# STUDIES ON THE ECOLOGY AND POPULATION BIOLOGY OF LITTLE KNOWN ECUADORIAN ANOLES

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## CONTENTS

ABSTRACT. Little is known about the ecology and natural history of South American anoles. This study reports the results of a variety of different studies on several relatively common species of Ecuadorian *Anolis*. In part I, habitat use and population density are compared among three species of *Anolis* that occur in sympatry at a number of sites in Ecuador. The three species—*A. chloris, A. festae*, and *A. peraccae*—are roughly the same body size. These species perch primarily on tree trunks, and *A. chloris* perches substantially higher than the other two species, which are similar in perch height. Large differences from one year to the next were observed both in mean perch height and in population densities.

In Part II, natural history, growth rates, and population densities are reported for two little known *Anolis* species, *A. bitectus* and *A. gemmosus*. Although the two species are from nearby regions and are similar in microhabitat use, they show more differences than similarities in most aspects of their biology. The species have similar ranges in active body temperatures, but *A. bitectus* is thermally passive, whereas *A. gemmosus* appears to thermoregulate. Populations of *A. gemmosus* tend to remain constant through time, whereas *A. bitectus* undergoes moderate population fluctuations. Both species exhibit little sexual size dimorphism, but in *A. bitectus* females are larger, and in *A. gemmosus* males are larger. *Anolis bitectus* has a fairly high characteristic growth rate, whereas that of *A. gemmosus* is quite low.

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# I. ECOLOGICAL INTERACTIONS IN THREE SPECIES OF ECUADORIAN *ANOLIS* LIZARDS

## INTRODUCTION

The iguanid lizards of the genus *Anolis* form a large and complex assemblage of species within three major evolutionary theatres: the West Indies, Central America, and South America. From the West Indies we find a large body of work on many aspects of the biology of the genus (see Williams, 1969, 1972, 1976a; Schoener, 1977, for summaries of some of this work).[1] These studies have led to many refinements in our understanding of the evolutionary forces that have shaped this rich and diverse fauna. The situation in the two mainland regions, however, is quite different. For the Central American anoline fauna, a few works deal with the ecology and systematics of certain species and certain specific faunas (e.g., Taylor, 1956; Fitch, 1972, 1973, 1975; Fitch et a1., 1976),[2] but general overviews have been lacking. Andrews (1976, 1979) has made some attempts to compare island and mainland anoles in terms of life history strategies, but no efforts have been made to make comparisons of entire faunas. For South America, ecological studies have been very limited in scope,[3] although some systematically oriented papers have made substantial contributions to understanding of major evolutionary patterns (Vanzolini and Williams, 1970).[4] The emphasis of South American anole studies on systematic problems has two underlying causes: the South American anole fauna is very complex and confusion abounds in trying to elucidate relationships and affinities of the various taxa because of extensive convergence and parallelism between and within lineages (Williams, 1976b),[5] and South American anoles are characteristically uncommon in the field, which discourages most field studies.

The little information available on the ecology of South American anoles has been largely anecdotal in nature, consisting mostly of brief comments made by various collectors. There have been no detailed population studies of any species of South American anoles, although some valuable information has been provided in general faunal studies of specific regions (Dixon and Soini, 1975; Duellman, 1978).[6] A few papers provide more than anecdotal information on specific species (Rand and Humphrey, 1968; Vanzolini, 1972; Fitch et al., 1976),[7] but this information is usually incomplete and covers only a tiny percentage of the South American anole fauna. Our knowledge of the population ecology of any one species of South American anole is scanty at best, and for most species we have no information at all.[8]

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[1] This and all other footnotes in the main text have been added by the editor: A summary of anole research conducted since Miyata wrote his thesis can be found in Losos (2009).

[2] More recent studies include Guyer (1986); Andrews and Nichols (1990); Andrews (1991); Andrews and Wright (1994); Parmelee and Guyer (1995); Vitt et al. (1995, 2001, 2003a,b, 2008); Vitt and Zani (2005); Schaepfer (2006).

[3] See Ávila-Pires (1995) and Vitt et al. (2008) for references to more recent publications on South American anoles.

[4] For a revised view of the situation with the *A. chrysolepis* species complex, see D'Angiolella et al. (2011).

[5] The phylogenetic relationships of South American anoles are slowly coming into focus Poe, (2004); Castañeda and de Queiroz, (2011, 2013); D'Angiolella et al., (2011).

[6] Avila-Peres (1995); Vitt and Zani (1996); Vitt et al. (1999); Mesquita et al. (2006), (2007); Wernick et al. (2009).

[7] Vitt and Zani (1996, 2005); Vitt et al. (2001, 2003a, 2003b, 2008); Molina and Gutiérrez (2007); Velasco and Herrel (2007); Bock, et al. (2010).

[8] Citations in previous footnotes indicate that the situation has improved in the last 30 years, although we still know little or nothing about most South American anole species.

The present paper provides a look into some of the interactions between several species of *Anolis* from the Pacific lowlands of northwestern Ecuador. Although detailed information on the population ecology of the three major species treated are not available, certain patterns and trends can be followed, and it is possible to make some inferences regarding the way these species interact with each other and the rest of the fauna of the region.

Because the three principal species of *Anolis* studied are poorly known, I will briefly characterize them.

*Anolis chloris* Boulenger: A small to medium-sized anole (maximum male snout-vent length [SVL] ca. 60 mm, females ca. 58 mm SVL). This species is uniform green in color. It ranges through the southern Darién Province in Panama and Chocó region to northwestern Ecuador.

*Anolis festae* Peracca: This is a small species of anole, reaching a maximum SVL of 55 mm in the study region. It is endemic to the lowlands of southwestern Ecuador. Fitch et al. (1976) referred to this species as *Anolis nigrolineatus*.

*Anolis peraccae* Boulenger: This is another small species, reaching a maximum SVL of 54 mm. It is found in the lowland forests of southwestern Colombia and northwestern Ecuador.

## STUDY SITES

The study sites visited in the course of the field work were all located within 25 km of each other in the lowlands of southern Provincia Pichincha, Ecuador. This area ranges in elevation from about 125 to 225 m above sea level. The topography is mostly flat, but with some steep bluffs dropping down into river valleys and low rolling hills. The entire region was once covered by rain forest and was transitional between the tropical moist forest and tropical wet forest formations of Holdridge (1967). Most of this forest has now been cleared, and the area is now rich agricultural land for the most part. The mean annual precipitation in the area varies from about 3,000 mm in the north to 2,000 mm in the south (Dodson and Gentry, 1978), with a distinct dry season running from June to December. During the dry season the region has an almost constant cloud cover, and the humidity remains rather high. Light morning rains or drizzles are an almost daily occurrence during the so-called dry season, although heavy rains do not occur very often. Most of the native forest trees do not drop their leaves during the dry season, and conditions probably do not often become severe.

The primary study site was the Centro Científico Río Palenque, located 47 km south of Santo Domingo de los Colorados on the road to Quevedo at an elevation of 220 m. A map and general discussion of the climate and vegetation of the area is presented in Dodson and Gentry (1978). Although scattered observations were made in the forest there, the major study site was along a row of balsa trees (*Ochroma pyramidale*) on both sides of Perimeter Road between Three Corners Road and Dodson Road (Fig. 1). This stretch of road was about 900 m long and was bordered on one side by rain forest and on the other by plantations of oil palm (*Elaeis guineensis*) and banana (*Musa paradisiaca*) with some small patches of secondary forest. The balsa trees were not planted but germinated shortly after the road was constructed in 1971. These trees grew very rapidly, and at the time the study began in 1974, most were about 20 m in height. At the beginning of the study they were spaced in a fairly uniform manner.

This site was first visited in June 1974, at which point the high population density of *A. peraccae* was noted and preliminary studies begun. At this time the balsas ranged from 15 to 25 cm diameter at breast height (dbh) and were between 15 and 20 m in height. The first planting of oil palm had been made about a month before the first visit, and the bananas had been cut down to clear the way for the new crop. The cut bananas sprouted immediately, and by the

Figure 1. Perimeter road at the Centro Científico Río Palenque balsa study site. The view includes section bordered by forest on left with open banana and oil palm to the right. Photo taken July 1975.

end of August 1974, scarcely 2 months after they had been cleared, they ranged in height up to 5 m. This mixture of bananas and oil palm continued through 1975, but by 1976 the bananas were kept cut back to promote growth in the palms.

At the same time, the balsas had continued to grow until most were more than 20 m in height and 25 cm dbh, and many began to break of their own accord from storms and heavy rains. Certain sections of the study area were consequently opened by these natural falls, and trees in parts of the site were cut and the wood sold. The entire study area was affected by this thinning, but the crowns of the balsas remained more or less continuous. By 1977 nearly all of the balsas had been removed, and no further quantitative studies were possible.

In 1975 a series of isolated tree rows along the Santo Domingo de los Colorados-Quevedo road were examined for anoles. Dense populations of anoles were found at several sites, and these were monitored between the months of June and September of that year (Fig. 2). These sites usually consisted of single rows of large trees, generally teak (*Tectona grandis*) or guayacan (*Tebebuia* sp.), bordered on one side by the road and on the other by open fields or banana plantations. The bases of the trees generally had a thick layer of rather dry leaf litter, and the only vegetation was grass. All of these study sites were destroyed by construction work between September 1975 and June 1976 when the road was widened.

Other study sites included a plantation of rubber (*Hevea brasiliensis*) at Hacienda Cerro Chico and old cacao groves (*Theobroma cacao*) near Buena Fe and just east of the city of Quevedo. Observations in these sites were carried out between 1975 and 1979 at irregular intervals. Additional observations were made at Tinalandia, a hotel located some 16 km southeast of Santo Domingo de los Colorados on the road to Quito at an elevation of 700 m.

Much of the information summarized in this report consists of scattered observations of lizards made at the above study sites, along with a few observations from elsewhere. Because of the nature of the anole populations, many of these observations were perforce opportunistic. It should also be emphasized that nearly all of these observations were made in disturbed habitats, for reasons which will be discussed later.

The daily censuses performed at the Perimeter Road study site at the Centro Científico Río Palenque consisted of slowly walking down the road and noting the following for each lizard seen: species, sex (if determinable—this was often not possible with *A. chloris*), height above ground and diameter of perch at first sighting, and exposure to sun and orientation with respect to the ground. In the censuses performed

Figure 2.    Roadside teak plantation at 41 km S of Santo Domingo de Los Colorados, on road to Quevedo. Photo taken July 1975.

after August 1975, the location of each lizard seen within the study site was noted, and the study strip was divided into 10-m-long segments. In 1974 and 1975 individual trees in the section of the study site nearest Three Corners were marked, and individual lizard sightings were associated with particular trees.

An attempt was made to mark and measure as many lizards as possible to obtain information on growth and movement and spacing patterns. This was later cut back because of several compelling reasons involving increased wariness of marked individuals (see below) and the virtual lack of juveniles, which are necessary to obtain reliable estimates of growth rates (Andrews, 1976, 1979; Schoener and Schoener, 1978). Nevertheless, a total of 65 *A. chloris* and 88 *A. peraccae* were captured and marked at the Centro Científico Río Palenque. For each animal captured, the snout-vent length (SVL) was noted, the reproductive state of adult females (obviously gravid or not) was observed, and an individual toe-clip mark was made. An initial attempt was made to color mark each animal individually, but these marks rarely lasted more than a day or two because of wet climatic conditions. Whenever possible, cloacal temperatures (BT) and air temperatures (AT—shaded bulb ca. 1 cm above perch at time of first sighting) were measured using a Schultheis rapid-registering thermometer.

A similar protocol was followed in all of the study areas, except individual positions were not recorded, and no attempt was made to mark the animals individually.

In several places individual behavior was observed for periods ranging up to one hour at a time. Most such observations were made on *A. chloris,* and none were made on *A. festae.*

In short, except for the Perimeter Road balsa site census area at the Centro Científico Río Palenque, my sampling was opportunistic. These observations did provide considerable insight into the biology of the animals which could have been obtained in no other way. The ephemeral nature of the characteristic habitats of the lizards was the justification for these observational techniques, which did prove to be quite useful.

Figure 3.   Body temperatures of *Anolis chloris* plotted against air temperature at time of capture. Open circles present multiple records. Diagonal line is for body temperature = air temperature.

Analysis of perch height data was performed using log transformations of perch heights, which were always estimated in inches, to normalize the distributions. Means were then transformed back into linear measurements. Perch dimensions in the field were always estimated in inches because I am more familiar with these units and found it much easier to make estimates. These units were retained in the analyses because conversions to metric units would have added nothing except apparent precision.

## RESULTS

### Thermal Biology

All three species of *Anolis* studied were thermally passive (Figs. 3–5). *Anolis chloris* was the only one of the three that was ever observed basking, and this basking was always observed early in the morning or late in the afternoon when the lizards were perched high in the trees and I was unable to sample their body temperature.

The mean body temperatures of all three species were similar (Table 1), reflecting their thermal passivity and similarity of habitat preferences. This similarity held even where the species were found in strict sympatry, rather than basing the comparison on total samples (Tables 2, 3).

### Structural Habitat

Ecological studies of anole communities in the West Indies have shown the importance of differences in structural habitat in the reduction of possible niche overlap (Rand, 1964; Schoener, 1968; Schoener and Gorman, 1968; Rand and Williams, 1969; Schoener and Schoener, 1971a,b). Structural habitat for anoles has customarily referred to both perch height and perch diameter, with sympatric species normally segregating along one or both spatial axes.
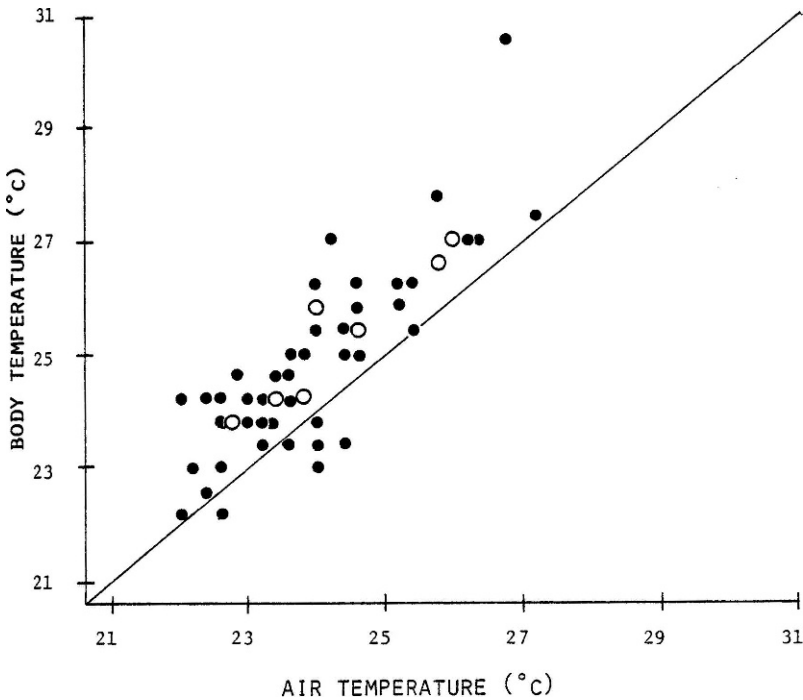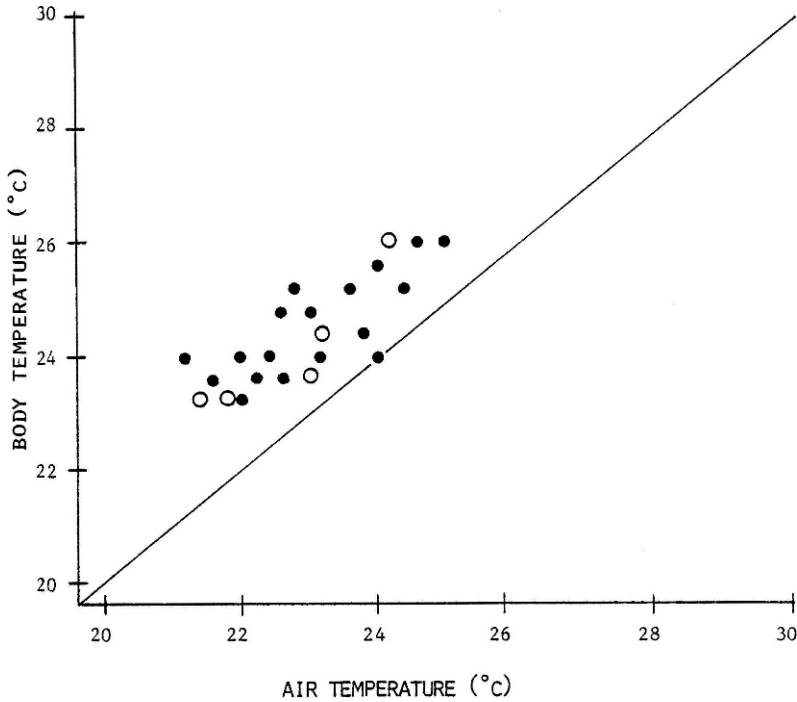
Figure 4.   Body temperatures of *Anolis festae* plotted against air temperature at time of capture. Open circles represent multiple records. Diagonal line is for body temperature = air temperature.

All three species in the present study appear to be obligate tree-trunk perchers (Table 4), and for all practical purposes, perch diameter can be ignored. Although a large number of *A. chloris* were perched on small-diameter perches, which suggests a possible difference in perch distribution with respect to the other two species, in every case, the small-diameter perches were over 25 ft (7.6 m) above the ground, and their presence on small-diameter perches is a function of their perch height.

Mean perch heights for the total data sets of each species (all localities, all times, both sexes) are presented in Table 5. The three species differ significantly from each other in mean perch height (p ≪ 0.001). *Anolis chloris* clearly chooses perches much higher than either *A. festae* or *A. peraccae*, and *A. peraccae* perches slightly higher than *A. festae*. Although these data appear to suggest that the three species are segregated by differences in perch height, the real pattern is obscured in this pooled data.

The slight differences in mean perch height between *A. festae* and *A. peraccae* dissolve if the situation is examined more carefully. Table 6 presents perch height data for these two species at two different localities where they occurred syntopically. At the more northern of these localities, 41 km south of Santo Domingo de los Colorados, there is no significant difference in mean perch height between the two species ($p = 0.68$). Both species typically perch very near the ground. On the other hand, at Hacienda Cerro Chico there are slight but marginally significant differences in mean perch height between the two species, with *A. festae* perched higher than *A. peraccae* ($0.01 < p < 0.05$). This is exactly the opposite of what the pooled data show. The slight differences in mean perch height between these two species is unlikely to be of much biological significance despite
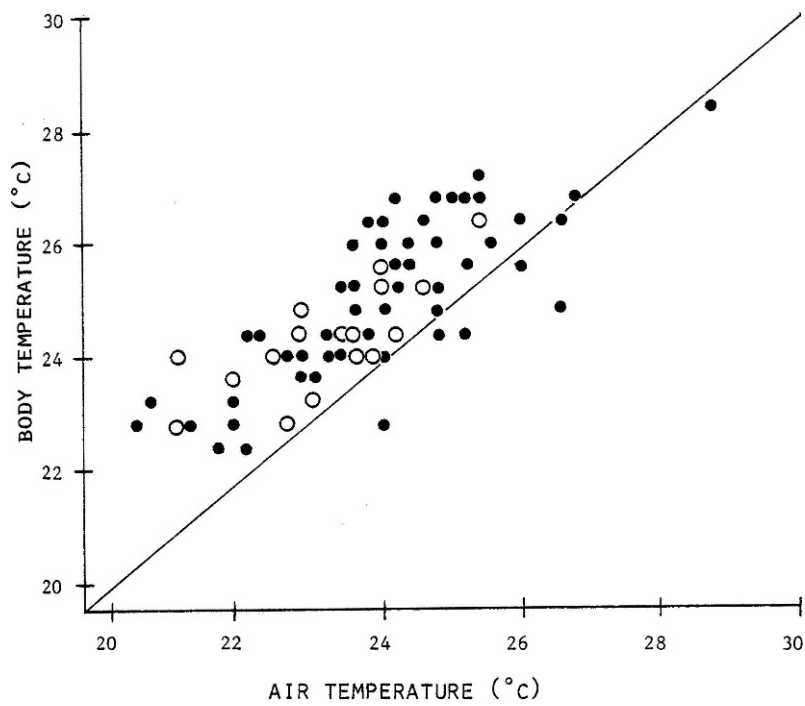
Figure 5.   Body temperatures of *Anolis peraccae* plotted against air temperature at time of capture. Open circles represent multiple records. Diagonal line is for body temperature = air temperature.

their statistically significant differences in central tendency.

Perch heights are subject to daily cycles of change. Figure 6 shows hourly shifts in perch height distribution of *A. peraccae* at the Río Palenque balsa site. There is a clear upward shift in perch height through the day. Both sexes, however, do not shift upward at the same time. Females show no difference in mean hourly perch height between 7:00 a.m. and 3:59 p.m. (ANOVA, $F_{8,261} = 1.88$, $p = 0.064$), whereas males show a steady increase in hourly mean perch height (Table 7). In late afternoon

both sexes are typically found on high perches, presumably as a preliminary movement to their normal sleeping perches in the tree crowns.

Because *A. chloris* is more difficult to sex in the field without capture, my data on perch height shifts are less extensive than for *A. peraccae*. Observations were pooled into bi-hourly samples for analysis, and not all individuals could be sexed (Table 8). Females showed no shift in perch heights through the entire day, whereas males showed a strong tendency to perch higher as the day went on. However, because it is easier to make a positive sex identification of males at long distances (particularly when they display, which they do often), this could bias the data. It does appear likely in any case that males perch higher than females regardless of the time of day.

Because of the much smaller total sample size, I was unable to analyze the perch height data for *A. festae* in terms of daily

TABLE 1.   MEAN BODY TEMPERATURES OF POOLED SAMPLES OF THREE SPECIES OF *ANOLIS* FROM WESTERN ECUADOR.*

|  | $n$ | MBT (° C) | $s^2$ |
|---|---|---|---|
| A. chloris | 58 | 24.8 | 2.36 |
| A. festae | 28 | 24.3 | 0.85 |
| A. peraccae | 87 | 24.7 | 2.28 |

* $F_{2,170} = 1.42$, $p = 0.25$.

TABLE 2.    BODY TEMPERATURE OF *ANOLIS FESTAE* AND *ANOLIS PERACCAE* AT TWO LOWLAND LOCALITIES IN WESTERN ECUADOR.

|  | A. festae | | | A. peraccae | | | |
|---|---|---|---|---|---|---|---|
|  | $n$ | MBT ($°$ C) | $s^2$ | $n$ | MBT ($°$ C) | $s^2$ | $p$ |
| 41 km S of Santo Domingo | | | | | | | |
| de los Colorados | 15 | 23.8 | 0.27 | 4 | 24.0 | 0.09 | 0.61 |
| Hacienda Cerro Chico | 5 | 24.4 | 1.04 | 7 | 24.8 | 0.52 | 0.52 |

shifts in perch height. As regards to sexual differences in perch height, the answer is unclear. For all of the observations pooled, males perch significantly higher than females (27.7 in [=704 mm] vs. 12.6 in [=320 mm]). However, if only the best-sampled locality is examined, mean perch height does not differ between sexes (Table 9).

In addition to these sexual differences in mean perch height and daily shifts in perch height distribution, species can also exhibit marked shifts in mean perch heights from year to year (Table 10). At the Río Palenque balsa site, both *A. chloris* and *A. peraccae* were perched much higher in 1975 and 1976 than in 1974. This was not due to sampling bias because the field protocol was not changed, and there is no reason to suspect that I was any better at spotting lizards perched higher in the trees in the latter 2 years.

The Río Palenque balsa site was divided into subsections about midway through the 1975 field season, and from that point on, all animals seen during the censuses were associated with a 10-m-long interval of the roadside. Two definite habitat types were associated with the balsas along this strip. The first section consisted of trees that were isolated from forest edge and secondary growth by a buffer zone of oil palms, and the second section consisted of trees that abutted either forest, secondary growth, or

both (Fig. 1). Table 11 summarizes the perch heights of *A. chloris* and *A. peraccae* from 1975 and 1976 in these two areas. The patterns that emerge are rather peculiar. *Anolis chloris* in both sections perched at the same mean height above the ground in 1975, but in 1976 the animals in Section 2 perched higher than those in Section 1. *Anolis peraccae* perched at the same mean height in both sections in each of the 2 years, but showed significant differences in mean perch height from year to year, perching somewhat higher in 1976 than in 1975.

The orientation of individual lizards with respect to the ground may be of possible significance when it comes to assessing how the lizards utilize their perches. Classical sit-and-wait predation in anoles typically involves a lizard perching with its head pointed downward, which allows it to scan the ground and vegetation below for prey. If the lizards are primarily searching actively for their prey, one might expect them to be oriented differently with respect to the ground, particularly if they are searching for prey on the trunk of a tree or in the

TABLE 3.    MEAN BODY TEMPERATURES OF *ANOLIS CHLORIS* AND *ANOLIS PERACCAE* IN SYMPATRY AT CENTRO CIENTÍFICO RÍO PALENQUE.*

|  | $n$ | MBT ($°$ C) | $s^2$ |
|---|---|---|---|
| A. chloris | 55 | 24.9 | 2.31 |
| A. peraccae | 54 | 25.0 | 2.86 |

* $F_{1,107} = 0.22$, $p = 0.64$.

TABLE 4.    PERCH OCCURRENCE OF THREE SPECIES OF *ANOLIS* IN WESTERN ECUADOR (% TOTAL OBSERVATIONS).*

|  | A. chloris | A. festae | A. peraccae |
|---|---|---|---|
| Ground | 0.7 | 1.2 | 0.6 |
| Tree trunks[1] | 89.4 | 95.2 | 97.0 |
| Branches[2] | 9.2 | 3.6 | 1.4 |
| Leaves | 0.7 | 0 | 0.5 |
| Banana stems | 0 | 0 | 0.4 |
| Lianas | 0 | 0 | 0.1 |
| $n$ | 433 | 83 | 1,144 |

[1] More than 7.5 cm in diameter, vertical or near vertical.
[2] Less than 7.5 cm in diameter, vertical or horizontal (includes small tree trunks as well).
* $x^2 = 93.18$, $p \lll 0.001$; $x^2 = 2.92$, $p = 0.232$ for comparison between *A. festae* and *A. peraccae*.

TABLE 5.    MEAN PERCH HEIGHTS (IN INCHES) OF THREE SPECIES OF TRUNK-PERCHING *ANOLIS* IN WESTERN ECUADOR. LOCALITIES, DATES, TIMES, AND SEXES LUMPED. ALL MEANS SIGNIFICANTLY DIFFERENT ($p \lll 0.001$).

|              | $n$   | Mean Height[1]  |
|--------------|-------|-----------------|
| A. chloris   | 426   | $120 \pm 1.1$   |
| A. peraccae  | 1,131 | $26 \pm 1.0$    |
| A. festae    | 79    | $20 \pm 1.3$    |

[1]  ±95% confidence limit.

TABLE 6.    MEAN PERCH HEIGHTS (IN INCHES) OF *ANOLIS FESTAE* AND *ANOLIS PERACCAE* AT TWO LOWLAND LOCALITIES IN WESTERN ECUADOR.

|                                              | A. festae | | A. peraccae | | |
|----------------------------------------------|-----|----------------|-----|----------------|-------|
|                                              | $n$ | Mean Height    | $n$ | Mean Height    | $p$   |
| 41 km S of Santo Domingo de los Colorados    | 40  | 11.9           | 8   | 13.9           | 0.681 |
| Hacienda Cerro Chico                         | 8   | 25             | 38  | 15.3           | 0.039 |

vegetation. Table 12 shows the orientation at first sighting for the three species; the percentage of lizards facing the ground is not significantly different between the three species.

## Daily Activity Cycles

Activity cycles in arboreal lizards are difficult to estimate because there is always some question as to whether their apparent absence at a given time is due to lack of activity or a shift of activity to an area that cannot be censused by a ground-based observer. Keeping this potential complication in mind, the activity cycles of *A. chloris* and *A. peraccae* at the Río Palenque balsa site are presented in Figure 7. Data were insufficient to make similar estimates of activity patterns in *A. festae*.

Even though these data on activity cycles might represent shifts in activity, rather than actual changes in activity, some interesting patterns emerge. *Anolis chloris* is not usually seen until after *A. peraccae* has begun its daily activity. Both species reach an apparent activity peak during the mid-morning hours. *Anolis chloris* seems to show a definite decrease in activity shortly after noon, with a slight afternoon peak several hours later; this pattern was seen in *A. peraccae* in 1976 but not in 1975. Both species become considerably less conspicuous in late afternoon, coinciding with their strong upward shift in perch height.

## Population Densities

It was not possible to make estimates of population size with conventional mark-recapture techniques because the central assumptions of such methods were not met. All of my comments on density are therefore based on a crude index of population density—the number of individuals seen per census on the Río Palenque balsa site. Although the total number of visible lizards in any given census could vary considerably depending on activity patterns of the lizards, these variations should be dampened out in the course of extensive sampling spread over a several month interval. In any case, the sampling biases from year to year should be comparable, and the resulting data are probably adequate to detect major shifts in abundance from year to year.

Because of the variation between different study sites and habitats, all my comparisons of population density are restricted to the populations of *A. chloris* and *A. peraccae* at the Río Palenque balsa site. These observations spanned the months of June to August from 1974 to 1976. The data from 1974 were taken only from Section 1 of the site. This site was extended in 1975, and from about halfway through the sampling period, note was taken of which section each individual sighting was made. The study was terminated in 1976 because the balsa trees in the study area were removed prior to my next visit in April 1977.

The mean number of observations of *A. chloris* and *A. peraccae* per census in the entire study area are presented in Table 13. These data suggest that populations of *A. chloris* remained more or less similar during these years, whereas *A. peraccae* underwent a drastic population decline between 1975
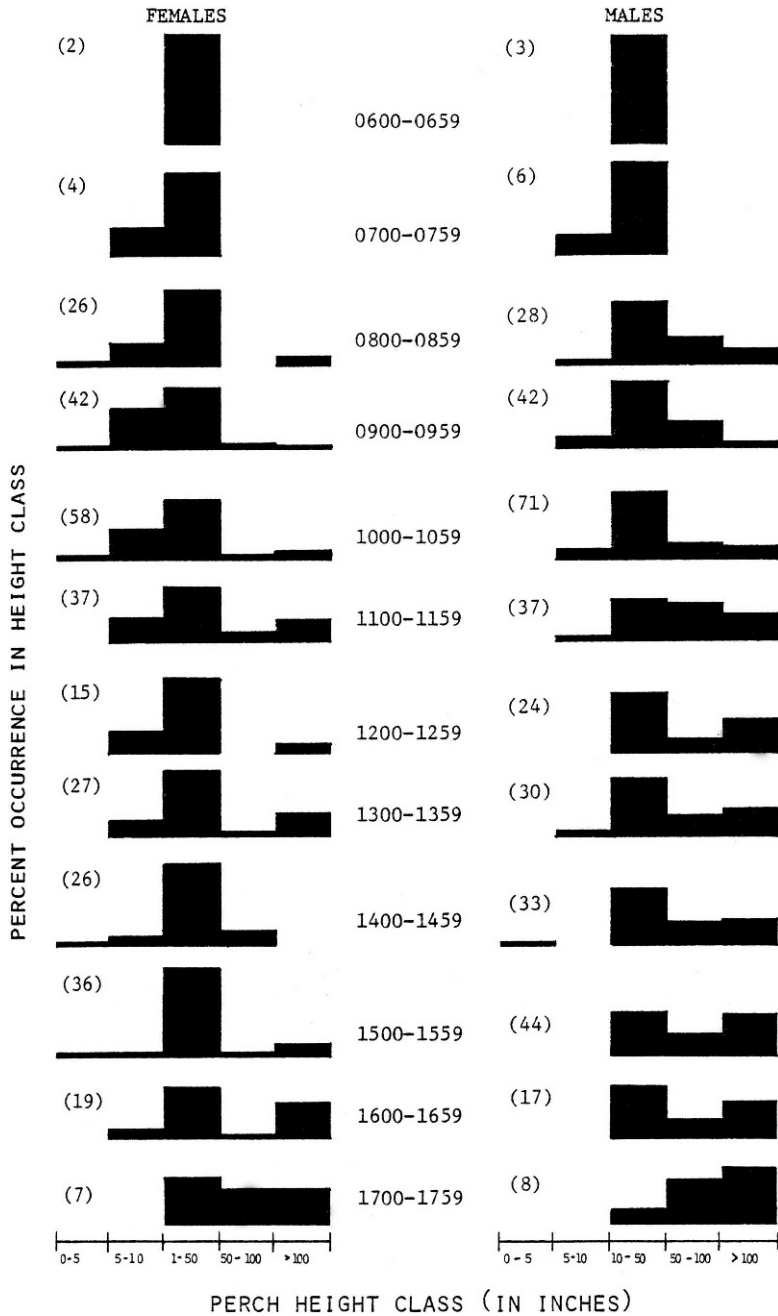
Figure 6.   Hourly shifts in perch height distributions of female and male *Anolis peraccae* at Río Palenque balsa study site in 1975 and 1976. Sample sizes in parentheses.

TABLE 7.    HOURLY SHIFTS IN MEAN PERCH HEIGHTS (IN INCHES) OF *ANOLIS PERACCAE* AT RÍO PALENQUE BALSA STUDY SITE. DATA ARE FROM 1975 AND 1976 ONLY.

| Time | Total[1] | | Females | | Males | |
|---|---|---|---|---|---|---|
| | n | Mean Height | n | Mean Height | n | Mean Height |
| 6:00–6:59 a.m. | 5 | 17.6 | — | — | — | — |
| 7:00–7:59 a.m. | 21 | 25.8 | 8 | 26.6 | 13 | 25.3 |
| 8:00–8:59 a.m. | 54 | 27.6 | 26 | 18.5 | 28 | 39.9 |
| 9:00–9:59 a.m. | 87 | 21.9 | 41 | 15.4 | 46 | 30.2 |
| 10:00–10:59 a.m. | 134 | 25.1 | 58 | 21.2 | 76 | 28.6 |
| 11:00–11:59 a.m. | 75 | 40.6 | 37 | 29.3 | 37 | 54.3 |
| 12:00–12:59 p.m. | 39 | 40.7 | 15 | 22.5 | 24 | 58.9 |
| 1:00–1:59 p.m. | 56 | 41.4 | 25 | 33.1 | 31 | 53.3 |
| 2:00–2:59 p.m. | 58 | 39.0 | 26 | 24.4 | 32 | 57.1 |
| 3:00–3:59 p.m. | 79 | 48.7 | 35 | 28.5 | 43 | 72.3 |
| 4:00–4:59 p.m. | 35 | 57.8 | 18 | 51.5 | 17 | 71.1 |
| 5:00–5:59 p.m. | 15 | 86.3 | 7 | 68.0 | 8 | 106.4 |

[1] Not all lizards could be positively sexed.

and 1976. Although there are no firm data, my observations in the forest at Río Palenque and elsewhere in the vicinity seemed to affirm this pattern: *Anolis peraccae* was much more difficult to find anywhere in the region after 1975.

If the two sections in the Río Palenque balsa site are examined separately, several interesting trends emerge (Tables 14, 15). In Section 1, *A. chloris* seemed to have undergone a decline before the 1975 sample, from which it subsequently recovered before the 1976 sample. Although statistically significant, this apparent decline in *A. chloris* might have been an artifact of the sampling procedure and is of questionable validity. On the other hand, the differences seen in *A. peraccae* (Table 15, top) are undoubtedly real and seem to constitute a strong downward trend in abundance over the 3 years of the study. This downward trend in populations of *A. peraccae* was apparently general throughout the region; it was considerably more difficult to locate *A. peraccae* in January 1979 than it was to find them in 1974 throughout the region.

The downward trend in *A. peraccae* populations was even more pronounced in Section 2 of the Río Palenque balsa site. Population densities appeared to be about an order of magnitude less in 1976 than in 1975, which accounted for the shift in relative abundances of the two species in this section (Table 16).

TABLE 8.    BI-HOURLY SHIFTS IN MEAN PERCH HEIGHTS (IN INCHES) OF *ANOLIS CHLORIS* AT RÍO PALENQUE BALSA STUDY SITE. DATA ARE FROM 1975 AND 1976 ONLY.

| Time | Females* | | Males** | |
|---|---|---|---|---|
| | n | Mean Height | n | Mean Height |
| 6:00–7:59 a.m. | 1 | 12.0 | 2 | 509.1 |
| 8:00–9:59 a.m. | 8 | 59.2 | 21 | 125.8 |
| 10:00–11:59 a.m. | 19 | 55.4 | 55 | 195.2 |
| 12:00–1:59 p.m. | 5 | 42.0 | 17 | 214.6 |
| 2:00–3:59 p.m. | 3 | 160.7 | 29 | 279.5 |
| 4:00–5:59 p.m. | 2 | 93.0 | 16 | 320.4 |

* $F_{5,32} = 0.63$, $p = 0.680$.
** $F_{5,134} = 3.43$, $p = 0.006$.

TABLE 9.    SEXUAL DIFFERENCES IN MEAN PERCH HEIGHTS (IN INCHES) OF *ANOLIS FESTAE* IN WESTERN ECUADOR.

| | n | Mean Height |
|---|---|---|
| All localities lumped* | | |
|   Females | 30 | 12.6 |
|   Males | 25 | 27.5 |
| 41 km S of Santo Domingo de los Colorados** | | |
|   Females | 19 | 9.2 |
|   Males | 8 | 9.5 |

* $F_{1,53} = 398.45$, $p \lll 0.001$.
** $F_{1,25} = 0.009$, $p = 0.93$.

TABLE 10.  SHIFTS IN MEAN PERCH HEIGHTS (IN INCHES) BETWEEN 1974 AND 1976 IN *ANOLIS CHLORIS* AND *ANOLIS PERACCAE* AT CENTRO CIENTÍFICO RÍO PALENQUE.

|  | 1974 | | 1975 | | 1976 | |
|---|---|---|---|---|---|---|
|  | $n$ | Mean Height | $n$ | Mean Height | $n$ | Mean Height |
| *A. chloris* | 48 | 35 | 160 | 131 | 160 | 171 |
| *A. peraccae* | 294 | 15 | 539 | 33 | 123 | 41 |

## DISCUSSION

### Ecological Segregation among the Anoles of the Río Palenque Region

The three species of *Anolis* studied were the most conspicuous members of the anole fauna of the region.[9] All three species were most abundant in secondary habitats, and one, *A. festae*, was restricted to disturbed habitats in the Río Palenque region. At first consideration the data on perch height seem to provide a suitable approximation of how the three species might partition resources. By perching at different heights above the ground, the three species may be able to scan different areas of the ground below and select a different range of prey items. However, a closer examination of the occurrence of *A. festae* and *A. peraccae* indicates that the rather slight, but statistically significant, differences in mean perch height could be of no apparent biological significance.

In sympatry, one or the other of the two species is always considerably more abundant. In the few places where both species occurred in sufficient number to obtain data on perch dimensions and body temperatures, there was almost complete overlap between the two species. Both species are practically identical in size, and a preliminary examination of the stomach contents of the two species reveals no obvious differences in the range of prey taxa or sizes taken. The two species appear to be very similar to one another and coexist along a rather narrow zone where populations may be in rather tenuous balance.

Although *A. festae* was seen on the Río Palenque balsa site only in 1976, after *A. peraccae* had undergone a severe decline in population density, only one or two *A. festae* were seen. With the removal of the balsa trees after the 1976 field season, it was not possible to see what this situation might have developed into. It seems clear, however, that competition with *A. festae* did not cause the decline in *A. peraccae* populations.

Competition between *A. festae* and *A. peraccae* would appear to be quite severe, given their general similarity in size and morphology and habitat preferences. These two species are quite different from *A. chloris*, which clearly segregates itself ecologically from the other two species by its utilization of high perches.

### Co-Adapted Complexes and Recent Interactions

One clue to the pattern seen between these three species lies in the historical patterns of distribution and the effect of recent human disturbance in the region. Both *A. chloris* and *A. peraccae* are elements of the Chocoan herpetofauna; *A. chloris* is found as far north as the Darién Province in Panama, and *A. peraccae* (along with a vicariant species in a superspecies complex) is widespread in the Chocó north of central Ecuador. *Anolis festae*, on the other hand, is a member of a peculiar southern Ecuador fauna that might be associated with the more seasonal and xeric lowlands of southwestern Ecuador. The entire region between Quevedo and Santo Domingo de los Colorados has recently undergone a burst of intensive agricultural development (Nelson, 1973; Dodson and Gentry, 1978), which could have opened pathways through which this southern fauna

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[9] Eight species of *Anolis* have been found on recent visits to the Río Palenque station (*A. fasciatus, A. festae, A. gracilipes, A. lyra, A. maculiventris, A. parvauritus, A. peraccae,* and *A. princeps*), although, interestingly, *A. chloris* has not been found there. Two other species— *A. lynchi* and *A. parilis*—likely occur at the station or nearby. Poe et al. have put together a pictorial guide to these species, available at http://www.oeb.harvard.edu/faculty/losos/jblosos/pdfs/PoeRioPalenque2012.0.pdf.

TABLE 11.   SHIFTS IN MEAN PERCH HEIGHTS (IN INCHES) OF TWO SPECIES OF *ANOLIS* AT RÍO PALENQUE BALSA STUDY SITE. HORIZONTAL LINES CONNECT VALUES WHICH ARE NOT SIGNIFICANTLY DIFFERENT ($p > 0.05$).*

| | 1975 | | | | 1976 | | | |
| | Section 1 | | Section 2 | | Section 1 | | Section 2 | |
| | $n$ | Mean Height | $n$ | Mean Height | $n$ | Mean Height | $n$ | Mean Height |
|---|---|---|---|---|---|---|---|---|
| A. chloris | 7 | 73.9 | 50 | 82.2 | 35 | 80.0 | 125 | 161.7 |
| A. peraccae | 94 | 23.1 | 99 | 25.2 | 100 | 38.1 | 20 | 57.8 |

* The differences in mean perch height between species are all significant ($p \ll 0.01$).

might have been able to invade what was formerly a wet Chocoan forest fauna. The interactions between *A. festae* and *A. peraccae* could thus be of very recent origin, at least in the area encompassed by the study, and the two species might not yet have had sufficient time or opportunity to become more finely tuned to each other ecologically. The interactions between *A. chloris* and *A. peraccae*, on the other hand, are of long duration, and the clear ecological differences between the two could partially reflect this opportunity for ecological integration and extensive sympatry.

## Generalizing from Limited Samples

Although the data presented here are rather limited, they do cover a fairly long time span, and strong differences between years and study sites were noted in several aspects of the biology of the three species of *Anolis*. The popular conception of the "unchanging tropics" is gradually eroding among the biological public, but this concept finds its way into the general public with disturbing frequency. The large fluctuations in population density observed in *A. peraccae* might be extreme (a 10-fold

TABLE 12.   ORIENTATION OF THREE SPECIES OF *ANOLIS* IN WESTERN ECUADOR WHEN FIRST SIGHTED.*

| | Head-Up | | Head-Down | |
| | $n$ | % | $n$ | % |
|---|---|---|---|---|
| A. chloris | 60 | 27.5 | 158 | 72.5 |
| A. festae | 25 | 32.9 | 51 | 67.1 |
| A. peraccae | 239 | 31.0 | 533 | 69.0 |

* $x^2 = 1.19$, $p = 0.55$.

decrease in a year), but they are well in line with similar fluctuations in Central American anole populations (Sexton et al., 1963; Sexton, 1967; Andrews and Rand, 1982).

Life history information is clearly needed for South American anoles. The only such information currently available are for two species of Ecuadorian anoles, *A. bitectus* from the lowlands and *A. gemmosus* from the cloud forests. I was unable to obtain any useful data on growth or longevity of any of the three species in the current study, despite the fact that almost 150 individual lizards were marked and released in the course of the study. All of the recaptures made were very short term (none more than 70 days), and all involved animals originally marked as adults.

The complete absence of recaptures between years does suggest that the three species might be short-lived. This is in keeping with current ideas concerning the life history of mainland anoles (Andrews, 1979).

The current concept of a typical mainland anole could be severely biased by the nature of the species studied. Mainland anoles are thought to be generally limited by predation, rather than competition, as in the case of island anoles. This fundamental difference in selective pressures leads to certain predictions regarding life history strategies that seem to be met by most of the species that have been studied to date (Andrews, 1979). However, relatively few mainland anoles have been studied in any detail, and what might be true for them might not necessarily be true for the majority of mainland species.
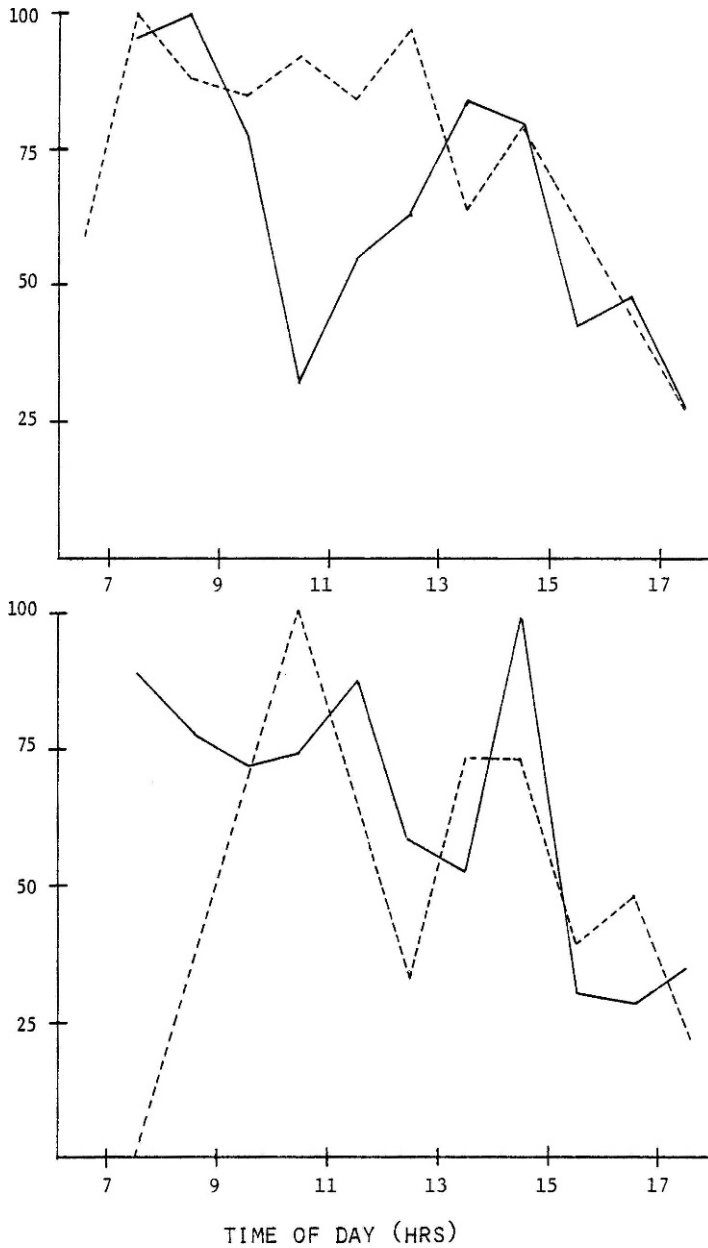
Figure 7.   Activity cycles of *Anolis peraccae* (top) and *Anolis chloris* (lower) at Rio Palenque balsa study site. Data for 1975 indicated by dotted line; data for 1976 indicated by solid line.

The relative scarcity of anoles in mainland habitats has been repeatedly emphasized (Vanzolini, 1972; Williams, 1976b; Andrews, 1979). Andrews (1979) has published a list of mainland and island species for which estimates of population density are available. From these data, and additional data in Schoener and Schoener (1980), it appears that island anoles have densities typically an order of magnitude or more higher than

TABLE 13.   NUMBER OF OBSERVATIONS OF *ANOLIS CHLORIS* AND *ANOLIS PERACCAE* PER CENSUS AT RÍO PALENQUE BALSA STUDY SITE, 1975–1976.

| | A. chloris* | | A. peraccae** | |
|---|---|---|---|---|
| | 1975 | 1976 | 1975 | 1976 |
| No. of censuses | 57 | 48 | 57 | 48 |
| Mean no. of observations per census | 2.84 | 3.42 | 9.35 | 2.60 |
| $s^2$ | 3.94 | 5.96 | 24.65 | 3.57 |

* $F_{1,74} = 1.06$, $p = 0.31$.
** $F_{1,74} = 89.88$, $p \lll 0.001$.

mainland species. However, even these figures might not portray the situation accurately. The figures presented for mainland anoles are much higher than for the two species of South American anoles known (see below), which suggests that South American anoles might typically be much less abundant than Central American and Mexican species. These low population densities make it extremely difficult to collect data relevant to life history studies.

Another equally serious problem that is closely related to the above phenomenon is the nature of the mainland species that have been examined. In most cases, only the most abundant species of mainland anoles have been studied. These species are largely found in high densities only in rather disturbed habitats, although some rather

TABLE 14.   NUMBER OF OBSERVATIONS OF *ANOLIS CHLORIS* PER CENSUS AT RÍO PALENQUE BALSA STUDY SITE BY SECTION, 1974–1976.

| | 1974 | 1975 | 1976 |
|---|---|---|---|
| Section 1* | | | |
| No. of censuses | 38 | 18 | 48 |
| Mean no. of observations per census | 1.13 | 0.39 | 0.94 |
| $s^2$ | 2.11 | 0.35 | 1.73 |
| Section 2** | | | |
| No. of censuses | | 18 | 48 |
| Mean no. of observations per census | | 2.83 | 2.48 |
| $s^2$ | | 3.94 | 5.96 |

* All three years: $F' = 4.89$ ($v_1 = 2$, $v_2 = 63.8$), $p = 0.011$; 1974 and 1976: $F_{1,84} = 0.41$, $p = 0.52$.
** $F_{1,64} = 0.30$, $p = 0.59$.

TABLE 15.   NUMBER OF OBSERVATIONS OF *ANOLIS PERACCAE* PER CENSUS AT RÍO PALENQUE BALSA STUDY SITE BY SECTION, 1974–1976.

| | 1974 | 1975 | 1976 |
|---|---|---|---|
| Section 1* | | | |
| No. of censuses | 38 | 18 | 48 |
| Mean no. of observations per census | 7.79 | 5.61 | 2.15 |
| $s^2$ | 14.69 | 13.68 | 3.5 |
| Section 2** | | | |
| No. of censuses | | 18 | 48 |
| Mean no. of observations per census | | 5.44 | 0.46 |
| $s^2$ | | 5.14 | 0.46 |

* All three years: $F' = 3558.75$ ($v_1 = 2$, $v_2 = 47.0$), $p \lll 0.0001$; 1974 and 1975: $F_{1,54} = 3.89$, $p = 0.054$.
** $F'_s = 75.13$ ($v_1 = 1$, $v_2 = 22.7$), $p \lll 0.0001$.

specialized species (e.g., the aquatic *A. poecilopus* and the saxicolous *A. gadovii*) are also found in high densities in undisturbed habitats.

Table 17 summarizes information regarding the relative abundances and habitat occurrence of the anoles of Ecuador. Although the vast majority of species occur in forest, relatively few are ever found in sufficient peak densities to allow ecological studies, and in nearly all cases these peak densities are only reached in disturbed habitats. Although it seems clear that a "typical" South American anole is an inhabitant of forest habitats, very few can be studied in a quantitative fashion, even in habitats that may not be typical. With this in mind it seems premature to make overly

TABLE 16.   NUMBER OF OBSERVATIONS OF *ANOLIS CHLORIS* AND *ANOLIS PERACCAE* IN TWO SECTIONS OF RÍO PALENQUE BALSA STUDY SITE BY SECTION, 1974–1976.

| | 1974 | 1975 | 1976 |
|---|---|---|---|
| Section 1* | | | |
| A. chloris | 43 | 7 | 48 |
| A. peraccae | 213 | 101 | 98 |
| Section 2** | | | |
| A. chloris | | 43 | 115 |
| A. peraccae | | 98 | 22 |

* $x^2 = 29.80$, $p \lll 0.0001$.
** $x^2 = 80.90$, $p \lll 0.0001$.

TABLE 17.  HABIT OCCURRENCE OF ECUADORIAN *ANOLIS* LIZARDS ON THE BASIS OF FIELD WORK BETWEEN 1974 AND 1979. (X) INDICATES PRESENCE IN HABITAT TYPE, (+) INDICATES THAT SPECIES REACHES MAXIMUM DENSITY IN THIS HABITAT.

|  | Forest | Edge | Analogue[3] |
|---|---|---|---|
| A. aequatorialis | + |  | + |
| A. bitectus | x |  | x |
| A. chloris | x | + |  |
| A. chrysolepis scypheus | + |  |  |
| A. eulaemus group[1] | x |  |  |
| A. fasciatus | x |  | + |
| A. festae |  | x | + |
| A. fitchi | x |  |  |
| A. fraseri | x | x |  |
| A. fuscoauratus | x | + |  |
| A. gemmosus | x | + |  |
| A. gracilipes | x |  |  |
| A. granuliceps | x |  |  |
| A. lynchi | x |  |  |
| A. lyra | x | + |  |
| A. maculiventris | x |  |  |
| A. ortonii | x | + |  |
| A. parvauritus[2] | + | x |  |
| A. peraccae | x | x | + |
| A. princeps | + | x |  |
| A. punctatus | x | + |  |
| A. trachyderma | x | + |  |

[1] Undescribed species from Puyo region.
[2] Editor's note: considered *A. biporcatus parvauritus* by many.
[3] Editor's note: by "analogue," the author apparently means forest-like habitats occurring in cultivated areas.

inclusive generalizations regarding ecological patterns in mainland anoles at the present time.

## II. GROWTH AND POPULATION STRUCTURE OF TWO SPECIES OF *ANOLIS* FROM THE PACIFIC SLOPES AND LOWLANDS OF ECUADOR

### INTRODUCTION

The iguanid lizard genus *Anolis* has been the subject of a large body of ecological research over the past two decades, concentrated largely on the islands of the West Indies and, lately, on selected parts of Central America and Mexico. The large and fundamentally important South American radiations have been largely ignored in this respect, although some important contributions have been made regarding the general natural history of some of the species (Vanzolini, 1972; Hoogmoed, 1973; Dixon and Soini, 1975; Duellman, 1978). However, there has been a dearth of quantitative studies regarding even the most common species of South American anoles. This lack of emphasis on quantitative ecological studies has been the result of two major factors. First, the systematics of South American anoles are poorly understood. As a result, most of the workers concerned with the biology of these lizards have directed their efforts largely toward unraveling the complex fabric of their evolutionary history on the South American continent, rather than focusing on ecological studies. This approach has been absolutely necessary; without some perspective in which to place observations concerning the natural history of the various species, it would be exceedingly difficult to employ many characters of the living animals in answering broad questions concerning the biology of the South American forms.

However, there is a second, even more fundamental, reason why some ecological studies have not been carried on concurrently with the systematic studies, as happened in the West Indies and is happening in Central America. A basic fact of life concerning the South American anole fauna in particular, and the entire forest lizard fauna in general, is that individuals tend to be rare. Although this fact in itself is of some interest, it virtually precludes the possibility of carrying on detailed quantitative studies. Most species of anoles in most places in South America are simply too rare to study in a quantitative manner. In most cases it requires a considerable effort to secure a sample adequate for even basic systematic studies, and the chances of collecting adequate amounts of ecological data are slim indeed.

The present paper is the first to present quantitative data concerning South American species of *Anolis*. The two species I studied are poorly known ecologically. The extent of the literature on the biology of *A. gemmosus* consists of a single paper (Fitch et al., 1976) and a short abstract of parts of

the present work (Miyata, 1977). *Anolis bitectus* remains completely unknown in the literature outside of a few systematic discussions (all rather old) and the brief abstract in Miyata (1977). These two species are rather typical South American anoles in many respects; both are small to medium in size and are associated with forest habitats. One species (*A. gemmosus*) is a member of the autochthonous South American alpha radiation, and the other (*A. bitectus*) is a member of the more recently arrived beta radiation (Williams, 1976b). Both have restricted distributions on the Pacific slopes of the Ecuadorian Andes.

## STUDY SITES

*Anolis gemmosus* was studied at Río Faisanes, a cloud forest locality on the west slope of the Ecuadorian Andes at an elevation of 1,380 m. The Río Faisanes is a small mountain river that crosses the La Palma–Quito road (Ecuador Highway 28) some 14.4 km northeast of La Palma. The general area consists of patches of cloud forest, generally confined to narrow stream beds, with considerable cleared agricultural land on the less precipitous slopes. The actual study area consisted of a narrow strip of edge vegetation made up primarily of ferns and small shrubs located along a narrow and steep road cut. The area covered by my censuses spanned some 150 m of this roadside vegetation on both sides of the road. Because of the steepness of the road cuts, perhaps 2 m on either side of the road were actually sampled in the censuses.

This roadside habitat was chosen for the mark-recapture study because of the high population densities of *A. gemmosus* observed there on initial surveys in June through August of 1975. These densities were fairly typical of the roadside habitats in the area, and lizards appeared to be in much lower densities in the adjacent forest. Furthermore, although the roadside vegetation was subject to some disturbance in the course of the study, this activity was confined largely to just the very edges of the vegetation and was intended primarily to keep the road shoulders clear. The small patches of cloud forest in the same area, in contrast, were being cut back at a steady rate during the course of the study, and drastic changes occurred in the structure of the forest along the banks of the Río Faisanes between 1976 and 1979.

*Anolis bitectus* was studied in an artificial plantation of rubber trees (*Hevea brasiliensis*; not indigenous to the region) at Hacienda Cerro Chico, a large plantation located some 45 km north of Quevedo in Provincia Pichincha at an elevation of approximately 125 m. The rubber groves were planted between 1969 and 1970, the area previously having been a banana plantation. The original forest in this area was probably cleared between 1960 and 1965. The rubber groves form a forest-analogue habitat, with a dense overhead canopy through which little light penetrates. The ground is covered with a thick layer of herbaceous vegetation between 0.3 and 1.5 m in height. The rubber trees were uniformly spaced and sized, with most between 15 and 25 cm dbh and perhaps 10–15 m in height. To facilitate harvest of the rubber, small paths were kept clear of understory vegetation, and most of the understory could be scanned thoroughly from these walkways.

## METHODS

Both species of *Anolis* were collected by hand, usually as they slept at night. This night sampling has several distinct advantages over conventional daytime capture: 1) The lizards do not become increasingly difficult to catch after they have been marked; this factor proved to be a major difficulty in other mark-recapture studies attempted in the same region on species that could only be found during the day; 2) the lizards are very easy to capture when they are asleep; 3) lizards that sleep on understory vegetation are usually very easy to see at night because the pattern of dew or

Figure 8.   Adult male *Anolis gemmosus* sleeping on fern at Río Faisanes study site.

rain beaded up on their skin is quite different from the surrounding leaves; one of the species, *A. gemmosus* has an extremely cryptic pattern (Fig. 8) that makes it very difficult to find while active. Nighttime sampling appears to be far superior to conventional lizard sampling techniques for population studies such as the present one.

Some daytime sampling was also conducted for *A. bitectus*. The first sampling of the population at Hacienda Cerro Chico was done by means of a common random quadrat sampling technique (see Lloyd et al., 1968; Scott, 1976), in which plots of 7.6 by 7.6 m were laid out on the floor of the rubber grove, and a group of eight people converged from the perimeter and captured the animals inside. In this manner, 12 quadrats of 58 m² each were sampled on 9 July 1976.

Subsequent visits to the Hacienda Cerro Chico study sites (April and November 1977, January and April 1978, and January 1979) employed a different sampling technique. A marked study plot was laid out in the rubber grove adjacent to the section sampled in 1976. This plot consisted of some 3,948 m² and had eight rows of rubber trees spaced approximately 6 m apart. The first tree in each row was adjacent to a service road, which provided an opening in the canopy, and the understory vegetation was somewhat denser along this edge. Each row contained 21–23 rubber trees, generally spaced about 3.5 m apart (range 2–6 m). This plot was worked by following the narrow paths along the tree rows and scanning the top of the understory vegetation for sleeping anoles at night. Each census required 1–3 hours to complete, depending on the number of people I had to assist.

The sampling procedure for *A. gemmosus* at the Río Faisanes site consisted simply of walking slowly along the road while carefully scanning for sleeping lizards on ferns and shrubs within reach. I was unable to place any markers here because of the constant minor disturbances, so individual positions of each lizard could not be recorded.

For each lizard captured, sex and SVL were noted. For *A. bitectus* in the marked

plot, the exact position was also noted. Measurements were taken with plastic dial calipers to the nearest 0.1 mm or with a plastic rule to the nearest 1 mm. In both species, sex was easily determined by the presence of a distinct dewlap on males; even the smallest juveniles exhibited this sexual dimorphism. Individuals were marked with a unique toe-clip which removed no more than a single digit from each limb.

Population estimates for the random quadrat sample of *A. bitectus* were calculated in the following manner:

$$\hat{N} = \frac{n}{ba},$$

where $n$ is the total number of individuals from all $b$ quadrats, and $a$ is the area of each quadrat in hectares. This gives a density estimate for number of individuals per hectare. Because the populations cannot be assumed to be randomly distributed, an unbiased estimate of the variance was calculated by the method of Cochran (1963):

$$\hat{\sigma}_N^2 = B^2 \frac{v}{b}\left(1 - \frac{b}{B}\right),$$

where $B = 1/a$ and

$$v = \sum_{i=1}^{b} \frac{(x_i - \bar{x})^2}{(b-1)}.$$

The 95% confidence intervals are then given by

$$\hat{N} \pm t_{b-1}[0.05]\hat{\sigma}_N.$$

The study plot population of *A. bitectus* was estimated by the weighted least squares method of Schumacher and Eschmeyer (1943). This estimate of mark-recapture analysis has been found to be reliable for lizard population studies by Turner (1977), who recommends its use for the evaluation of lizard population densities because of its consistently "realistic" results. This tech-

nique employs multiple recaptures and assumes that the population is closed during the sampling period. Each census within a given sampling period was regarded as a sample, and estimates were made independently for each sampling period (i.e., marked animals from previous sampling periods were not included in the calculations unless they were found in the present sample or a later sample). The population size is estimated by

$$\hat{N} = \frac{\sum_{i=2}^{s} n_i M_i^2}{\sum_{i=2}^{s} m_i M_i},$$

where $s$ is the number of samples, $m_i$ is the number of marked individuals in the $i$th sample, $M_i$ is the number of marked individuals in the population just before the $i$th sample, and $n_i$ is the number of individuals in the $i$th sample. The variances and confidence intervals for the estimates were calculated in the manner of DeLury (1958):

$$\hat{\sigma}^2 = \frac{1}{s-2} \left[ \frac{\sum_{i=2}^{s} m_i}{n_i - \left(\sum_{i=2}^{s} m_i M_i \middle/ \sum_{i=2}^{s} n_i M_i^2\right)} \right].$$

The 95% confidence intervals are then given by

$$\frac{\sum_{i=2}^{s} n_i M_i^2}{\sum_{i=2}^{s} m_i M_i \pm t_{s-2}[0.05]\left(\hat{\sigma}^2 \sum_{i=2}^{s} n_i M_i^2\right)^{1/2}}.$$

To obtain density estimates for the study plot population of *A. bitectus*, $N$ was multiplied by 2.53 to obtain the estimated number per hectare of rubber grove habitat.

Population estimates of the *A. gemmosus* populations at the Río Faisanes were calculated using the Jolly–Seber method

(Seber, 1973). This method allows for the death, recruitment, immigration, and emigration of animals into and out of the population. Turner (1977) has suggested that this method could result in unrealistic estimates if its assumptions are not met, but the data for the *A. gemmosus* study seem to fit the assumptions fairly well (Seber, 1973). In particular, some individuals persisted in the population through the entire duration of the study. Using this method, the population size is estimated by

$$\hat{N}_i = \frac{(n_i z_i / r_i) + m_i}{m_i / n_i},$$

where $n_i$ is the number of animals in the $i$th sample, $m_i$ is the number of marked animals in the $i$th sample, $r_i$ is the number of marked animals released after the $i$th sample that are subsequently recaptured, and $z_i$ is the number of animals caught before, but not during, the $i$th sample that are subsequently recaptured. The variance is calculated by

$$\hat{\sigma}^2 = \hat{N}_i (\hat{N}_i - n_i)$$

$$\left[ \left( 1 + \frac{r_i}{z_i} \right) \left( \frac{1}{r_i} - \frac{1}{n_i} \right) + \left( \frac{1}{m_i} - \frac{1}{n_i} \right) \right].$$

Population densities were estimated in very crude terms because the study area was never accurately delineated. The study area consisted of both sides of a road over a ca. 150-m stretch. Because of the steepness of the road cut, only 1–3 m of vegetation could be sampled on either side of the road. For the purpose of having a crude density estimate for comparative purposes, I estimated the area of the study area as $150 \times 5 = 750$ m$^2$. To get an estimate of density per hectare, $N$ was multiplied by 13.3.

Growth rates for the two species of anoles were calculated separately for each sex. The characteristic growth rate ($r$) and the asymptotic maximum SVL were calculated using a logistic-by-weight growth model and fitting a curve by means of a nonlinear least squares regression. The computer program

for this calculation was provided by Jon Seger. Choice of the particular growth model was based on the results of a comparative study of lizard growth models by Schoener and Schoener (1978), who found that the logistic-by-weight model consistently resulted in the best fit.

## RESULTS

### General Observations and Natural History

Both species of anoles are members of relatively simple lizard communities. The montane *A. gemmosus* is known from lower cloud forest localities on the western slope of the Ecuadorian Andes as far north as the Colombian border. The known elevation range is from 1,150 to 2,100 m, with the highest population densities normally found between 1,200 and 1,600 m. Over this range it is sympatric with at least four other species of *Anolis*, but only two of these are regularly found in sympatry with *A. gemmosus*: the giant, crown-dwelling *A. fraseri* and the large trunk-ground *A. aequatorialis*. *Anolis bitectus* has a restricted distribution in the lowlands of west-central Ecuador near the base of the Andes, where it seems to be associated with tropical moist forest vegetation. It is known from relatively few localities, and before the present study, it was very poorly represented in collections. The small samples collected in the course of my field work easily doubled the number of specimens in museum collections. Although possibly found in sympatry with as many as 10 congeners at various points over its range, it has been recorded in sympatry with only four: *A. fasciatus*, *A. festae*, *A. peraccae,* and *A. princeps*. In the study area at Hacienda Cerro Chico it was found with only two congeners: *A. festae* and *A. peraccae*, both small species of the trunks along forest edge (see above).

*Anolis gemmosus* is by far the most abundant species of lizard in all of the cloud forest localities I have visited in northwestern Ecuador. Although abundant by South American standards, their presence is often very difficult to detect if the

area is sampled by day. My limited observations on active *A. gemmosus* agree with those of Fitch et al. (1976). All of the individuals they saw were perched above the ground, with the majority in foliage rather than on tree trunks or stems. The majority of my observations of active animals were of lizards perched on ferns along road cuts and in other disturbed habitats, but I did see several adult males perched on tree trunks several meters off the ground in small clearings in otherwise undisturbed cloud forest. *Anolis gemmosus* would appear to be a bush-dwelling anole for the most part, although individuals might utilize higher perches when available.

My body temperature data are scant, reflecting the lack of time spent searching for these lizards during the day. The mean body temperature of four lizards was l6.2° C, with a mean air temperature of l6.l° C. Fitch et al. (1976) gave a mean body temperature (MET) of 21.0° C for their sample of 34 temperatures. The discrepancy in METs occurs because three of my four temperatures were of animals found shortly after dawn, when air temperatures were still very low and the lizards were not obviously active. Interestingly enough, the sleeping perches of *A. gemmosus* generally seemed to be oriented so that the lizards would be exposed to any early morning sunlight; on three occasions when I observed sleeping anoles before dawn and watched the sun rise, all of the lizards were met by the first rays of direct sunlight.

*Anolis bitectus* was found only in the single rubber grove at Hacienda Cerro Chico, despite extensive collecting efforts over a 6-year period in the surrounding region. This species remains known from a very few scattered localities in west-central Ecuador.

*Anolis bitectus* is active in the understory vegetation at the Hacienda Cerro Chico rubber grove and is very rarely seen on the trunks of the rubber trees. Active individuals seem to spend most of their time within the dense foliage; nearly all of the undisturbed individuals seen were perched on small stems and vines within 20 cm of the ground, where they were hidden from above by the dense vegetation. It was exceedingly difficult to find undisturbed individuals, and most of the lizards found during the day were seen after vegetation was disturbed and they revealed their presence by flight movements.

At Hacienda Cerro Chico, *A. bitectus* seems to be essentially restricted to the rubber plantation. Despite some searching, both by day and by night, in adjacent plantations of African oil palm and second growth forest, no specimens were found. Even within the rubber groves it seems to be restricted to the more deeply shaded interior sections and avoids the more open edges of the groves.

Body temperature data for *A. bitectus* are summarized in Figure 9. Individuals were never observed basking. The intensity of thermoregulation, $k$ (Huey and Slatkin, 1976), is 0.89.

## Population Densities

The estimated population sizes for the Río Faisanes population of *A. gemmosus* are presented in Table 18. The density estimates presented are based on the rough approximation of the sampled area and are best regarded as maximum density estimates for two reasons. First, this study site was originally selected because it appeared to have the highest population density of *A. gemmosus* along a 15-km stretch of road leading through appropriate cloud forest habitat. I roughly estimated it to have from two to five times the density of other similar areas along the road when the initial surveys were made in 1975 and 1976. Second, the entire habitat sampled was ecotonal in character, lying at the edge of a large patch of closed-canopy cloud forest. Within the adjacent forest, population densities were much lower; whereas sampling periods along the road resulted in from 13 to 31 individuals observed, sampling in the adjacent forest on the same night would generally result in fewer than five individuals being found, even though much more time was spent and
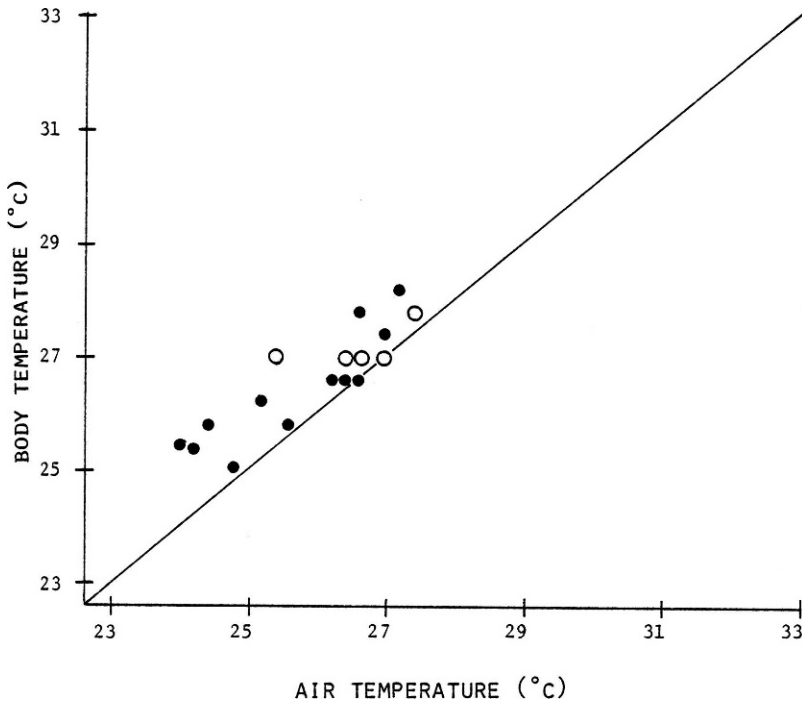
Figure 9. Body temperatures of *Anolis bitectus* plotted against air temperature at time of capture. Open circles represent multiple records. Diagonal line is for body temperature = air temperature.

several times the area was covered. It seems doubtful that this discrepancy was due to differences in sleeping perch preferences because the forest lizards were found on similar perches to those along the edge. The estimated population densities in Table 18, therefore, are estimates of maximum densities of *A. gemmosus* observed in edge habitats, and areal estimates of density for large patches that include considerable cloud forest would be much lower, perhaps as much as an order of magnitude or more.

The populations of *A. gemmosus* remained more or less constant over the course of the

study and from season to season within each year. The rather large variances obtained in the estimates are fairly typical of the Jolly–Seber technique (Seber, 1973), but the close agreement of the estimates makes this constancy seem realistic.

The estimates of population size and density of *A. bitectus* at Hacienda Cerro Chico are presented in Table 19. Populations of *A. bitectus* appeared to be spread

TABLE 18. POPULATION AND DENSITY ESTIMATES OF *ANOLIS GEMMOSUS* AT RÍO FAISANES, ECUADOR. SEE TEXT FOR DISCUSSION OF ESTIMATION TECHNIQUE.

|  | *n* | Variance | Density/ha |
|---|---|---|---|
| August 1976 | 98 | 65 | 1,304 |
| April 1977 | 75 | 38 | 995 |
| November 1977 | 80 | 34 | 1,065 |

TABLE 19. POPULATION AND DENSITY ESTIMATES OF *ANOLIS BITECTUS* AT RUBBER GROVE STUDY PLOT AT HACIENDA CERRO CHICO, ECUADOR. SEE TEXT FOR DISCUSSION OF ESTIMATION TECHNIQUES.

|  | *n* | 95% Range | Density/ha |
|---|---|---|---|
| July 1976[1] | — | — | 445[2] |
| April 1977 | 139 | 105–203 | 352 |
| November 1977 | 308 | 219–516 | 780 |
| January 1978 | 298 | 105–618 | 755 |
| April 1978 | 183 | 107–630 | 464 |
| January 1979 | 113 | 43–178 | 286 |

[1] Different sampling technique used.
[2] The 95% confidence interval for this density estimate is 256–644.

out more or less uniformly throughout the rubber plantation, although densities appeared to be somewhat lower near the margins of the groves, so the density estimates provide a reliable picture of the actual densities of the population.

The populations of *A. bitectus* varied somewhat from one sampling period to the next, but with no clear pattern related to seasonality. The lowest population densities were recorded in January 1979 and April 1977, corresponding roughly to the beginning and end of the wet season in this area. However, population densities in January and April 1978 were higher, and the 95% confidence limits overlapped with the highest recorded density in November 1977. In 1977 it appeared as though recruitment into the population occurred during the dry season, with the estimated population density perhaps doubling in a 7-month period. In 1978, however, the population appeared to decrease during the dry season.

## Size and Growth

*Anolis gemmosus* reaches a maximum recorded SVL of 66 mm (Fitch, 1976), although the largest individual marked at the Río Faisanes locality was only 62.5 mm SVL. Fitch also recorded a maximum female SVL of 63 mm, whereas the largest female at the Río Faisanes was 56.8 mm. The mean SVLs that Fitch recorded for his sample of *A. gemmosus*, taken from Tandapi, a locality some 20 km due south of the Río Faisanes at 1,460 m elevation, were as high as (males) or higher than (females) the maxima I recorded. Fitch found significant sexual dimorphism in his sample, with the sexual dimorphism ratio (SDR = female SVL/male SVL) equal to 0.94. The SDR for the Río Faisanes population was 0.92, also highly significant. Only adults were used to calculate the mean SVLs; adults were considered all those individuals with SVL > 50 mm (size of the smallest females with oviducal eggs).

There were no apparent shifts in the size-frequency distribution of the Río Faisanes population (Table 20) during the course of

TABLE 20.    SIZE FREQUENCY DISTRIBUTION OF *ANOLIS GEMMOSUS* AT RÍO FAISANES DURING FOUR SAMPLING PERIODS, 1976–1978.

|  | July 1976 | April 1977 | November 1977 | January 1978 |
|---|---|---|---|---|
| Female SVL (mm)* | | | | |
| 21–30 | 0 | 1 | 0 | 0 |
| 31–40 | 1 | 2 | 0 | 0 |
| 41–50 | 4 | 3 | 3 | 1 |
| 51–60 | 17 | 7 | 7 | 15 |
| Male SVL (mm)** | | | | |
| 21–30 | 3 | 0 | 0 | 0 |
| 31–40 | 5 | 0 | 2 | 3 |
| 41–50 | 1 | 1 | 0 | 1 |
| 51–60 | 6 | 4 | 4 | 6 |
| 61< | 3 | 0 | 0 | 3 |

* $x^2 = 9.91$, $p = 0.36$.
** $x^2 = 11.88$, $p = 0.46$.

the study. Adults made up a large proportion of the population (70%), with adults comprising 62% of the males and 75% of the females. This difference in the proportion of adults is not significant ($x^2 = 2.16$, $p = 0.14$).

Growth rates using the logistic-by-weight growth model and unfixed data (Schoener and Schoener, 1978) were calculated for each sex (Figs. 10, 11; Table 21). The calculated asymptotic SVL is somewhat smaller than the recorded maximum SVLs,[10] but the SDR calculated from them is quite close to that actually found in the population (0.95). *Anolis gemmosus* appears to be quite long-lived for a small lizard; adult females first marked in July 1976 remained in the population until at least January 1978 (data for April 1978 were lost, but at least one adult female from the original marked cohort was still present at that time). Growth appears to cease once sexual maturity is reached, at least in the case of females. Because it was not possible to determine at what size males attained maturity, it is not clear whether they continue to grow after that point. If the assumption made above that they reach maturity at the same size as females (and the same age, since the

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[10] A common finding in studies on anoles (Stamps and Andrews, 1992).

Figure 10.    Absolute growth rate of *Anolis gemmosus* females plotted against initial size. Open circles represent multiple records.



Figure 11.    Absolute growth rate of *Anolis gemmosus* males plotted against initial size. Open circles represent multiple records.

TABLE 21.  GROWTH RATES OF *ANOLIS BITECTUS* AND *A. GEMMOSUS* IN WESTERN ECUADOR.

|  | $n$ | Maximum Estimated SVL | $r$ | SSQR |
|---|---|---|---|---|
| *A. bitectus* | | | | |
| Male | 16 | 48.8 | 0.0248 | 39.783 |
| Female | 31 | 52.0 | 0.0211 | 69.919 |
| *A. gemmosus* | | | | |
| Male | 13 | 57.7 | 0.0104 | 24.662 |
| Female | 41 | 54.5 | 0.0094 | 31.799 |

characteristic growth rates are essentially the same) holds, then males would continue to grow somewhat past this point.

*Anolis bitectus* reaches a maximum male SVL of 56.0 mm, and females reach 56.5 mm. Females reach sexual maturity at about 45 mm SVL, and this was taken as the minimum adult size for the Hacienda Cerro Chico population. Adults show significant sexual dimorphism in size, with the females slightly larger than the males (SDR = 1.02, $p = 0.03$). Although the lumped data show significant size dimorphism, three of the six sampling periods show no significant dimorphism (Table 22). In all cases, however, females are slightly larger than males, and the slight dimorphism in adult size is probably real.

There were no significant shifts in the size-frequency distribution of *A. bitectus* females (Table 23). Males may show some degree of shifting in the size distribution, however, but larger samples would probably

be necessary to demonstrate this. Adult males compose a smaller proportion of all males (51%) than adult females do of all females (62%; $x^2 = 4.88$, $p = 0.03$).

Growth curves for the *A. bitectus* population at Hacienda Cerro Chico are shown in Figures 12 and 13, and the growth rate parameters for the logistic-by-weight model are presented in Table 21. The asymptotic maximum SVLs are again lower than those actually recorded in the population, and the SDR calculated from these asymptotes (1.07) is slightly higher than the one recorded for the lumped sample, although it is similar to some of the individual sampling period SDRs (Table 22). Unlike *A. gemmosus*, female *A. bitectus* appear to continue growing after sexual maturity is reached (Fig. 12).

By substituting the calculated values of the characteristic growth rate $r$ and the asymptotic maximum SVL into the logistic-by-weight growth equation, it is possible to calculate the time needed to reach sexual maturity provided the size at hatching ($SVL_0$) and at sexual maturity ($SVL_{sm}$) are known. The equation is

$$T_{sm} = -\frac{1}{r} \ln \frac{SVL_0^3 \left( SVL_{max}^3 - SVL_{sm}^3 \right)}{SVL_{sm}^3 \left( SVL_{max}^3 - SVL_0^3 \right)}$$

Although I have no data on the hatchling size of either species, I have used the smallest individual recorded of each species as an indication of hatchling size, assuming

TABLE 22.  SEXUAL SIZE DIMORPHISM IN *ANOLIS BITECTUS*, ADULTS ONLY (SVL ≥ 44 MM).

|  | Males | | | Females | | | |
|---|---|---|---|---|---|---|---|
|  | $n$ | $\overline{SVL}$ | $s$ | $n$ | $\overline{SVL}$ | $s$ | SDR[1] |
| July 1976 | 4 | 48.4 | 0.522 | 10 | 51.3 | 8.800 | 1.06* |
| April 1997 | 19 | 50.0 | 3.222 | 27 | 50.1 | 8.165 | 1.00 |
| November 1977 | 20 | 48.8 | 5.735 | 24 | 49.4 | 7.986 | 1.01 |
| January 1978 | 26 | 48.1 | 5.969 | 27 | 50.3 | 2.612 | 1.05** |
| April 1978 | 18 | 48.2 | 4.916 | 18 | 50.8 | 3.838 | 1.05** |
| January 1979 | 21 | 50.7 | 8.776 | 17 | 51.1 | 7.232 | 1.01 |

[1] Female $\overline{SVL}$: Male $\overline{SVL}$.
* Dimorphism significant at $p < 0.01$.
** Dimorphism significant at $p < 0.0001$.

TABLE 23.  SIZE FREQUENCY DISTRIBUTION OF *ANOLIS BITECTUS* AT HACIENDA CERRO CHICO DURING SIX SAMPLING PERIODS, 1976–1979.

|  | July 1976 | April 1977 | November 1977 | January 1978 | April 1978 | January 1979 |
|---|---|---|---|---|---|---|
| Female SVL (mm)* | | | | | | |
| 21–32 | 2 | 8 | 5 | 3 | 6 | 8 |
| 33–44 | 5 | 5 | 17 | 10 | 3 | 5 |
| 45> | 10 | 26 | 24 | 28 | 18 | 17 |
| Male SVL (mm)** | | | | | | |
| 21–32 | 6 | 9 | 4 | 16 | 7 | 4 |
| 33–44 | 4 | 9 | 13 | 13 | 16 | 4 |
| 45> | 4 | 19 | 20 | 26 | 18 | 17 |

\* $x^2 = 13.44$, $p = 0.20$.
\*\* $x^2 = 17.47$, $p = 0.06$.

that hatchling males are the same size as hatchling females. These values are 21.6 mm for *A. bitectus* and 26.8 mm for *A. gemmosus*. Both sexes were assumed to reach sexual maturity at the same SVL (see above), and the minimum SVL of gravid females was used as this parameter; for *A. bitectus* this was 45 mm, and for *A. gemmosus* this was 50 mm. Substituting these values and the appropriate values of $SVL_{max}$ and $r$ from Table 21 into the above equation, the following results were obtained. Both male and female *A. bitectus* reach sexual maturity in about 150 days (males 147, females 150); male *A. gemmosus* take 271 days to reach maturity, and female *A. gemmosus* require almost a full year (343 days).

### Reproduction

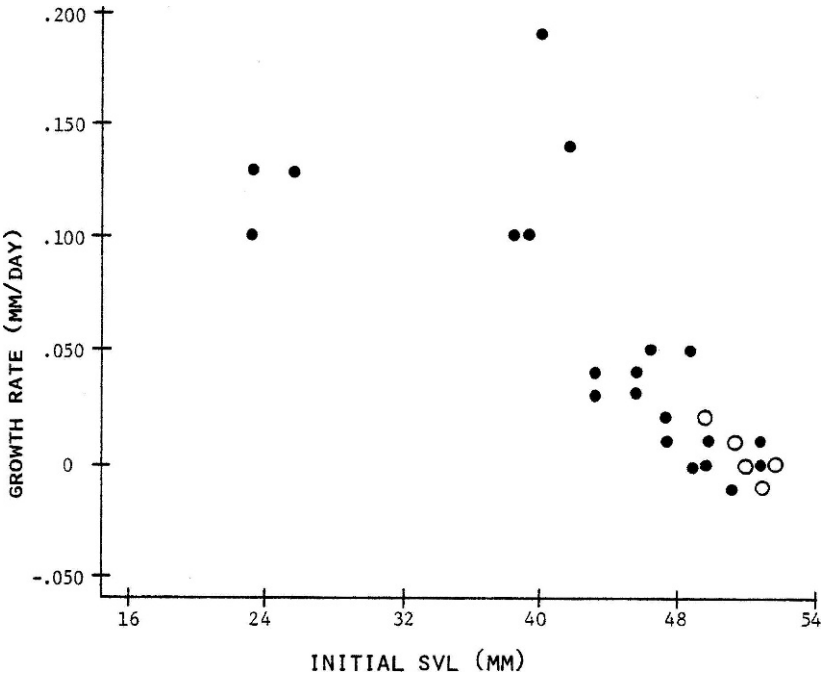In both species the same basic pattern of reproductive activity was noted. In nearly all



Figure 12.   Absolute growth rate of *Anolis bitectus* females plotted against initial size. Open circles represent multiple records.
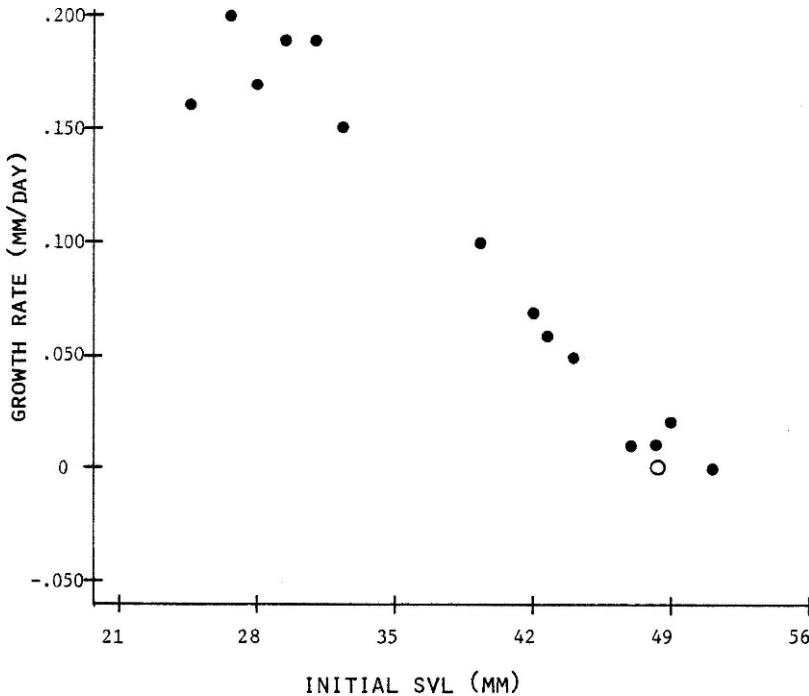
Figure 13.    Absolute growth rate of *Anolis bitectus* males plotted against initial size. Open circles represent multiple records.

cases, adult females sampled at all seasons were gravid. At least one large oviducal egg could be felt or seen in almost every female lizard more than 2 mm larger than the minimum adult female size mentioned above. The few cases of non-gravid females could very well have been of lizards which had just laid their egg. I have no information on clutches for the marked populations, but anoles are known to generally have single-egg clutches (Fitch, 1970).

Hatchling-sized juveniles were not present in every sample. This size class was poorly represented in *A. gemmosus*, comprising no more than two individuals in any sampling period, and I am unable to make any statements regarding the seasonality of their appearance. For *A. bitectus*, the percentage of hatchlings (20–26 mm SVL) in the population varied from 2% in November to 3% in January to 11% in April to 19% in July ($x^2 = 7.67$, $p = 0.05$). This suggests a peak in hatching some time near the end of the rainy season and a consider-

able decrease in hatching toward the end of the dry season. Because females continued to be almost uniformly gravid throughout the year, this suggests either a decrease in hatching success during the dry season or an increase in egg retention and longer intervals between clutches. I have no data that can distinguish between these alternatives.

## DISCUSSION

Although the two species of *Anolis* considered in this paper are both from nearby regions and are basically similar in perch preferences, generally perching on vegetation rather than on tree trunks, they show more differences than similarities in most aspects of their biology. Although both species exhibit similar ranges in active body temperatures (see Fitch et al. [1976] for more temperature data on *A. gemmosus*), *A. bitectus* is thermally passive in the strictest sense (Huey and Slatkin, 1976), whereas *A. gemmosus* appears to exhibit some thermoregulatory behaviors. The populations of *A.*

*gemmosus* also tend to remain constant through time, with a stable size-frequency distribution, whereas *A. bitectus* undergoes moderate population fluctuations and may show some shifts in size-frequency distribution (at least in the case of males). Both species show similar slight degrees of sexual size dimorphism, but in *A. bitectus* the females are larger, and in *A. gemmosus* the males are larger. *Anolis bitectus* has a fairly high characteristic growth rate, whereas that of *A. gemmosus* is quite low. To what extent are these differences due to differences in the local environment and to what extent might they be due to different competitive milieus?

The apparent difference in thermal strategies between the two species probably reflects differences in the climates to which the species are exposed. *Anolis bitectus* lives in an area where temperatures tend to be warm, rarely dropping below 20° C even at night. These lizards are still quite mobile at that temperature and probably can begin their daily activity early in the morning. The cloud forests that *A. gemmosus* inhabits, on the other hand, are characteristically cool, and air temperatures before dawn can be as low as 10° C or even lower. At this temperature the lizards are virtually immobile, and it might take a considerable amount of time for the air to reach temperatures commensurate with activity temperatures of the lizards. By selecting sleeping perches exposed to any available morning sun, they are able to reach activity temperatures more quickly, and they can do so behaviorally rather than relying on more complex physiological adaptations to low temperatures. Furthermore, because early mornings are the only times of reliable sunlight in the cloud forest habitat, it might be important for these lizards to begin activity early so that when the almost inevitable cloud cover settles in an hour or two after dawn they can already be going about their business. Behavioral adaptations to thermoregulation appear to be much more easily evolved in the genus *Anolis* than physiological responses, and a trend to increasing thermoregulation with altitude has been noted in the West Indies (Hertz and Huey, 1981).

The relative constancy of the *A. gemmosus* populations is also probably a reflection of the cloud forest environment. Although precipitation in the cloud forests of western Ecuador show some degree of seasonality, more or less paralleling that of the adjacent Pacific lowlands, cloud cover is almost constant in this region, and afternoon mists and drizzles occur virtually daily. In terms of productivity, the cloud forest environment is probably quite constant as periods of water shortage are scarce and of short duration. Given a relatively constant level of productivity, it is not surprising that populations of at least some animals might be relatively constant as well. The lowland areas that *A. bitectus* inhabits, on the other hand, have a definite dry season, and although this period is not generally severe enough to result in deciduous vegetation, there is no question but that seasonal variation in productivity exists. Furthermore, this area is subject to considerable annual variation in precipitation, both with respect to total amount and to the exact timing and duration of the wet season. This adds more possible variation to productivity, which is difficult to assess over short-term studies such as the present one but which could easily result in the moderate population fluctuations observed in the *A. bitectus* population.

Andrews (1979) provided compelling evidence to suggest that mainland species of *Anolis* differ fundamentally from island species in a number of important aspects of life history, which are related to the basic roles the lizards play in their respective communities. Her basic thesis is that island species, which tend to be dominant members of their terrestrial vertebrate faunas, are basically food-limited, and intraspecific competition has resulted in life history strategies that tend to be K-selected (MacArthur and Wilson, 1967; Pianka, 1970). Mainland species, on the other hand, are generally not dominant members of their

terrestrial vertebrate faunas and are subject to intensive predation pressure from a wide variety of potential predators that are absent from the West Indies (certain families of birds in particular); intraspecific competition is therefore not as severe as on the islands, and the mainland species are more r-selected. These conclusions were reached after a consideration of a variety of studies dealing with the ecology of West Indian, Mexican, and Central American anoles. How do the two species of South American anole fit into this general picture?

One of Andrews' predictions concerning mainland species is met by both *A. bitectus* and *A. gemmosus*. Both species exhibit very small degrees of sexual size dimorphism. This slight difference in mean adult size is probably not of any consequence in terms of resource partitioning. Slight, but statistically significant, differences in adult size could be due to a number of factors. The smaller sex might be more susceptible to predation than the larger because of differences in behavior. If males tend to live shorter lives, perhaps because of more conspicuous perches subjecting them to increased danger from predation, this could account for a slight difference in mean adult SVL. This might be the case for *A. bitectus*. The longest interval between recaptures for males was 197 days, whereas 11 females were recaptured after intervals of more than 200 days, and the longest recapture interval was 349 days. No similar pattern was observed in the *A. gemmosus* population, as individuals of both sexes persisted in the population for more than 600 days. The larger size of males could be due to more growth after sexual maturity is reached because they do not have to allocate part of their energy intake to production of eggs.

Both species of South American anoles differ in one major respect from the Central American anoles. Both *A. bitectus* and *A. gemmosus* require long periods to reach sexual maturity. For the small, lowland *A. bitectus,* approximately 5 months is required to reach the minimum SVL at which oviducal eggs are noted. This is considerably longer than most small Central American anoles require and is comparable to the amount of time needed by a large species like *A. frenatus* (Andrews, 1976). This is more or less in keeping with the maturation time required by the West Indian species. *Anolis gemmosus* requires even longer to reach sexual maturity, with females needing almost a year to reach minimum adult SVL. However, the maturation time of male *A. gemmosus* is fairly similar to that of a Central American montane species, *A. tropidolepis* (Andrews, 1976), which suggests that the cloud forest environment might play a major role in determining the slow growth rate.

It is not immediately clear why South American anoles might require longer to reach sexual maturity than the Central American species. The lowland communities that *A. bitectus* is from are certainly quite similar in most respects to lowland habitats in Central America in terms of possible competitors and predators, and there is no reason to believe that the basic structure of the communities differs in any significant and obvious way. The answer to this problem could in fact be quite simple; *A. bitectus* might not be ecologically similar to the Central American species studied. Unlike most of the Central American species, which tend to be associated with edge and disturbed habitats in general, the South American species allied with *A. bitectus* are typically forest-restricted species. Because no populations of *A. bitectus* aside from the study population were discovered in six years of field work, it might be reasonable to assume that their presence in high densities there is the result of a historical accident. I strongly suspect that *A. bitectus* is primarily a forest species and that its presence in the rubber grove at Hacienda Cerro Chico might be most unusual.

Most Central American anoles that have received detailed study are characteristically species of the forest edge, and most of the studies have been conducted in disturbed habitats. It is generally only in these habitats

that mainland anoles reach population densities high enough to warrant study. However, by restricting the species studied to those normally associated with edge situations, the possibility of mistaken generalization could set in. Although anoles are abundant in edge situations, and many species inhabit these habitats, a large percentage of species, particularly in South America, are essentially restricted to forest interiors. Unfortunately, these species are nearly always quite rare, and there exists little possibility of conducting quantitative field studies on a species that might only be seen once every 2 weeks. If, as I believe, *A. bitectus* is normally such a species, then the Hacienda Cerro Chico rubber grove might have provided an opportunity to obtain some insight into the biology of one of these species normally difficult to study, and this could account for some of the differences in life history.

It is in precisely those species that are characteristic of edge situations that one might expect to encounter relatively r-selected life history strategies. Because most West Indian anoles abound in such habitats, the comparisons that Andrews (1979) made between Central American and West Indian anoles are legitimate, and the patterns she found are of real and general significance. However, I do not believe that it is possible as yet to determine whether these patterns are typical of mainland anoles as a whole. Given the implausibility of much of the field work necessary to establish whether these patterns are typical, a thorough understanding of the ecology of mainland anoles probably lies far in the distant future.

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