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## Ecological Observations on *Anolis lionotus* and *Anolis poecilopus* (Reptilia, Sauria) in Panama

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### ABSTRACT

*Anolis lionotus* and *A. poecilopus* were studied in central Panama during most of an annual cycle. Both species are semiaquatic, utilizing the borders of streams in heavy forest, with *A. poecilopus* occurring only in permanent streams of the Pacific side and *A. lionotus* in permanent or intermittent streams of the Caribbean side of the region studied.

Few ecological differences were noted between the species, the ability of *Anolis lionotus* to utilize intermittent streams being the most significant. Reproduction in both species living in streams with continuous flow appears to be continuous throughout the year; a suggestion of cessation during the dry season was noted in *A. lionotus* populations inhabiting intermittent streams. Growth and mark-recapture data for *A. poecilopus* indicate it to be an annual species, reaching sexual maturity in two months after hatching with a growth rate of 0.3–0.48 mm./day.

Population density estimates for both species range from 1/10 m<sup>2</sup>–1/45 m<sup>2</sup> in the wet season to 1/40 m<sup>2</sup>–1/75 m<sup>2</sup> in the dry season. Variation in the amount of sunlight reaching the forest floor appeared to be the dominant factor influencing densities and distribution of the species along the streams, highly insolated areas not being frequented.

The primary behavioral adaptations to a semiaquatic niche appear to be the positive orientation to the stream side area and the use of the aquatic phase in the escape behaviors. Both species might be considered “specialists” in the restriction of their activities to a narrow portion of the available habitat but “generalists” in the breadth of their utilization of the resources within this zone.

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## INTRODUCTION

Lizards of the genus *Anolis* occupy a wide variety of microhabitats throughout the neotropics, from arboreal to terrestrial, scansorial, and even semiaquatic. Few species are known ecologically in any detail, despite their abundance and diversity.

Throughout the majority of 1968, field studies on several populations of two of the semiaquatic species in the genus, *Anolis lionotus* Cope, 1861 (fig. 1) and *Anolis poecilopus* Cope, 1862 (fig. 2) were conducted in the Canal Zone area in central Panama. The data obtained are believed to be of considerable interest in elaborating the exploitation patterns of these species in this unusual saurian niche.

Only one species of lizard of the few that have succeeded in adapting to this habitat has received any ecological scrutiny beyond the anecdotal. *Anolis barkeri* Schmidt of Mexico has been examined by several investigators as regards its temperature relationships, habitat selection, and feeding behavior. Similarities and differences between it and the topical species are discussed later in the appropriate sections.

Details of the distribution and systematics of these species are unsettled; these aspects of their biology are currently under study and will be reported at a later date. In the study area they are morphologically distinct and display minor differences in the use of their habitat, which justifies their treatment as distinct morphological entities. A detailed morphological analysis of each species is not yet possible. The majority of the characters previously utilized in defining these species have been found to overlap broadly or to be identical in both species. Until a detailed analysis of the species throughout their ranges is completed, a brief comparison of the salient characters is offered here to differentiate the forms. The most reliable characters are the relative size of dorsal and ventral scales and the presence of keels on the dorsal scales. The dorsal scales of *Anolis poecilopus* are strongly keeled and of approximately the same size as the ventral scales, whereas the dorsal scales of *A. lionotus* are smooth, or at best only a few have faint keels, and the dorsal scales are about twice the size of the ventral scales.

While one suspected area of sympatry exists in this region (S. R. Telford, pers. commun. Gaspar Sabana sample, April, 1969), *Anolis lionotus* was chiefly found in the Caribbean versant of the Canal Zone and to the west, and *A. poecilopus* was chiefly found in the Pacific versant of the Canal Zone and to the east (in both Caribbean and Pacific drainages). *Anolis poecilopus* was the chief object of study. The majority of the field work was conducted along the Frijoles River, Frijolito Creek, and Quebrada Juan Grande, all between 3 to 5 miles north of Gamboa, Canal Zone (fig. 3). Visits were

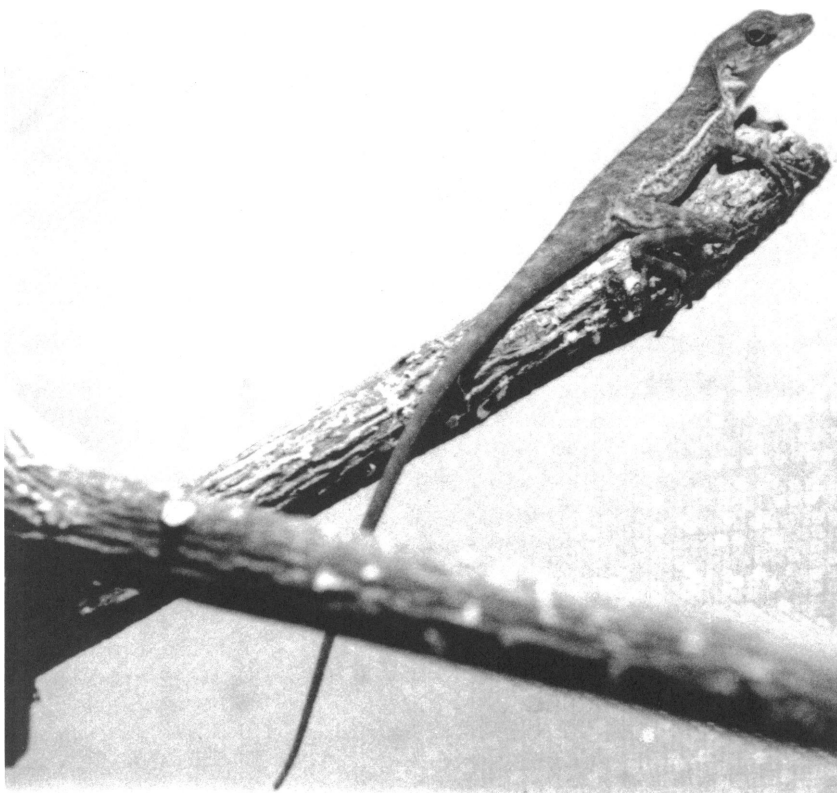


FIG. 1. Adult *Anolis lionotus* Cope from El Aquacate, Panama Province, Panama. Photo by S. R. Telford, Jr.



FIG. 2. *Anolis poecilopus* Cope from near Santa Rita, Colon Province, Panama. Adult female.

also made to tributaries of the Rio Agua Clara, east of Santa Rita, Colon Province, and the Rio Tocumen, Panama Province. A number of specimens were also available for examination from the "Gaspar Sabana," in

the mountains north of Chepo, Panama Province, and from Sasardi, San Blas territory.

The bulk of the field observations of *Anolis lionotus* were obtained in the vicinity of Achiote, Colon Province, in tributaries of the Rio Providencia. Visits to El Valle de Anton and Cerro Campana, Panama Province, were also made and a large series of specimens was available from El Aguacate on the slopes of Cerro Trinidad, 40 miles west of Panama City, Panama Province.

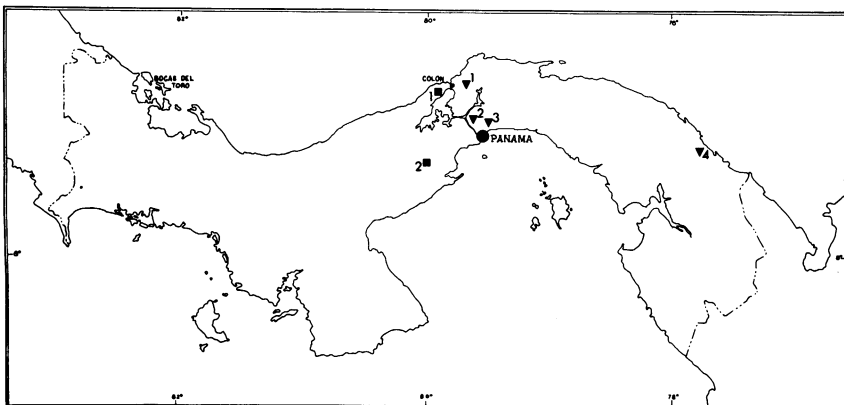


FIG. 3. Collecting localities for *Anolis lionotus* Cope and *A. poecilopus* Cope in Panama. Squares represent *A. lionotus* (1, Achiote. 2, El Aguacate). Triangles represent *A. poecilopus* (1, Santa Rita area. 2, Frijoles River area. 3, Gaspar Sabana. 4, Sasardi).

The total number of preserved lizards, by month, studied from each locality is given in table 1.

Studies were begun in December, 1967, and continued through August, 1968. A second trip to the area was made in April-May 1969, to reexamine and verify specific aspects noted in the original study. More than 600 observation hours were logged in the various localities in addition to laboratory observations. Specific methodological approaches are covered in the appropriate sections to follow.

#### HABITAT

Although both species are restricted to streamsid es throughout the study area, there are numerous slight differences in the microhabitats utilized, which requires that they be treated separately for maximum clarity.

TABLE 1  
PRESERVED SPECIMENS OF *Anolis lionotus* COPE AND *Anolis poecilopus* COPE EXAMINED<sup>a</sup>

	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Total
<i>A. lionotus</i>	25	30	9	24	29	16	16	14	0	45	10	20	238
<i>A. poecilopus</i>	9	61	15	43	13	14	14	17	3	21	0	19	229

<sup>a</sup>Specimens collected between January, 1968 and October, 1969.

In the study area *Anolis poecilopus* was encountered only along clear, rapidly flowing streams running through rather heavy forest with a complete canopy cover. Along the streams the lizards were concentrated in areas with exposed rocky surfaces and well-developed stands of the Panama-Hat Palm, *Carludovica palmata*. Figures 4 and 5 illustrate several sections of optimum microhabitat for this species.

Adults were almost exclusively found near the edge of the water on rocks, the basal stems of the Hat Palm, or on the buttresses of large trees that extended down into the water. Younger lizards would also occasionally be found in this portion of the habitat but were more often taken farther away from the immediate proximity of the water. The hatchlings were seldom seen near the water but seemed to spend most of the time up in the Hat Palm or in other bushes along the edge of the water.

*Anolis poecilopus* is tightly bound to the water; no individual was ever observed more than 10 feet away from the edge and only two observations were made of lizards more than 6 feet away from the water. In the area investigated the species occurs only along permanent streams. Several streams were examined numerous times without locating the species; all



FIG. 4. Optimal habitat for *Anolis poecilopus* Cope on the Quebrada Juan Grande, 1 mile North Gamboa, Canal Zone. In this circumscribed area lizard density was as high as 1/10 m<sup>2</sup>.

these streams underwent a partial drying of the streambed and cessation of water flow during the dry season.

*Anolis lionotus* was somewhat more catholic in its habitat requirements. While closely bound to the water and seldom straying more than 5 feet from the edge, it was found in a wider variety of streamside situations and is capable of utilizing watercourses that dry to isolated pools during the dry season. The Hat Palm is lacking in the majority of *A. lionotus* localities, the streams are smaller than those inhabited by *A. poecilopus*, and rocky outcrops are not so dominant an aspect of the habitat (figs. 6, 7). *Anolis lionotus* was also found in streams similar to those in which *A. poecilopus* occurred, and in these areas its behavioral orientation and responses to the physical surroundings appeared identical with *A. poecilopus*. *Anolis lionotus* differs from *A. poecilopus* chiefly in the degree that it is capable of using the open flat areas along the stream bank; on one occasion an individual was observed on a mud bank along a stream (S. R. Telford, pers. commun.), a situation in which *A. poecilopus* has never been observed. The streams used by *A. lionotus* tended to accumulate large piles of logs and brush heaped up during flood stages owing to their narrow channels and high banks. The lizards showed a decided preference for these areas, utilizing them much as did *A. poecilopus* the rocky outcrops along its streams. These log-jams were likely to shift position with shifts in the river, and this was responsible for considerable fluctuation in *Anolis* density at any given spot over any period of time.

#### POPULATION DENSITIES

A number of attempts were made to estimate population density of *Anolis poecilopus* and *A. lionotus* using several techniques. Mark/recapture data were not satisfactory as the lizards did not behave in a manner compatible with the basic assumptions underlying the logic of the Lincoln Index; that is, marked individuals did not mix freely throughout the population but remained in the capture area.

Consequently, density estimates were based on the total number of individuals counted in a walk over a 500 meter length of stream and by counting the individuals present in randomly selected 20 square feet quadrates along the full length of the stream.

Several factors obviously affected these estimates; seasonal differences in daily activity cycle resulted in low counts during mid-afternoon in the dry season but not in the wet season. The activity of other humans or large animals (coati mundis, *Nasua narica*, for example) was common in the study area and these disturbances drove the lizards into retreats. High water periods also resulted in lower estimates.

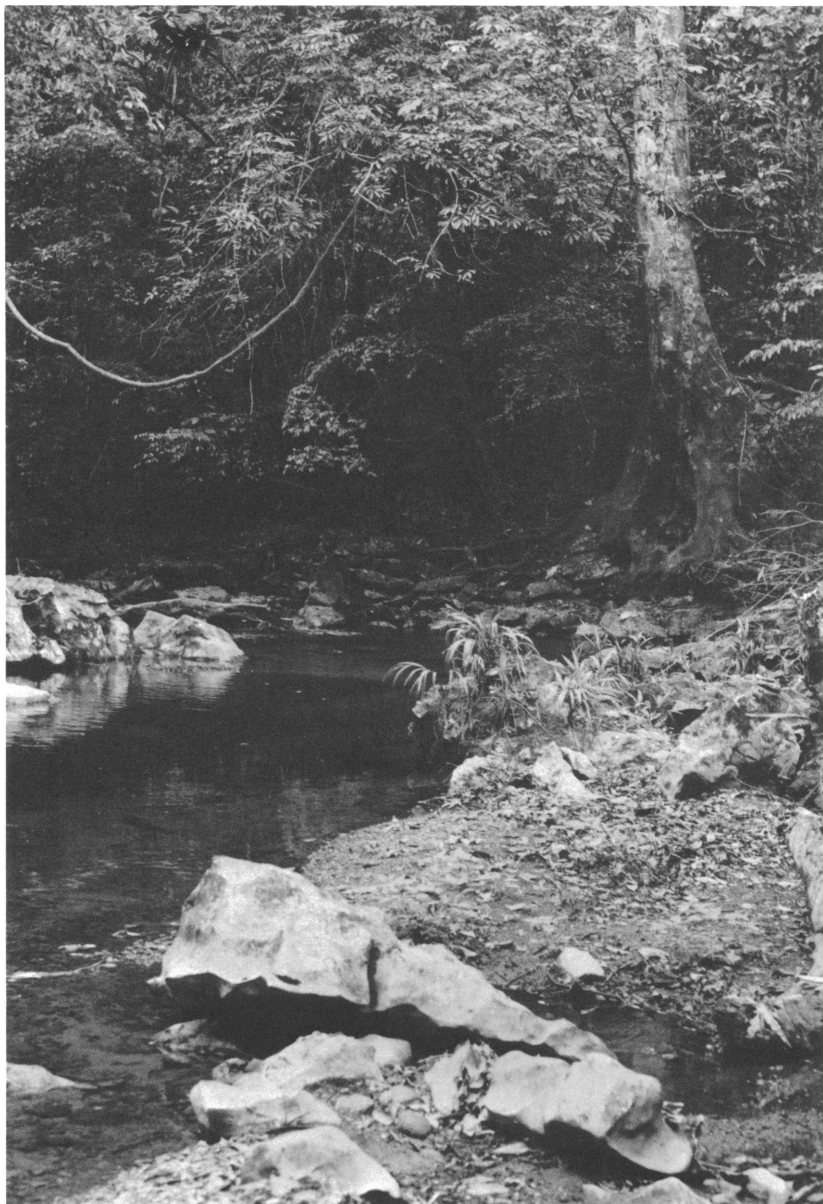


FIG. 5. View of *Anolis poecilopus* Cope habitat along the Frijoles River, 3 miles North Gamboa, Canal Zone. Lizards were maximally abundant on the rocks in the shaded zone.



Maximum densities for both species estimated by both techniques varied from  $1/10 \text{ m}^2$  to  $1/45 \text{ m}^2$  in the wet season and  $1/40 \text{ m}^2$  to  $1/75 \text{ m}^2$  in the dry season.

Density, of course, varied along the stream with the lizards being concentrated in areas offering both rock and Hat Palm or brush tangles. Figure 4 illustrates the optimum habitat-type along the Quebrada Juan Grande. In this particular location, 10 by 13 meters, frequently we counted as many as 13 *Anolis poecilopus* in the wet season, whereas immediately above and below this area few lizards were ever seen.

*Anolis lionotus* at the Achioté locality exhibited considerably greater densities during the early part of the study, in the wet season, than it did toward the end in the dry season. Estimates, based on total number of individuals observed were as high as  $1/11 \text{ m}^2$  over a 150 meter length of stream. At the end of the dry season densities had fallen to about  $1/45 \text{ m}^2$ . It is not clear whether this decline was because of physical alteration of the habitat owing to the dry season or to the heavy removal of animals in previous months. Fifty-four adult individuals were removed from this population in the preceding four months, and it seems likely that this constitutes a sizable percentage of the resident population. Very few individuals were removed from the population in 1969 (10 only), and a recheck of the density in May, 1969, gave an estimate of  $1/60 \text{ m}^2$ . This would suggest that the lower densities recorded are a seasonal event and not the result of excessive collecting. However, ecological specificity in conjunction with the disjunct distribution of suitable habitat should hinder recruitment into the local areas through immigration, and it is possible that it would be relatively easy to temporarily "wipe-out" local populations by repeated sampling.

Density estimates for a species with similar habitat requirements in Mexico, *Anolis barkeri* (Meyer, 1968), are similar to those reported here for *A. poecilopus* and *A. lionotus* in the dry season but lower than the wet season estimates. Meyer gave figures of  $1/40 \text{ m}^2$  to  $1/75 \text{ m}^2$  for *A. barkeri*, and suggested total population sizes in two localities of 200 to 300 individuals (in  $14,000 \text{ m}^2$ ) and 1000 individuals (in  $80,000 \text{ m}^2$ ). These estimates were made during the summer months and thus are presumably comparable with the wet season estimates for *A. lionotus* and *A. poecilopus*. If true, it appears that *A. barkeri* may not exist at population levels as high as those achieved by *A. lionotus* and *A. poecilopus* in Panama.

#### SEASONAL CHANGES

Seasonal changes in the behavior and distribution of these lizards were noted although no changes in population densities could be discerned that



FIG. 6. Habitat of *Anolis lionotus* Cope three miles southeast of Achioté, Colon Province, Panama. Photo during dry season.

could definitely be related to climatic fluctuations.

Throughout the wet season (April-January) the streams are full and the forest canopy effectively shades the area throughout the day. During this period, the lizards are active throughout the day and over a wide range of microhabitats along the edge of the stream, adequate shading apparently being a major factor influencing their distribution. With the advance of the dry season in February and March the canopy loses leaves and the water levels drop. At Achiote the forest floor never experiences high insolation; however, drying of the streambed concentrates the lizard population along small flowing trickles of stream and small pools (fig. 6). They remain active throughout the day in these areas.

With *Anolis poecilopus* along the Frijoles and Frijolita rivers the situation is reversed; these larger streams never dry but reduction of the canopy density allows considerable sunlight to reach ground level in some areas during the midday hours. During these hours, *A. poecilopus* ceased activity and remained sequestered in holes in the bank, beneath dense patches of Hat Palm, in contact with the water, or in the air pockets formed where water ran rapidly over rocks. In areas where insolation of the streambed occurred more than an hour or so a day the lizards disappeared.

Concurrent with the increased insolation in the *Anolis poecilopus* habitat was an influx of other, more thermophilic, species of lizards, most notably *Basiliscus vittatus* Wiegmann. In several areas the resident *Anolis* disappeared totally and were replaced over a two-month period by small to medium-sized *Basiliscus*. The fate of the displaced *A. poecilopus* is a moot point; many of the individuals were marked and none were later recaptured at different points, so predation by the larger *Basiliscus* is a possibility. However, arguing against this was the invasion with the *Basiliscus* of a smaller species of *Anolis*, *A. tropidogaster* Hallowell. *Anolis poecilopus* and *Basiliscus* do utilize the same physical locations on the edges of the bank and on rocks, whereas *A. tropidogaster* was invariably in the vegetation and perhaps out of the foraging zone of the *Basiliscus*.

The available data are inadequate to determine the mechanics of the displacement process, whether through predation, competition, or incidental environmental change, but the actual displacement was an obvious and dramatic process.

Another aspect of seasonal change with which both *Anolis* species had to contend was the prevalence of flooding of the stream beds during the wet season. During rains, the beds of these streams were filled to overflowing, water levels frequently rising 3 to 4 feet or more. During these periods all the normal habitat of the lizards was under water. Numerous unsuccessful attempts were made to determine where the *Anolis* took



FIG. 7. View of a small (4-foot wide) pool along stream 3 miles southeast of Achioté, Colon Province, Panama. During dry season *Anolis lionotus* Cope was concentrated around such pools, as many as six adults being observed together at this one.

refuge under these conditions. We made intensive searches in the vegetation along the edges of the flooded streams and farther back in the forest, both visually by day and with the aid of a head lamp at night. Not one *A. poecilopus* was ever found under these conditions.

I tentatively conclude that the animals remain under water in refuges (air filled?) or simply cling to rocks, during the flood conditions. The duration of the flood stage, several hours or more, weighs against this possibility but it cannot be discounted. These animals do enter the water to escape pursuit, diving to the bottom to hide beneath leaves, or rocks, or whatever, but the longest voluntary dive I was able to record was four minutes, 35 seconds.

This is an issue of considerable significance in the ecology of these species, and to other species in this uncertain environment. Flood stage conditions, while of relatively short duration (two to six hours usually), caused considerable rearrangement and modification of the physical streamside habitat. Sandbars were frequently eliminated at one point and rebuilt some distance away, log piles appeared and vanished, and the whole streamside area showed considerable evidence of "scouring" by water and transported debris.

Lloyd, Inger, and King (1968) have suggested that similar conditions in Borneo might prevent the streamside community from achieving its theoretical equilibrium. In Panama the flooding did not appear to be related to any variations in species composition in the streamside habitat. Immediately, within one to 10 hours after a flood stage, amphibian and reptile activity was minimal in the habitat with only an occasional frog or *Anolis poecilopus* being observed. Within 48 hours, however, the area presented a "normal" appearance. Sandbars and gravelly areas that had shifted position were repopulated with their characteristic amphibian species, and lizard populations would have returned to normal activity levels. This observation, although not quantitative, does indicate that the major effect of the flood conditions was to redistribute, on a local scale (< 200 yds.), some species populations, most notably the frog species, and to depress activity in the lizard populations without causing any noticeable relocation. It is possible that the rapid turnover in the lizard populations, as indicated by the large number of marked individuals that were never recaptured or were observed only briefly in the population, could be due to some degree to flood-related mortality. The present data are inadequate to shed any light on this.

#### PREDATION

Only three positive instances of predation, all concerning *Anolis poe-*

*cilopus*, are available. On January 28, 1968, a vine snake, *Oxybelis brevirostris* (Cope), was observed feeding on an *A. poecilopus* at the Santa Rita, Colon Province, area. A hatchling *A. poecilopus* was taken from the stomach of an adult lizard of the same species from the Frijolita River. In several instances unidentified fish were observed making passes at subadult lizards swimming across pools; on one of the occasions I chased the lizard back across the pool several times and on the third exposure it was caught and eaten.

Predator-avoidance behavior was observed on several occasions. Coati-mundis are abundant along the streams and are potentially important predators. On one occasion a Coati was seen moving through a rocky area in which three *Anolis poecilopus* were visible. One of the lizards, sitting at the mouth of a crack between some rocks, withdrew into the cavity out of sight, a characteristic defense response of the species (fig. 8). The other two in exposed positions took to the water, one immediately, and the other after running along the stream bank for 10 feet. Both dove to the base of the rocks sitting in the water. The Coati nosed about the crevice where the first lizard had disappeared and then moved on. On another occasion a *Chironius carinatus* (Linnaeus) 3-feet long was released about 10 yards from a concentration of *Anolis poecilopus*. One lizard fled through the Hat Palm, covering a distance of about 30 feet before stopping. The others, four visible, remained immobile until the snake had approached to within approximately 3 feet then dashed off a short distance and dove into the water. Three submerged immediately, the fourth crossed the stream (2 feet wide at this point) and ran behind a small rock pile grown over with Hat Palm.

Escape behavior from humans is identical. In several hundred observations only three cases were recorded where a lizard left the immediate vicinity of the stream to escape. On one occasion a lizard ran up the steep bank and into a hole about 9 feet from the water, on another, one ran 10 feet from the stream and disappeared under a log, and on the third the lizard, resting on a large tree trunk at edge of the water, ran up the tree about 20 feet. When pressed, it moved down rather than up the tree and slipped into the water.

*Anolis poecilopus* uses an unusual avoidance tactic in areas where water flows rapidly over rocks, or down small waterfalls and forms small pockets of air. The lizards utilize these air pockets as refuges and may stay sequestered after a pursuit for as long as a half hour. Usually they entered the retreat in full flight but, on two occasions, first dove into the water, submerged, moved around the rock and emerged into the air pocket. This retreat is also utilized by the frog *Eleuthrodactylus bufoniformis* (Boulenger)

in this area and on four occasions an *A. poecilopus* and an *E. bufoniformis* were recovered from the same refuge. A total of 47 *A. poecilopus* were flushed from these retreats during the study, although only 17 were observed to enter the air pockets. *Anolis lionotus* was not observed to use this tactic.

The most frequently used avoidance behavior of both species is submergence, either following a short dash along the bank or among the rocks, or immediately when pursuit begins. In most cases the individual simply runs into the water at the base of a rock and clings to it about 2 to 8 inches beneath the surface; occasionally, however, individuals dive into the water and swim underwater some distance (2 to 11 feet) before stopping. The longest dive duration recorded was four minutes, 35 seconds, and the average dive time was two minutes, eight seconds ( $n=31$ ).

Both species were also capable of utilizing the surface film to run across the surface of the water as frequently reported for the "Jesus Cristo" lizards (*Basiliscus*) and for *Anolis pulchellus* Dumeril and Bibron (Heatwole, Diaz-Collazo, and Jiminez-Velez, 1961). This behavior was frequently incorporated into their escape reaction; they would run across the stream or into the middle before diving, and often run across the stream or pool and take refuge in the Hat Palm or behind the rocks on the opposite side. This appeared hazardous for the smaller lizards, at least, for they often attracted the attention of the fish in the area (see Predation above).

Overall, any given individual appeared capable of varying its escape response. If a surface retreat was immediately available, a rock crevice or recess in a log pile, for instance (fig. 8), they would utilize it immediately, but, if exposed, might respond by diving immediately, running either along the streamside or across the stream before diving or hiding behind a rock or in a clump of Hat Palm either immediately or after a short run across the stream or along it. This escape response appears to be an advantageous strategy for a species restricted to such a narrow and limited activity zone.

#### TEMPERATURE RELATIONSHIPS

Detailed temperature data for these species has been presented elsewhere (Campbell, 1971), however, pertinent highlights can be repeated here. *Anolis lionotus* and *A. poecilopus* are both nonheliothermic and are most commonly active with body temperatures between 24°–26° C. Their body temperatures are usually between water and air temperatures at the point of capture, occasionally equal to the water temperature, but never equal to or above air temperature. In 600 hours of field observation no lizard was ever observed basking or in a position where exposure to direct



FIG. 8. Habitat of *Anolis poecilopus* Cope near Santa Rita, Colon Province, Panama. A lizard is visible in a recess in extreme foreground, just right of center (arrow). *Anolis lionotus* Cope occurs in similar habitat at Achioté, Colon Province, Panama.

sunlight was probable. They were invariably found in areas of deepest shade, or, where the overall light level was high, beneath the foliage at the edge of the water (usually Hat Palm) or beneath overhanging rocks, logs, or the overhanging edge of the bank. They occasionally took refuge in holes in the streambank as far as 4 feet from the water during the dry season when the leaf-fall had exposed a greater proportion of the stream bed to afternoon sunlight.

This behavior seems to differ from that of the aquatic anole found in Mexico, *Anolis barkeri*. While the mean body temperature of all three species is approximately the same (*barkeri* = 24.4° C., Kennedy, 1965, *poecilopus* = 26.5° C., *lionotus* = 26.4° C.), Kennedy, 1965, observed basking behavior in *A. barkeri* and a sizable proportion of his temperatures were equal to, or slightly above, the ambient air temperatures. The ambient temperatures he recorded at his locality were lower than those generally encountered in the Panamanian localities. Meyer (1968), however, stated that *A. barkeri* is definitely shade-loving and seldom basks. *Anolis lionotus* and *A. poecilopus* under thermal conditions similar to those



in the *A. barkeri* habitat, soon after emergence in early morning and in the evening, made no effort to elevate their temperature by basking although potential basking sites were available.

The similarities of the mean body temperatures of the three species should not be considered to indicate a similar thermal ecology; *Anolis barkeri* is a species that can and apparently does on occasion utilize basking behaviors to elevate its temperature to the preferred range; *A. lionotus* and *A. poecilopus*, at least in the localities studied, do not. This fact is indicative of some basic differences in the behavioral and ecological organization of these species, which should not be lost in the overall similarities of gross temperature data or in superficial ecological resemblances.

#### INTERSPECIFIC RELATIONS

Interspecific interactions of both species vary with age and season. Small to half-grown individuals, as noted above, are generally active in elevated positions in the Hat Palm or other vegetation along the edge of the water. This habitat is also occupied on occasion by *Anolis limifrons* Cope young and adults. On one occasion a half-grown *A. poecilopus* and an adult *A. limifrons* were found within 3 inches of each other under a large piece of tin 2 feet from the edge of the stream.

The proximity of these two species may possibly result in some competition for food and perching positions, although only once was any behavioral interaction noted. On this occasion an adult *Anolis limifrons* male displayed at a subadult *A. poecilopus* that approached it. They were both 2 feet up in the Hat Palms, 3 feet back from the edge of the water. The *A. poecilopus* moved toward the *A. limifrons* which retreated several feet, displayed again, and then left the clump of Hat Palm. The *A. poecilopus* made no attempt to follow and did not display at any time during the encounter.

Throughout the wetter months of the year the *Anolis limifrons* are distributed throughout the forest with minimal population densities along the streambeds. During the dry season, however, they appear to concentrate around the streams and their density may approach, locally, the *A. poecilopus* numbers. During this time also the large aboreal anole, *Anolis frenatus* Cope, concentrates around the streams. This large anole is quite capable of feeding on both *A. poecilopus* and *A. limifrons*, although no natural occasion of such predation was noted. *Anolis frenatus* restricts itself to the trunks of the larger trees, a habitat which *A. poecilopus* only rarely utilizes (three observations), while *A. limifrons* is frequently found in this situation. If *A. frenatus* poses a substantial threat to the other anole species

in this habitat during the dry season it appears that *A. limifrons* would take the brunt of the burden. During the wet season *A. frenatus* is only occasionally seen in the trees immediately along the edge of the streams. It, like *A. limifrons*, appears to disperse into the forest with the onset of the rains.

The lizard *Ameiva leptophrys* Cope is frequently seen foraging on the ground beneath the Hat Palms and between the rocks on which *Anolis poecilopus* spends the majority of its time. Juvenile *Ameiva* are especially common in this situation. Several interactions between *A. poecilopus* and *Ameiva* were observed; in every case a foraging *Ameiva* moved beneath an *Anolis* perched in a Hat Palm. The *Anolis* became agitated, repeatedly cocked his head to watch the activity of the *Ameiva* and usually displayed vigorously at the larger lizard. The *Ameiva* took not the slightest notice of the frantic *Anolis*. On one occasion in the laboratory, however, under similar conditions, an *Anolis* attacked an *Ameiva* thrice his size, seizing him by the upper jaw. The two lizards rolled over several times and struggled before the *Ameiva* broke free and ran off, the *Anolis* returned to his perch, displaying vigorously before settling down.

*Basiliscus vittatus* juveniles and subadults replace the *A. poecilopus* in many of their habitats with the advance of the dry season (see section on Seasonal Changes). Despite the similarity in size and activity areas of the two species, no behavioral encounters were ever noted. Although positive data is not available, it appeared that the alteration of the habitat was the decisive factor in the replacement, and that the *Anolis* were vacated before or as the *Basiliscus* moved in. This replacement process, and the reverse situation as the rains begin and the canopy thickens, deserves more attention. The local nature of this phenomena, and the low densities of the populations involved, might make it quite feasible to eliminate all individuals of one or the other species in specific areas to determine whether the replacement is due strictly to climatic or competitive factors, or a combination of these.

### HOME RANGE AND TERRITORIALITY

*Anolis poecilopus* appears to be remarkably sedentary, although there is considerable apparent individual variation. One individual was marked as a hatchling, for example, and recaptured 37 times in seven months. It was observed within inches of the same position on the same branch at the base of a large boulder on every occasion. The greatest distance the lizard ran during a chase was 9 feet before entering the water to hide at the base of a rock. Usually the lizard would not leave the 3-foot diameter boulder during a chase, but circled around when pursued. Others were less restricted to a particular spot, the average distance covered between

recaptures was 4 feet, but not one was ever recaptured more than 30 feet from the original marking site.

On one occasion a whole marked population of adults (13 individuals) vanished over a six-day period from one restricted section of prime habitat. Their disappearance corresponded to a period of human activity in the area. Within 20 days the density of adults (late subadults and small adults versus full adult-sized specimens which had been marked) had returned almost to the previous level (11 as opposed to 13). This suggests a large floating population that rapidly moves in to replace lost territory holders. Further support for this can be taken from the mark-recapture data. During the course of the initial field work, 147 lizards were marked by clipping their toes in individual combinations. Of these, 51 were never recaptured, 33 were recaptured either only once or twice, seven were recaptured three times, and 16 were recaptured more than three times. This suggests that the great majority of the individuals were transient (either through emigration or predation) in the population and that only a few were resident. These data are, however, only suggestive and open to alternate interpretation; additional observations in this area are needed to resolve this point.

#### INTRASPECIFIC BEHAVIOR

Numerous observations of intraspecific agnostic behavior were obtained for *Anolis poecilopus* on the Frijoles River and Quebrada Juan Grande. Dewlap displays were observed frequently and several attempts were made to obtain movie sequences for detailed analysis. Under the prevailing low light conditions these attempts failed and no detailed analysis of the behavioral sequence is available. Basically the behavior consists of, first, a moderate extension of the dewlap and a sequence of head-bobs. This is followed by a complete extension of the dewlap with extension of the forelimbs, elevation of the anterior portion of the body, and a more vigorous sequence of head-bobs. Highly agitated individuals gape the jaws and engorge and protrude the tongue just prior to attack.

Chase behavior was observed on several occasions. Two adult individuals of different or the same sexes would often occupy one large boulder or log. Chases about these sites were frequent with the final result of both individuals ending at their original positions on opposite sides of the site and out of sight of each other.

Mating behavior was observed on three occasions, twice at the Frijolito River (*A. poecilopus*) and once at Achiote (*A. lionotus*). In all cases the lizards were in copulation on rocks along and above the water. The male grips the female in the shoulder/neck region and, lying alongside her,

inserts the hemipenis by twisting his body laterally and curling his tail beneath the tail of the female in "typical" lizard copulatory fashion. No obvious courtship behavior was observed during the study, although it may be presumed to occur.

#### FOOD AND FEEDING

Feeding behavior was observed on numerous occasions. Lizards most commonly perched on the basal portions of Hat Palm, on rocks, or dead branches, or at the edge of the water, and pounced on suitable prey either on the land or at the edge of the water. On several occasions lizards were observed to actually jump up off the substrate after flying insects. As the lizards generally incline to perch with their head uppermost or nearly horizontal, in contrast to many other anoles that perch facing downward, they were well positioned to observe prey moving above in the Hat Palm as well as below by just slight movements of the head.

Juvenile and subadult lizards assumed the same hunting position as adults, but they were generally much higher in the bushes and a bit farther away from the water. Their hunting radius appeared somewhat smaller than that of the adults and most observations of prey pursuit were of lateral or upward chases. Only 13 actual prey pursuits by these size classes were observed, however, so little reliance can be placed on these apparent differences in the size classes.

The feeding behavior and stomach contents of *Anolis barkeri*, a species with superficially similar ecology, has been described by Robinson (1962), Kennedy (1965), Brandon, Altig and Albert (1966), and Meyer (1968). These observations led Meyer to suggest that the majority of prey items taken by *A. barkeri* were immediately associated with the water even though more than 70 percent of their stomach contents was nonaquatic invertebrates. While *Anolis lionotus* and *A. poecilopus* are as closely bound behaviorally to the immediate vicinity of the water, their feeding habits do not leave them dependent on water-borne prey. The majority (73%) of successful prey chases involved prey on the land near the water or in the bushes or on the rocks on which the lizard perched. It seems doubtful, furthermore, that the lizards can regularly catch prey in the swifter, rocky portions of the stream where they are maximally abundant. This was "tested" twice by floating small insects of known prey species past lizards perched in appropriate positions. The lizards did attend to the floating insect on several occasions but the insect was out of the pursuit radius before the lizard mobilized for pursuit. On one of these occasions the lizard subsequently ate an insect dropped on the ground nearby. This is, of course, scant data on which to base firm conclusions, but the overall

impression of the feeding behavior of these species indicates that they are not at all bound to the stream as a food source but rather take their prey wherever they find it in the streamside area. It is thought that the orientation to the aquatic habitat is the behavioral substrate upon which the feeding behavior is superimposed rather than a result of a feeding specialization to the aquatic situation as suggested by Meyer (1968) for *A. barkeri*.

Goodman (1971) has demonstrated that another species of semiaquatic *Anolis*, *A. aquaticus* Taylor, in Costa Rica, will readily feed on dead insects in contrast to the other *Anolis* species tested. This suggests that they are capable of recognizing as prey dead insects that come to rest along the banks of the streams. No actual observations of *A. lionotus* or *A. poecilopus* feeding on prey of this nature were made, although struggling insects near the bank in backwashes and quiet areas were taken on several occasions. It might be interesting to examine this aspect of the prey recognition in these species in subadults, which do the majority of their prey-seeking away from the water in the higher areas in the vegetation, and in adults, which feed mainly near the edge of the water. The perceptual environment associated with prey recognition in these two areas is obviously quite distinct and might require quite different sensory orientations in the different age classes.

No attempt was made to quantify the amount or variety of food items accepted by either species. Low absolute numbers of individuals argued against heavy removal sampling in any given area and specimens removed were generally maintained alive in captivity for a variety of reasons and periods of time. Thus, stomach content data for a reasonable sample are not available. A few specimens were examined and contained remains of spiders, ants, Lepidoptera larvae, and one adult male *A. poecilopus* contained a hatchling-sized specimen of the same species.

A great variety of insects was observed to be eaten under natural conditions, but no identifications are available. In general, the lizards appeared to accept almost any insect of appropriate size that lacked obvious defensive capabilities. Army ants, leaf-cutting ants, and ponerine ants were frequently seen in the immediate vicinity of perching lizards and were never utilized as food. Wasps and other Hymenoptera were also common in the immediate vicinity of the lizards and active individuals were never approached. One lizard was observed, however, to eat an almost dead specimen of an unknown wasp species that was struggling in an eddy of the stream.

#### REPRODUCTION

Standard monthly sampling of the study populations was deemed

inadvisable due to the low absolute numbers of lizards in any given area. Thus a detailed analysis of seasonal variation in reproductive physiology cannot be attempted. Some general patterns can be discerned, however, based on irregular samples from several different localities, field observations on the presence of shelled eggs in females captured for marking, and the appearance of hatchling-sized specimens in the population. Data of this sort do not allow for any quantitative estimates of the proportion of females breeding in any given period but they do permit cautious statements on the presence or absence of active breeding.

In the Gamboa area *Anolis poecilopus* hatchlings enter the population in every month for which data are available, December through August. Females with shelled eggs were present in every month of the year and field observations suggest that the proportion of females with shelled eggs remains constant throughout the year. Data from other populations of this species from Sasardi, San Blas Territory, Santa Rita, Colon Province, Cerro Campana, Panama Province, and Gaspar Savanna, Panama Province, are available from February, March, April, May, and September, 1969 (table 1). The majority of the mature females in all of these samples contain one or two shelled eggs.

In the Gamboa area yolk deposition is first initiated at a body length of 48 to 50 mm. and appears to be continuous thereafter. The left ovary begins development first and appears to remain slightly advanced over the right throughout the reproductive life. Both oviducts frequently contain shelled eggs at the same time, with the left egg being somewhat larger, apparently to be oviposited first. The egg in the right oviduct is laid as yolk deposition begins again in the left, and this sequence apparently continues throughout life. Only 4 percent of the females over 58 to 60 mm. snout to vent (S-V) from all months sampled (with exceptions noted below) lacked either a large (7 to 10 mm.) yolked follicle or a shelled egg in at least one ovary. A similar alternation of oviducts with continuous breeding through the reproductive season has been suggested for *Anolis barkeri* (Kennedy, 1965) and demonstrated for *A. carolinensis* Voigt in Louisiana by Hamlett (1952).

Shell formation in both species begins at a follicle length of 11 mm. and the eggs are oviposited at 12 to 14 mm. in length. No data are available on the natural nest sites or on natural incubation duration. Eggs laid in the laboratory were adhered to solid objects and deposited occasionally in clusters with more than one female contributing to a group.

*Anolis lionotus* appears to undergo a decrease in reproductive activity in at least two populations (Achiote, Colon Province, and El Aquacate, Panama Province) in April and May. The data do not allow a vigorous

defense of this point, but the April samples from both areas (autopsy and field observations) lack any females ( $n = 26$ ) with shelled eggs. In the Achiote sample no female contained any yolked follicles larger than 5 mm. and none larger than 7 mm. was present in the females collected from El Aquacate. In the May sample from El Aquacate one female contained a shelled egg in the left oviduct and the remainder contained large (9 to 11 mm.) yolked follicles in the left ovary, smaller yolked follicles in the right. At Achiote no females with shelled eggs were present in May; all specimens larger than 55 mm. had an enlarging follicle in the left ovary (3 to 7 mm.) and a small one in the right (3 mm.). In all other months almost all adult females contain one or two shelled eggs. Hatchlings are present in the Achiote populations in all months; no data on this point is available for El Aquacate.

These data suggest that egg development is arrested to some degree toward the end of the dry season in these localities, perhaps to a greater degree at Achiote than at El Aquacate. This, if valid, is an interesting point. Both Sexton et al. (1971) and Licht and Gorman (1970) have suggested that the seasonal reproductive cycle in *Anolis* is related to seasonal variation in rainfall. Rand (1967) has further pointed out that reproduction in stream-associated populations of *Anolis limifrons* in Panama does not show as dramatic a seasonal cycle as populations removed from streams, thus supporting an association of reproductive activity and available water.

The data of Sexton et al. (1971) show a correlation between seasonal variation in rainfall in Central Panama and reproductive activity in *Anolis limifrons*. Those from the Pacific side where a definite dry season exists show a pronounced decrease in the drier months, whereas those from the Caribbean side where the dry season is less marked show a less marked decrease. Superficially, *Anolis lionotus* apparently fails to fit this pattern: the Achiote locality is on the Caribbean side of Panama and receives more rainfall than does the El Aquacate locality on the Pacific side. The Achiote populations, however, are located on small streams that undergo considerable reduction during the dry season. Flow virtually ceases in the late dry season and the streams dry to a sequence of small pools around which the *A. lionotus* populations become concentrated (fig. 7). The El Aquacate populations also are located on small streams for the most part, but these are generally larger than those at Achiote and maintain a continuous, if reduced, flow throughout the dry season. Thus, the *A. lionotus* populations appear to be affected by, or respond to, a reduction in the quantity or quality of the available water, although some water area is invariably present.

The *Anolis poecilopus* populations, in contrast, are all found on larger streams which experience only minor seasonal variation in extent or rate of flow; the available habitat along the banks is approximately the same, overall, in all seasons (but see section on Seasonal Changes). Streams of smaller sizes, which undergo partial seasonal drying, do not appear to be utilized by *A. poecilopus* in this area.

Thus, the reproductive cycles of these species appear to be regulated by seasonal fluctuations in the availability of water, if on a different scale from that experienced by *Anolis limifrons*. Obviously, "feast" or "famine" are relative values, dependent on the norm within a specific microhabitat and not necessarily on any absolute quantities. This a point perhaps often overlooked in considerations of the comparative "quality" of the tropical versus temperate environment for various groups of animals.

#### SIZE AND GROWTH

Hatching, in both species, occurs at a snout-vent length of 28 to 30 mm. Growth is rapid, as much as 0.48 mm./day during the first two months (fig. 9), and a S-V length of 52 to 55 mm. is reached in 50 to 70 days. Both sexes are reproductively active at this size; testicular enlargement begins in males at about 46 to 48 mm., and yolk deposition in females begins at 48 to 50 mm. In the April and May samples of *A. lionotus* from Achiote some delay in yolk deposition is indicated, although the samples are small. In these samples yolk deposition is not evident below a S-V length of 53 mm., possibly as a result of the dry season (see Reproduction).

Males of both species attain a larger maximum size and are, on the average, larger than the females, although the magnitude of these differences does not approach that seen in some other species in the genus (Schoener, 1967). The largest male *A. lionotus* collected measured 76 mm. S-V, the largest female 70 mm. The average length of sexually mature males of this species was 67.5 mm. S-V ( $n = 59$ ), the average length of sexually mature females was 60.6 mm. S-V ( $n = 44$ ). The largest male *A. poecilopus* was 71 mm. S-V, the largest female 66 mm. S-V. Sexually mature males averaged 61.6 mm. S-V ( $n = 60$ ), females 58.2 ( $n = 37$ ).

Males of *Anolis lionotus* are significantly larger than any of the other sample sets ( $p = 0.001$ , Students "t," two-tailed). Male *A. poecilopus* are significantly larger than females of the species at the 0.05 level, and there is no significant difference between the females of either species. No significant difference in average length of either sex was evident between any of the population sampled from within the range of either species.

These size differences do not appear to be reflected in any differential resource utilization by the sexes. The present level of analysis, however,



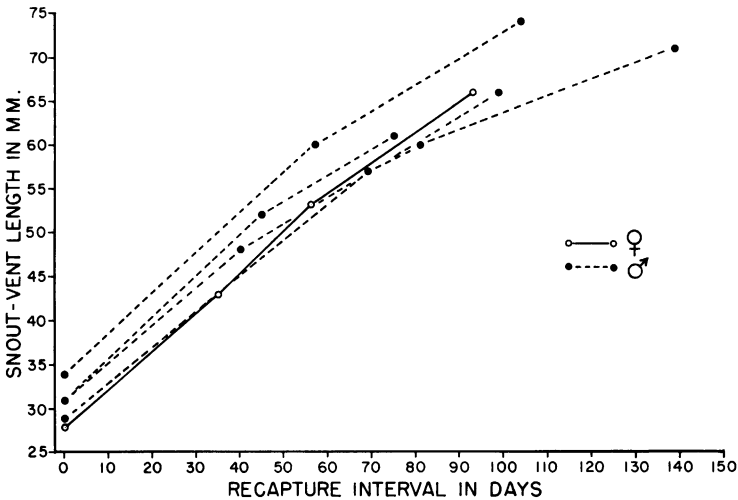


FIG. 9. Growth curves for five *Anolis poecilopus* Cope from Quebrada Juan Grande, Canal Zone.

may be too coarse-grained to reveal subtle differences if they exist.

The growth data suggest that both species are “annuals” that grow to maturity within two to three months and reach the “average” adult length by five months of age. Their “annual” status is supported by mark-recapture data. No males of 70 mm. S-V or larger ( $n = 11$ ), or females of 65 mm. S-V or larger ( $n = \text{six}$ ) were ever recaptured more than three months after they attained this size.

#### PARASITISM

The parasitic burden of the various populations was sampled throughout the study period and beyond by S. R. Telford. He is currently analyzing these data and will report them elsewhere. It can be noted here that both species of *Anolis* were host to the same two species of saurian malaria (Telford, 1969) and to apparently identical worm species. Thus it could appear that the constellation of parasites that these species host is primarily a function of the host ecology and is not species specific. This is further evidence of the ecological similarity of these two species in central Panama.

#### DISCUSSION

The stream-edge life style displayed by *Anolis lionotus* and *A. poecilopus* is, while rather unusual, by no means unique among lizards. The genus *Anolis* contains several other species which have similar ecologies, *Anolis*

*aquaticus* of Pacific Costa Rica and western Panama, *Anolis barkeri* of Mexico, and several species of South America and the Caribbean. Little detail is available for the other species, excepting *Anolis aquaticus* and *A. barkeri*, and it is not now possible to state to what degree their physiological and behavioral capacities reflect a specialization for this life style.

In the species in question the principal adaptive substrate appears to be the strong positive orientation to the immediate vicinity of stream edges. They seem never to leave this habitat, even under conditions of hot pursuit. The sensory cues utilized in maintaining this orientation are unknown. Anoline lizards are generally considered to be microsomatic with poorly developed olfactory capabilities (Armstrong, Gamble, and Colby 1953), but a wealth of visual and auditory information, as well as thermal and humidity gradients, is available to them for orientation purposes.

Aside from their orientation to this specific zone within the available habitat these species show few specific adaptations for an aquatic or semi-aquatic existence.

The behaviors associated with predator avoidance show the most obvious adaptations to the semiaquatic habit. Both species utilize the water in the escape behaviors in two manners; they may cross it in their flight, seeking refuge on the opposite side, or dive into it, hiding on the bottom or in air pockets. Both of these strategies appear well suited to the avoidance of olfactory-oriented predators. In conjunction with these habitat-specific responses, both species utilize a typical array of lizard escape devices, retreating into crevices (fig. 8), straightforward flight, and the interposition of objects between potential predator and self. A typical encounter is met first by immobility and/or object imposition, followed, on close approach (from 6 feet to actual contact), by flight, usually involving stream crossing or submergence. Specimens encountered at the entrance to or within a short distance of holes or crevices will usually run or withdraw into these retreats as soon as disturbed.

In contrast to species that live in more exposed habitats (Heatwole, 1968), the "flight distance" appears to vary with circumstance. While this cannot currently be quantified, the overall impression is that lizards situated on exposed areas, rocks, logs, and so on, will resort to flight at greater distances (30 to 50 feet), whereas those in more "secure" situations, such as thickets of Hat Palm, will not flee until approached to within 6 feet or closer. These escape responses are conceivably advantageous to a species which confines its activity to a narrow spatial zone that affords few absolutely secure retreats completely removed from the foraging zone of the predator.

Perch selection is at once highly specific and highly generalized and

varies with age class and social situation. Adults will utilize almost any available perch site; sticks and twigs of various dimensions, flat, round, or vertical rock surfaces, buttresses of large trees, the stiff but flattened leaves of the Hat Palm, etc., as long as it is in the proper position at the edge of the land-water interface. Optimally, perches are within 12 to 18 inches of the interface and continuous with it. Juveniles and, to a lesser extent, subadults, utilize smaller twigs and branches, leaves of various textures and dimensions, and rock surfaces, generally at a greater vertical distance from the water. Their activity zone is most commonly farther than 2 feet from the edge of the water either vertically and/or horizontally. These size class distinctions are not rigid, however, and frequently subadults or even juveniles are found in typical "adult" perching locations immediately adjacent to and above the surface of the water. This occurs only in the absence of adult territory holders in the immediate vicinity. Thus, the perch utilization of any given lizard is a function of the physical proximity of the perch to the water surface and his social position within the population and, within a wide range, is independent of the nature and dimensions of the perch itself.

The feeding behavior of both species is not so responsive to the stream-side situation as has been suggested for *Anolis barkeri* of Mexico which utilizes the same stream-edge physical regime (Meyer, 1968). Both *Anolis lionotus* and *A. poecilopus* appear to feed on any small invertebrates of proper size and palatability that wander into their pursuit zone. They take their prey in the air (or attempt to), from the vegetation along the stream edge, from the ground, or from the edge of the water. As concluded earlier, their feeding behavior reflects their orientation to the stream-edge situation and does not determine this orientation.

The demonstration by Goodman (1971) that *Anolis aquaticus* will accept dead and immobile insects for food suggests that drowned insects along the edge of the water form an important food source for this species. It is not known if *A. lionotus* and *A. poecilopus* share this ability with *A. aquaticus*, but if they do the present observations suggests that this resource is of minor importance. The majority of their feeding activity was directed toward live, active, prey.

One major aspect of the biology of both of these species for which data are totally lacking is their ability to weather the frequent, irregular and violent floods to which their streams are subject. The data indicate that they do not abandon the habitat during these periods and thus must have some mechanism(s) for confronting this circumstance. This may prove to be an area of major adaptation and is well worth continued study.

No aspects of the biology of these two species other than those noted

above, appear to reflect a specialization to a semiaquatic existence. This appears to reflect a situation where "niche specialization" has been achieved by behavioral adaptations to a particular zone in the habitat and not to any of the standardly measured physical resources. While both species could be considered highly specialized in their habitat selection, being restricted to a narrow physical zone in the habitat, they are generalists in their feeding habits as measured by stomach contents or prey-capture strategies. They are specialized only in the restriction of the area in which they seek it. Similarly, their perch utilization is generalized in nature but specialized in location. Thus, a standard *Anolis* "niche size" analysis might well document these species to be more ecologically versatile than other species in the habitat that are more ecologically diverse in total utilization of the forest. Clearly, care is called for in studies of "niche size" and species diversity where faunal components are grouped along a single or only a few arbitrarily chosen measures of the niche.

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