarily, there must often have been extinction. The montane local faunas may have their peculiar and unbalanced aspect because they have long remained disjunct, i.e. island-like.

The larger islands: lowland faunas: Cuba, Hispaniola

It has become clear that a possibly serious difficulty in the interpretation of faunal diversity and its history on the larger islands is the absence in all the Greater Antilles of native lowland wet forest. All the areas on any of the big islands which could have had such a forest appear to have been cleared at least once. The dry forests, in contrast, especially the extreme areas, may have natural forest, but even here subsistence farming or charcoal-making have destroyed more than is at first sight obvious. However, it is in the dry forest that local endemics have been found: *Anolis whitemani*, *Anolis longitibialis*, both *cybotes* relatives, the new relatives of *Anolis brevirostris* (See below.). In the moister cultivated areas some interesting studies may still be made of geographic variation, but only with the reservation that these areas have been immensely disturbed.

In the moister lowland forests *Anolis distichus* has been of interest, since the meaning of the complex pattern of subspecies described by Schwartz and differing primarily in dewlap color has been and remains a problem. Rand and Williams see in dewlap color an important element in species recognition on complex islands. Schwartz's dewlap races are in this regard especially interesting. Do they in fact show clinal change from one population to another or could there in some cases by sharp changes, or even overlap, which might imply sibling species?

In 1971 Williams, Roughgarden, Webster and Huey ran a transect between *A. distichus ignigularis* (dewlap with red central spot and yellow margin) and *A. distichus dominicensis* (dewlap uniform pale yellow) along the main road from Santo Domingo to Santiago, across the supposed subspecies border. Censuses of dewlap color at regular intervals made it clear that the change was clinal, but not in a simple sense. There were both some irregularity in the cline and a situation best described as a clinal change in the *frequency* of a spectrum of morphs ranging from strongly bicolor dewlaps to uniform pale dewlaps. (Webster has demonstrated clinal change in dewlap color in the *distichus* races of extreme Southwestern Haiti, where again dewlaps bear very strikingly different colors/patterns - vinosus, dark red with a white border, aurifer unicolor orange, suppar very pale yellowish; in this case, however, some elevational changes are involved.) No correlation with terrain or ecology was evident.

The transect from Santo Domingo to Santiago revealed also some very striking color variation in A. chlorocyanus, blue patches irregular in size and shape on head and body, largest just north of Santo Domingo and diminishing in frequency and amount both in the city and northward. Again the variation is clinal and not obviously associated with any vegetational or physiographic feature of the transect. The whole area of the transect has, of course, been so much modified by man that its original aspect can no longer be guessed at.

Webster has been especially concerned with the anoles of the arid lowlands of Hispaniola. He has utilized both field studies and electrophoresis very profitably to elucidate the relationships of populations of the distichus-brevirostris complex of siblings.

There is little morphological differentiation of the populations in either of the two types within this complex. A. brevirostris is the more arid-adapted of the two and differs from distichus in the modal condition of one variable scale character and in the presence of shoulder pattern always absent in distichus. There are also in both types striking differences in body color and especially dewlap color. In A. distichus all population transitions thus far carefully examined have shown gradual change in dewlap color, i.e. apparent true inter-gradation between populations clearly below the species level. In what has been called brevirostris the situation is different. In collaboration with J. M. Burns 15 populations of the brevirostris type have been examined electrophoretically. The resulting genetic analysis indicates complete isolation of populations in those areas where there are discontinuities in dewlap color i.e. brevirostris in the areas thus far studied is three species, not one. Species A in the northern part of Haiti has a dewlap in which all of the skin is bright orange; a dense area of scales along the edge gives the dewlap a pale yellow margin. To the south of this species B occupies an area of coast approximately 30 miles long and 2-3 miles wide. As especially demonstrated in a transect taken in the summer of 1970, at the northern end of the range the individuals of this species have dewlaps that are entirely white or which have only a small basal orange spot. At the other extreme of the distribution of this species, the dewlaps are predominantly light orange. Between the two localities there is a gradual cline in dewlap color, but great constancy in electrophoretic characters. Finally in the Cul de Sac Plain of Haiti is a third species which has its dewlaps dull or unpigmented.

This contrast between subspecific differences in distichus and species difference in the brevirostris series is intriguing. Since at most localities in which Webster has found both distichus and brevirostris they differ significantly in dewlap color, he suggests the possibility that dewlap color in distichus has evolved as a response to the local populations of brevirostris. If this be true it is necessary to suppose that brevirostris once had wider sympatry with distichus than it does now.

The larger Islands -- *montane faunas:* It is certainly a major feature of interest in the island of Hispaniola that there occur on that island strongly differentiated montane faunas, interesting in themselves and for their zones of overlap with lowland faunas.

Part of our energies under the grant have been directed to repeated exploration of the montane faunas to establish their content and their character. The following are some of the results:

A. *new distributional records:* Examples are discovery of *Chamaelinorops*, in the Cordillera Central of the Dominican Republic, (It is an archaic anoline genus previously known only south of the Cul de Sac trough, on the "south island" of Hispaniola) and of A. *aliniger* in the Cordillera Septentrional and in the vicinity of San Jose de Ocoa.

B. *new species:* One example is a new species allied to A. *monticola* and syntopic with it, differing in size and color. Another instance is provided by confirmation both from ecological observations and electrophoretic study that the red-dewlap "morph" of A. *cybotes* occurring with typical A. *cybotes* at San Jose de Ocoa and replacing it on the slopes of the Cordillera Central north of the town is in reality a distinct species.)

These alpha level discoveries are genuinely important because in their absence we have an incorrect idea of the faunal diversity in the montane regions and of the units that are interacting. Though some species still appear rare (and hence to some workers unimportant constituents of the community) it seems more probable that rarity is merely an index of our ignorance of the ecology of these "rare" species and of inappropriate or inadequate methods of observation and collection. Cases in point are A. *aliniger* and A. *singularis* (the last was so named because of its apparent rarity). Both have within the last two years been found to be very abundant at appropriate elevations, but only because very systematic and careful observation and/or massive collections by native helpers revealed their true numbers.

C. *further ecological data:* A. *aliniger* and A. *singularis* have both been observed in open situations at lower elevations, there co-occurring with A. *chlorocyanus* and A. *coelestinus* respectively, but at higher elevations and with greater abundance alone. (A. *singularis* appears remarkable in that when occurring alone the males are much larger than the females and about the size of A. *coelestinus*; where it co-occurs with A. *coelestinus* sex dimorphism is much diminished and the males are much smaller than A. *coelestinus*.)

D. cross-comparisons between montane faunas. Some of the interest attaching to montane faunas is the fact that they show far more local difference than do the lowland faunas. This is not surprising since they are in many respects island faunas, with ample opportunity, therefore, for local specialization. More surprising is the lack of parallelism in terms of ecomorphs. For example, two montane areas have had special attention: La Palma, (Williams et al.), Les Platons (Moermond). Each has been disturbed by man, but none to an extent that explains the differences tabulated below:

La Palma:

forest		*open formations*	
species:	ecomorph:	species:	ecomorph:
ricordii	giant	*aliniger*	trunk-crown
insolitus	twig	*distichus*	trunk
christophei	trunk	*cybotes*	bush
etheridgei	bush		

Les Platons:

forest			
species:	ecomorph:	species:	ecomorph:
ricordii	giant	*koopmani*	grass
distichus	trunk	*semilineatus*	grass
hendersoni	bush	*cybotes*	rocks
coelestinus	trunk-crown		
monticola	rocks		

It is true that these areas are not strictly comparable in terms of vegetation, but this is, conspicuously, far from a sufficient explanation. In the lowlands vegetation may change greatly without altering more than the relative frequency of the common species and the relative frequency within each species of the spectrum of perch-preferences usual in each. At Les Platons it is, for example, extraordinary that there should be two conspicuous grass anoles, while at La Palma none have been seen in many visits.

It is in fact this last peculiarity of Les Platons that has stirred Moermond's special interest. His study shows that one grass anole *koopmani*, prefers denser and higher herbs than the sparse vegetation utilized by the other *semilineatus*, but in terms of the main sequence of lowland ecomorphs both are still *equivocally* grass anoles. These montane "islands" may be very useful in knowing what are the *permissible* co-adjustments between similar ecomorphs, while the lowlands may show better which are in a long term sense stable co-adaptations.

We are very conscious that it is possible that some of the discrepancy commented on by Rand and Williams (1969*) between the "north island" in which La Palma is located and the "south island" in which Los Platons is placed will disappear with further collecting. The discovery, mentioned above, of *Chamaelinorops* in the north island, when it had seemed a true south island endemic is a warning that this may be true. Schwartz also has reported that he has discovered a new twig anole like *A. insolitus* of La Palma on the Sierra de Baoruco in the south island. Perhaps his other large new anole in the Cordillera Central may be a representative of *A. darlingtoni*. Discoveries like these will obviate but will not diminish the differences between local montane faunas.

The Larger Islands -- *overlap faunas*: Some special effort has been directed to the study of the overlap of siblings or of ecological counterparts, whether or not closely related. Schoener has been particularly interested in this. The following are the more interesting or better studied cases:

1. On the road to Cabral north of the city of Barahona, Dominican Republic. Two overlap zones are found adjacent to one another: (1) in open fields a contact zone between *A. brevirostris* and *A. ravitergum*. In the summer of 1970 this was seen as an extraordinarily sharp division within one field, dividing the field almost in halves and with actual species overlap on a few trees only. In the summer of 1971 the overlap was observed to be substantially wider but both years there was the obvious ecological difference between the two species in perch or climatic preference. (2) Quite nearby, where more trees provided greater shade and there were many palmettos *A. chlorocyanus* and *A. coelestinus* appeared to occur randomly in the palmettos but with an overlap zone estimated as between one and two kilometers in breadth.

2. In a ravine on the road from La Vega to Jarabacoa at *ca* 1500 feet the montane species *A. christophei* co-occurred at the bottom of the ravine with *A. distichus* and *A. cybotes*. On the slopes of the ravine *A. semilineatus* and *A. chlorocyanus* were also seen, and at the top *A. distichus* was very common. In the well-shaded bottom along an intermittent stream *A. distichus* and *A. christophei* were about equally common, *A. cybotes* much scarcer. Careful census over several days here showed a significant difference between *A. distichus* and *A. christophei*. The latter on the average perched lower than *A. distichus*, closer to water and in deeper shade.

These (and other less dramatic overlaps) need to be investigated in winter as well as in summer and we hope so to do. Beyond this larger term studies may be desirable to establish the stability of such overlap zone.

Disturbed faunas. The results of human disturbance are at times illuminating. Jenssen has studied a small area cleared of underbrush and with well-spaced small trees at edge of Long Mountain. Mona Jamaica. He had previously much experience with the two species *A. opalinus* and *A. lineatopus* near Mandeville in the center of the island. At Mandeville he found *opalinus* to perch low as if it were a trunk-ground species and to share essentially the same perch height with the Mandeville *lineatopus* population. There was little aggressive interaction between the two species at Mandeville; such agonistic encounters as were observed were infrequent and brief and appeared to be an intrusion of one animal

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* Breviora No, 327: 1-19.

into another's individual distance. In Kingston in the cleared area (normal dry forest on either side) *opalinus* and *lineatopus* again occurred, but their interactions were very different. *Opalinus* again would often perch near the ground *but only* if *lineatopus* were not on the same tree. Whenever *lineatopus* was present, *opalinus* consistently (36 instances) perched above *lineatopus*. *Lineatopus* invariably perched low, but *opalinus* did so only if *and* when *lineatopus* was absent. There was a dramatic shift upward of *opalinus* whenever male *lineatopus* reached an "opalinus" tree.

In more complex nearby habitats Jenssen saw *opalinus* perched below two meters when an adult male *lineatopus* was only a leap away in an adjacent trunk. As Jenssen interprets the case, the increase in possible avoidance routes made possible this proximity at similar perch heights.

The case is instructive in making very clear that perch habitat for anole species is very much influenced by both other congeners and by the nature of the vegetation.

Mainland studies: Most of the focus of our work is still on the West Indies, since the greater breadth and depth of knowledge makes study there more profitable. However, since one of the associate investigators (Rand) is based in Panama, those species of Panamanian *Anolis* which come readily to hand have been utilized. *Anolis auratus* in particular has turned out to be an admirable experimental animal, very hardy in captivity and an active and aggressive species. *A. auratus* therefore has been used in experimental work by Rand, Feldmann and Kiester. *A. limifrons*, as a forest rather than grassland animal, has been more susceptible to study in the field. Andrews and Rand are doing a mark and recapture study on *A. limifrons* on a small plot on Barro Colorado Island. A long-term project, the intent is to study survival and recruitment. (Parallel studies on reproductive activity in *A. limifrons* under several climatic regimes have long been underway by Sexton; this is supplementary.)

Williams has in hand a revision of South American *Anolis* but is impressed by the necessity of seeing more species in life. He hopes to do so in the Chocó or Ecuador during the third year of the grant.

Mainland compared with the West Indies: Robin Andrews has compared resource utilization by *Anolis* in Costa Rica and in Dominica. She chose cacao habitats as study areas in both cases in order to ensure minimal environmental differences. At La Lola, Costa Rica, she collected 250 *A. limifrons* and 80 *A. humilis* for stomach contents and additionally worked 111 *limifrons* and 22 *humilis* to determine home ranges, individual movements and rates of growth during the 11 day study period. Arthropods were simultaneously collected from the local litter by pit traps and from tree trunks and from the low understory vegetation by sweeping. Parallel study of *A. oculatus* was accomplished during a month in Dominica. 191 *A. oculatus* were collected, and 129 individuals were marked for future study. Arthropods were taken by the same techniques as in Costa Rica.

Preliminary interpretation of the data is as follows: Arthropod size differs in similar habitats, differs in Dominica as compared with Costa Rica; there are few large arthropods on the island. Even this, however, does not fully account for amount of small prey items taken by the insular anoles. It appears that the relatively higher density of *A. oculatus* and the resultant high intra-specific competition tend to shift its diet to smaller, more abundant prey. On the continent, therefore, the relationship between prey size and lizard size involves the ability of lizards to subdue and swallow large prey items, while on the islands lizard size relates to feeding primarily in the sense that greater size ensures social dominance and the ability to maintain a territory against intruders.

Other Studies:

1. *Karyotype evolution.* Webster has now succeeded in karyotyping most of the anoles of Hispaniola. That he has not quite finished the job is due (1) to failure to re-discover one species - *darlingtoni* and (2) to the fact that new valid species continue to be discovered (two very recently by Schwartz).

The vast majority of *Anolis* species have a diploid number of 36, which is considered ancestral for the genus, the family Iguanidae, and probably lizards as a whole. For anoles the interest is in those species with derivative karyotypes. Gorman determined that Hispaniolan *distichus*, like many of the species of Puerto Rico and the northern lesser Antilles, has a reduced chromosome number, and an XXY chromosome mechanism as opposed to an XY. *Anolis brevirostris*, the closest relative to *distichus*, also has that karyotype.

Of greater interest, four Hispaniolan species are now known to have karyotypes in which the macrochromosomal complement is partially or entirely fissioned, producing diploid numbers in excess of 36. *A. insolitus*, an osteologically primitive species, has a 2N of 44, with 4 of the 6 macrochromosome pairs fissioned. *A. monticola* of Haiti's Tiburon Peninsula has a diploid number of 46, 47, or 48. Of 46 individuals examined, 4 have a diploid number of 46, 1 has 47, and the remainder are 48: all with numbers less than 48 are from localities at the western end of the known distribution. A number of chromosomes have undergone inversion, resulting in conversion of telocentric fission products to submetacentrics or metacentrics. The extent of fissioning is variable both between and within localities, but seems less developed at the western localities. While this situation awaits further analysis of present preparations and more collecting, it would seem that the eastern populations have become stabilized for the fully fissioned karyotype and undergone substantial secondary modification of chromosome morphology, while the western populations are as yet not fully fissioned and have experienced less inversion.

The *monticola* species group includes six species, one undescribed, which form a small radiation within the Hispaniolan fauna. The two species morphologically and geographically closest to *monticola* are *koopmani* and the undescribed species. Both have partially fissioned karyotypes. *A. koopmani* is 2N of 40, while the situation in the undescribed species is more complex.

Of two specimens taken at the type locality, both have 13 rather than the common 12 pairs of microchromosomes: one is homozygous for one fission, heterozygous for a second, and homozygous for 4 metacentric macrochromosomes; the second is homozygous for two fissions, heterozygous for a third, and homozygous for 3 metacentrics. This suggests that within this one population diploid numbers range from 40 to 44.

In the context of the known information on karyotypes and phylogeny of the West Indian anoles, it is possible to interpret the karyotypes of *insolitus*, *monticola*, *koopmani*, and the undescribed species as unequivocal examples of fission. Other studies have firmly established the occurrence of fission; the matter of frequency and importance remain undetermined, and it is to this that the anoles make a contribution. In particular, Todd (1970*) has suggested that multiple fission may result in speciation and adaptive radiation. Since it seems most likely that *monticola*, *koopmani*, and the undescribed species may be a case in point, this would be a very interesting problem for further study. The polymorphism in chromosome number in *monticola* and the undescribed species and the extent of inversioning might upon further analysis provide useful information on the events in full fissioning of a karyotype. The three species differ in size and proportions and apparently in structural niche and/or microclimate preference; they do in fact seem to form a small adaptive radiation. Further studies of ecology and distribution are also needed.

In many studies of comparative cytogenetics only one or two preparations are used to describe the karyotype for a species. Since those individuals might not be typically of the population or the species, this approach needs to be evaluated in terms of studies of intra- and inter-population variation in the karyotypes of one or a few species. Modest sample sizes are now on hand for several Hispaniolan species; they indicate that intra- and inter-population variation are not particularly uncommon. A. *etheridgei* males show either 12 or 13 microbivalents in meiosis. Similarly, A. *brevirostris* seems to be variable for the number of microchromosomes: both cases may involve supernumerary chromosomes, as has been suggested for A. *cristatellus* (Gorman et al.; 1968**). In A. *whitemani*, Haitian specimens have a normal complement of microchromosomes, while in two specimens from the Dominican Republic one of the 12 pairs is greatly enlarged. No A. *cybotes* has been found with a number other than 36, but a small proportion of individuals have the morphology of a chromosome substantially modified. While this casts some doubt on the validity of assuming one or two individuals provide a representative karyotype for a species, the variations observed are sufficiently small that they do not compromise the larger conclusions drawn from chromosome studies.

While chromosome number and morphology are the characters most frequently used to define a karyotype, in anoles an obvious additional trait is chiasma frequency. Preparations from male meiotic tissue are the easiest to make, and within such preparations diakinesis figures are usually the most common.

* Journ. Theoret. Biol. 26: 445-480.

** Breviora No. 293: 1-13.

In general, anole species have either a low frequency, with two chiasmata located terminally for each macrobivalent, or a high frequency, with several relatively unlocalized chiasmata per macrobivalent. The low frequency condition is characteristic of all the osteologically primitive species examined; of many species with the ancestral karyotype of 2N of 36 examined, only osteologically advanced *angusticeps* has high chiasma frequency. Apparently all the West Indian alpha anoles with XXY sex chromosome mechanism have a high chiasma frequency; the two species within the *bimaculatus* subsection with an XY sex system are *cybotes* (2N 36) and *evermanni* (2N 26), both with a low chiasma frequency.

There is no evidence of terminalization in anoles, so that differences in chiasma frequency may indicate real differences in the amount of genetic recombination. It is therefore of interest to consider the species with a high frequency and examine them for special evolutionary or ecological characteristics. In doing so it is assumed that females have a chiasma frequency similar to that of males of the species, or at least that the amount of genetic recombination in species of the high chiasma category is on the average higher than that in the low chiasma category.

It has been suggested that a high chiasma frequency may be of advantage to a colonist attempting to adapt to a new environment. Six anole species have colonized from one of the Greater Antilles to other islands. Only two have been exceptionally successful, but both *sagrei* and *carolinensis* have a low frequency. On the other hand, *distichus*, *cristatellus*, and *angusticeps* all have high frequency. *A. cristatellus* occurs on several of the southern Bahamas, although its source area, Puerto Rico, is much more distant than Hispaniola, the home of the ecologically comparable *cybotes*. *A. angusticeps* have a high frequency. Chiasma frequency is only one characteristic affecting colonization success, and at best the anoles have provided only a weak case for its importance.

On Puerto Rico all but 2 of the 10 species are known or presumed to have the high frequency. On Hispaniola, of at least 25 species only *distichus* and *brevirostris* and their siblings have the high frequency: they represent only one of the ecomorphs in the Hispaniolan fauna. While it may be significant that *distichus* is the most abundant Hispaniolan anole, there is no known difference between the Hispaniolan and Puerto Rican faunas that can be attributed to chiasma frequency.

Another approach to the study of the significance of chiasma frequency is just now being investigated. *A. cybotes* and *A. distichus* are the most widely distributed anoles on Hispaniola; as reiterated above, they differ in chiasma frequency, yet their chromosome numbers are very similar; if anything, *distichus'* 7 pairs of macrochromosomes give it an additional boost in recombination index. Samples of both species have been or will be obtained from different parts of the island, with both geographical distance and ecological difference being emphasized. Electrophoresis will be used to estimate the genetic similarity of the populations of each species. If higher chiasma frequency gives some advantage in local adaptation, it is to be expected that *distichus* will show greater local differentiation.

2. The problem of niche width with varying numbers of congeneric competitors is being explored by Jonathon Roughgarden. He is attempting an empirical test of an interpretation of niche width already in press in the *American Naturalist*. For *Anolis* his measure of niche width is the variance in prey size utilized by the population. Underlying this he sees two components: (1) an interphenotypic (polymorphism) component which is the contribution to niche provided by the presence in a population of a polymorphism of phenotypes specialized in specific ways for resource utilization (in *Anolis* for taking specific sizes of prey). (2) an intraphenotypic component which is the contribution made by the actual spectrum of resources taken by each phenotype (in the Anole range of prey size taken by each phenotype). Total niche width is then the sum of the interphenotype component, measured as the phenotype variance in the population (e.g. in *Anolis* variance in jaw length) plus the intraphenotypic component measured as the variance in resources taken by each phenotype (in *Anolis* the variance of prey size taken by each phenotype).

The field samples which are to test this idea are (1) *A. cybotes* from Jarabacoa where it occurs with three other common species (2) *A. cybotes* from San Jose de Ocoa where it occurs with an as yet unnamed close relative differing in dewlap color and with four additional species. (3) *A. shrevei* a *cybotes* relative occurring alone at high elevations.

Jaw size measurements (interphenotypic variance) have been taken on each sample and have been analyzed. Prey size (intraphenotypic variance) is not yet analyzed. The results on interphenotypic variance are as follows: *A. cybotes* at Jarabacoa (low diversity) and at San Jose de Ocoa (high diversity) have the same variance, but *A. cybotes* at San Jose de Ocoa is a larger animal. Thus the niche position of *A. cybotes* has been displaced upward by the presence of a smaller relative (the red dewlap species); variance has not been affected, just average jaw size. *A. shrevei* at Valle Nuevo shows another picture: variance itself is low.

3. *Habitat choice*: A. Ross Kiester, partially with grant support, has been engaged in theoretical and experimental analysis of resource utilization by lizards, particularly with regard to conspecifics as cues. Fifteen months were spent in the Panama Canal Zone as a predoctoral Intern at the Smithsonian Tropical Research Institute. He reports his activities as follows:

Within the broad field of behavioral ecology I have been concentrating on the idea that conspecifics may be used as cues which provide information about the distribution, of probable distribution, in space and time of a resource which a lizard must utilize. In this sense a cue is a statistic on a resource, providing some kind of average information about the variability of the resource. I have done work on the use of conspecifics as cues in four areas of behavioral ecology: A. habitat selection, B. daily movement patterns, C. social systems, and D. interspecific relations.

A. Habitat Selection. In selecting a habitat a lizard moves through the heterogeneous environment and attempts to settle in a favorable area. The lizard can make a more efficient choice if it has information about the temporal variation of the factors that determine that a given area will make a favorable habitat. The values of the factors at the point in time when the habitat is actually selected may not necessarily reflect how those factors may be expected to vary as time goes on. By its assumed continued presence, a conspecific provides the information that the values of the factors have varied within tolerable limits through some past period. Thus we expect that, other things being equal, conspecifics may be important clues in habitat selection.

A series of choice experiments run on the Panamanian grass anole (Anolis auratus) have provided support for this idea. If one displaces an individual of this species to an unfamiliar area which contains grassland nearby, and places it at the base of a bare pole which rises above the dense vegetation it will often climb slowly to the top of the pole, turn around, and then climb down and head off. This and similar behaviors indicated that it would be possible to separate habitat selection behavior from escape or flight behavior. Freshly caught animals were placed in the center of a long cage which had glass enclosures at either end which contained the various experimental stimuli, and the stimulus that was approached first was recorded. Over 170 animals were run according to a specific protocol in the cage, and each animal was used only once. For a given pair of stimuli we were able to get results significant at the 5% level consistently with samples of 15 animals. We found that most anoles of both sexes and all sizes would approach another anole, regardless of its sex or size, rather than a bare perch. Because this behavior was independent of the animal's sex, we ruled out an interpretation based solely on mate selection such as had been suggested by other workers. Because small animals approached large animals which could easily defeat them in any agonostic encounter and from which they would flee immediately if involved in an aggressive encounter, we ruled out aggressive behavior as the key to the interpretation. Experiments using a bush anole (A. tropidogaster) whose habitat partially overlaps that of auratus and whose morphology is superficially similar gave the result that auratus would approach a tropidogaster rather than a bare perch, again regardless of size and sex. However, when given the choice between the two species, auratus would usually approach its own species. The auratus always approached a small patch of grassland rather than a small perch. But, if given the choice between a patch of grassland and a small perch with a conspecific the animals would sometimes go one way and sometimes the other. This balance needs to be further clarified, but seems that conspecifics can be important, but certainly not the only, cues used in habitat selection.

B. Daily Movement Patterns. From both the theoretical and experimental points of view the next step in this analysis is to look at daily movement patterns. Daily movement patterns can be considered as a fine structure habitat selection where the animal has variable resource needs which have a spatial distribution within the broader habitat which was originally selected. The next logical extension of the choice experiments is to ask what the longer term behavior of the animals is in a more elaborate choice situation. That is, we need to continue beyond the initial approach movement.

These considerations led to an experimental system called the maze cage. Three separate cages each with three rooms are arranged so that two of the rooms in one of the cages look into one of the rooms of each of the two other cages. The arrangement is such that the view from all rooms with windows is identical.

A single lizard is placed in each cage. Thus one of the lizards has two neighbors whereas the other two have one neighbor each. All of the rooms have a uniform amount of habitat in them and each doorway between the rooms has a photocell tripping device attached to an event recorder to monitor movement between rooms. Preliminary runs indicate that the animals move into the rooms with windows in proportion to the frequency that the conspecific appears in the room opposite the window, although all of the animals regularly visit all of the rooms in their own cage. Further, it appears that the lizard with two nieghbors may undertake more actual movement than the individuals which have only one neighbor. This experiment was originally constructed in Panama for A. auratus. It has now been reconstructed in Cambridge with slight modifications for A. carolinensis. Further experiments are planned to have the habitat differ in quality between the rooms.

C. Social Systems. Much of an animal's daily movement pattern is closely connected with encountering conspecifics and engaging in social behavior and sexual behavior of a much broader kind than merely acquiring information about the distribution of resources as it is indicated by the conspecifics. Nonetheless, it should be possible to analyze an important part of the ecology of social systems from that point of view and to tie this analysis in with the work reviewed above. Much theoretical analysis has been developed to understand the effects of a group of animals using each other as cues to variable resources on the structure and function of their social system. This theory has been developed both along qualitative and quantitative lines. I am now in the process of writing up the qualitative theory, and discussing its application to the social systems seen in lizards of the family Iguanidae. The mathematical model which grew out of the theory was developed by M. W. Slatkin and myself. The model leads to a partial differential equation in both space and time which describes the movement of lizards over a variable resource where the lizards are using each other as cues. The equilibrium behavior and linear perturbation analysis of this equation has been completed. Future work will involve analog simulation of the system.

D. Interspecific Relations. I have begun to extend to analysis of the use of conspecifics as cues to the use of other species as cues. I am now beginning work on the analysis of interspecific territoriality, mixed flocks, and cleptoparasitism. The use of the notion of the conspecifics versus heterospecifics as cues has already provided a powerful explanation of the striking patterns of bird abundance along altitudinal gradients reported by Jared Diamond.

4. Dewlap and Display evolution. Rand has been concerned with the significance of both dewlap and display in inter-and intra-species communication. He has worked on most of the Lesser Antilles, attempting to film the full repertoire of each species. Both males and females were filmed. Where possible naturally occurring displays were recorded, but also displays provoked by introducing lizards of the same and opposite sex. Selected individuals were watched for 20 minute periods and their displays, interactions and movements recorded.

In Panama a colony of captive individuals was established and still maintained. Most of the animals are kept singly or in pairs in cages so designed as to allow any two cages to be put together with the result that the lizard in each cage suddenly finds an intruder in his territory. The resulting displays are filmed from a blind. Special attention has been given both in the field and in captivity to *A. oculatus* of Dominica. Two large cages are being used to establish small populations under semi-free conditions. Home ranges, displays and social interactions are recorded. So studied are not only Lesser Antillean species but some from the Greater Antilles and from Panama. (e.g. *A. krugi*, *A. biporcatus*, *A. auratus*). *Polychrus* and *Corythophanes* are maintained also for comparison.

Results and ideas to date are as follows: 1. In one anole islands, even those with remarkable local differentiation in body color (such as Dominica), there is little variation in dewlap color or display pattern. There is some poorly understood variation in the frequency of usage of displays. 2. A basic ethogram constructed for *Anolis* of the *bimaculatus* group suggests that the individual species have a basic repertoire and differ in the "form" of the various displays and in usage. It seems possible from preliminary looks at other species that the basic repertoire can be generalized for all or most of the genus. 3. Two mainland species show some interesting differences: The grass anole *A. auratus* displays very often but seems to have an intergrading set of displays best described as a continuum. The tree crown species *A. biporcatus*, on the contrary, displays very little and the repertoire seems small and stereotyped.

With Williams the function and evolution of dewlaps are beginning to be sketched out. The dewlap was originally, Rand and Williams believe, a device for increasing the apparent size of the animal in all aggressive encounters, inter- and intra-specific.

Initially its pattern and color had no function in species recognition. Rand and Williams see the situation in the Lesser Antilles as ample demonstration of this: Whether on one anole islands with little or with great variation in body color, or two anole islands, dewlaps have a standard color for all populations and species - light yellow or orange yellow. This is even the commonest color among anoles on multi-species islands.

In fact it is only when an island has species which are very similar in both adult male size, shape and color pattern that species differ in dewlap color.

On one anole islands body color seems of primary importance in species/population recognition, (Guadeloupe, Dominica). In two anole islands size *and* body color serve the purpose.

On the multispecies islands, however, ecomorphs have evolved. If there are series of species belonging to one ecomorph -- climatic or geographic vicariants -- they will be of very similar size and shape since this is a part of the ecological adaptation that defines each ecomorph. In such cases the dewlaps may be very strikingly different in color.

The dewlap functions as a flag the color of which is adapted to achieve maximum visibility and distinctiveness. Dewlap display is used 1. to draw attention to the displaying animal, 2. to indicate its motivational state (likelihood of attack, copulation...). These two functions are important interspecifically and intraspecifically. Only when two species which are very closely similar occur together is dewlap color used to signal species identity and hence mate and associate recognition.

Thus in Puerto Rico the three grass anoles have remarkably different dewlap colors: *krugi* yellowish, *pulchellus* crimson, *poncensis* white (and small). In Cuba the extensive series of the trunk-ground anoles are the species most different in dewlap colors: *homolechis* white, *allogus* yellow with three red stripes, *ahli* red central spot surrounded by yellow white, *rubribarbus* 4-5 thin red lines or yellow ground plus white margin, etc. In Hispaniola the two lowland grass anoles have (*semilineatus*) white or *olssoni* (orange) dewlaps.

In those cases in the Greater Antilles in which dewlaps are similar, the species may be very different in size (e.g. Cuba *allisoni*, *angusticeps*, *isolepis*) or in color (*angusticeps* grey in body color) or have special features that are very distinctive (*argillaceus* and *loysiana* are similar in size and not very different in dewlap, but *loysiana* is uniquely provided with randomly arranged spines over all of its body. In the *equestris* series which Schwartz now believes to be at least 5 species, although dewlaps are not very different, body pattern differs extraordinarily.

5. *Habitat Shift*: Schoener has devoted special attention to the problem of habitat shifts and the parameters involved. Data on frequency of occurrence in structural habitat categories (defined as intervals of perch height and perch diameter), collected prior to the present grant for several widespread *Anolis* in each of twenty localities in the western Caribbean has been analyzed.

The following five variables were specified where appropriate:

Niche shift and competition: data analysis

The analysis of the data (collected prior to the initiation of this grant) on niche shift in several widespread *Anolis* species has been nearly completed during the first two years of the grant. The data are of the following form. For each of 20 localities in the western Caribbean, the frequency of occurrence in structural habitat categories (defined as intervals of perch height and perch diameter) of these five variables was measured where appropriate:

V_1 - Structural habitat of the widespread species where it occurs with competitors;

V_2.- Structural habitat of the widespread species where it occurs alone;

V_3 - Structural habitat of a competing species;

V_4 - Availability of vegetation on islands where the widespread species occurs alone (surface area or some other measure);

V_5 - Availability of vegetation on islands where the widespread species occurs with competitors.

Using these data, we have attempted to answer three kinds of questions: (1) How can one show that habitat shift occurs? (2) What is the mathematical form of habitat shift? and (3) What is the biological distribution (presence and absence) of habitat shift among species and size classes in *Anolis*?

1. *Detection*. At the simplest level, the structural habitats of the widespread species from two islands can be considered separate frequency distributions subject to the sort of statistical tests used for within-habitat comparisons of different species (as in Ecology 51: 408). These tests provide estimations of the statistical significance of differences in distributions but little information on the possible causal mechanisms.

2. *Mathematical form*. An attempt was made to incorporate causally important factors into a set of predictive equations. All equations of simplest type used as the dependent variable V_1 above, and as independent variables combinations of V_2-V_5. The equations were derived from various competition models whose isoclines specify a certain relationship between competing species and habitat variables at equilibrium, e.g., linear, concave downward, etc. Most models were invented *ad hoc* for the *Anolis* data but should have wide application elsewhere. The parameters in the models, e.g., the "competition coefficient" are fitted linear or nonlinear regression coefficients. The variables, V_1-V_5, are indexed by microhabitat category; thus there are as many data vectors $(V_1\ V_2\ V_3\ V_4\ V_5)$, as structural habitat categories. The method is quite different from the usual way of calculating competition coefficients over microhabitat categories (Levins, 1968) but in some cases seems to provide very satisfactory descriptions of the *Anolis* data. Information thus gathered on the form of competition is useful not only to falsify competition models (or their particular application), but also to describe the way in which per capita increase in a given species abundance decreases the abundance of the competing species. The second kind of information, in turn, allows us to decide when ecological shift looks like it is the result of competition: if the relationship is highly concave, competition may be intense yet not detectable at low abundances of the widespread species.

For linear models, data-fitting was done by ordinary least-squares regression. For nonlinear models, two quite different algorithms were used: Davidson's minimization method as programmed by W. J. Raduchel (Harvard) in RAPE (Regression analysis program for economists) and Marquardt's algorithm as programmed by J. Wilcox *et al.* (Davis) and extensively modified by D. Schmalz (Harvard). Since nonlinear regression is still somewhat of an art, using two algorithms should forestall many of the artifactual results a particular method can generate. In fact, the methods gave rather similar results for most of the models, and the ranking of the models in terms of goodness of fit was different in only about 12% of the cases examined.

All possible combinations of species and islands were used in the linear regression. A selected sample of these, for which the signs of the competition coefficients indicated that competition in fact might have occurred, were used in the nonlinear analysis.

In addition to using V_1 as the dependent variable and using a single V_3, two other classes of equations were tested. These were 1) comparisons between islands (a and b) on both of which the widespread species had competitors (then V_{1a} and V_{1b} had to be used in separate regressions) and 2) comparisons between islands where the widespread species occurred alone and where it occurred with more than a single competitor. Equations for the isoclines can be generated from the same set of models now extended, and they are a good bit more complicated.

Results for these studies indicate that concave models in general seem to fit the data better than linear models with the same number of parameters and that purely exploitative models fit better than do purely interference models ("Exploitative" and "interference" as types of competition are used in the sense of Park, 1962).

3. *Biological distribution.* The following major global results arise from the above analysis:

a. Exploitative models fit relatively better situations involving species or classes of the same size; interference models relatively better situations involving species of different sizes. This might be expected if competition for resources is greatest among species of the same size, whereas interference is most deleterious for at least the smaller member of a pair of species of different sizes.

b. Females and other small-sized individuals show ecological shift more often than do the large adult males. This is expected if smaller individuals are pushed around more by larger individuals.

c. Males have their ecological shift predicted best by using as the competing class members of the same sex from other species; females by using members of the opposite sex. Again, the relation of size and sex to aggressive propensity may be important here.

Beyond these general results, certain species seem to show less shift than others. *Grahami*, for example, shows the least shift but is quite broad in its structural niche on its home island (with many competing species). *Sagrei* males on Abaco (a 1-species island) also show little shift; in that case, it appears that climate limits the kind of vegetation within which they can be common to edge of low structural diversity: thus the opportunity to shift and expand along one niche dimension is curtailed by physiological restriction along another dimension. *Carolinensis* as a species shows a remarkable tendency to shift its structural habitat, and this shift is accompanied by major correlated changes in body color and pattern.

Peripheral Studies:

I have not reported above researches primarily funded in other ways or not directly germane to the research topic of B 019801X, but in minor ways using grant funds or facilities purchased by the grant. Such researches are

(1) the elaborate studies by W. P. Hall III on the chromosomal "races" of *Sceloporus grammicus* in Mexico. Hall was provided with funds primarily to procure and karyotype Mexican *Anoles*. Hall has provided the specimens and the slides of karyotypes. These are still unstudied. Because his problem does have indirect interest for us (we are interested in the role of chromosomes in speciation) and because grant funds did assist his general Mexican work, I have listed under "publications" below the one publication by Hall and Selander which is now in manuscript. Other papers in the series will also allude to partial support by B 019801X.

(2) Webster, as a digression or diversion from his electrophoretic studies of anoles, has used grant equipment to investigate the genetics of color polymorphism in the salamander *Plethodon cinereus*. This is germane only to the extent that this is (a) a further study of intraspecies differentiation in a vertebrate and (b) an additional demonstration of the utility of the electrophoretic technique so valuable for *Anolis*. Webster has uncovered interesting linkage disequilibrium in these studies, but no manuscript has yet emerged. When one does, there will again be mention of partial support by B 019801X.

(3) Very germane to the problems studied under B 019801X is the research of Thomas Jenssen. However, only the last two months of his more than year long study was funded by the grant. A great amount of data was collected, most of it still unanalyzed. Populations of *Anolis opalinus* were worked and followed on three separate study areas in the Mandeville area for up to 13 months. During this time weather data were taken.

Studied were: growth rate as influenced by age, sex and time of year; territorial size as influenced by the animal's size, sex, time of year and habitat; seasonal coefficients of condition based on weight and length of animals; behavioral repertoire and its social context.

Jenssen is currently working up the annual reproductive cycle for *A. opalinus* from biweekly samples. The sound producing mechanism of *A. grahami* is being investigated. A hybrid between *A. lineatopus neckeri* and *A. grahami* has been verified as such karyotypically and electrophoretically with the aid of T. P. Webster and its filmed behavior and external morphology are also under study.

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