

## Behavior, Ecology, and Locomotor Performance of the Giant Anole, *Anolis frenatus*

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**ABSTRACT.** – We provide data on the diet, microhabitat use, home range size, behavior, sexual dimorphism, recruitment, density, and locomotor performance of the little known Central American giant anole, *Anolis frenatus*. This lizard is in some ways similar to the large anoles of the West Indies, but the similarities probably result solely from its large body size. In terms of microhabitat use and behavior, *A. frenatus* is not particularly similar to the “crown-giants,” nor to any of the other “ecomorph” types, of the West Indies.

### INTRODUCTION

Approximately 300 species of *Anolis* occur in Central and South America and on the Caribbean islands. Extensive ecological, behavioral, and evolutionary research (summarized most recently in Williams, 1983) has made this genus one of the best known among vertebrates. Nonetheless, some aspects of the anole radiation are poorly known. In particular, the biology of mainland (i.e., Central and South American) anoles has been investigated less extensively than that of West Indian species. Further, “giant” (i.e., greater than 100 mm snout-vent length [svl]) anoles have received relatively little attention. Here we provide data on the Central American giant anole *Anolis frenatus* Cope observed at Barro Colorado Island (BCI), Panama, and compare its biology to large West Indian *Anolis*.

### METHODS

#### *Size Distribution, Reproduction, Density, and Home Range*

Animals were collected and measured during censuses conducted from 1971-1982

(data on *A. frenatus* collected during censuses of *A. limifrons* Cope; see Andrews and Rand, 1982; Andrews et al., 1983). The few individuals represented more than once in summaries of size distributions were caught in different censuses. Home range areas were estimated by multiplying  $r^2$  (mean squared distance from the center of the home range to each capture point) by a factor of 5.2 to give home range area in  $m^2$  (Schoener, 1981; Andrews and Rand, 1983). Home ranges were estimated for individuals with three or more mark-recapture records.

#### *Microhabitat Use and Behavior*

Microhabitat use in *Anolis* is quantified from measurements of perch height and diameter (Rand, 1964, 1967; Schoener and Schoener, 1971a, b). For each adult individual encountered in Nov.-Dec. 1988, height above the ground and the diameter of the object upon which it was perched was recorded. In 1963, the orientation of lizards ( $n = 34$ ) and the objects upon which they were perched were recorded. The position of one male (svl = 80 mm) was recorded repeatedly ( $n = 51$ ) over a two-week period in 1963.

Lizards discovered along trails were quietly observed from a distance of 5-15 m for 15-70 min (1963,  $n = 3$ ; 1988,  $n = 17$ ; all lizards were adults except one female

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observed in 1963). All movements were noted as walks, runs, or jumps, and the amount of time spent displaying (bobbing and/or dewlapping) was recorded as a percentage of the total observation time (protocol following Losos [1990a]).

### *Performance Capabilities*

Sprinting and jumping capabilities were determined using established protocols for *Anolis* (van Berkum, 1986; Losos, 1990b). Sprint speed was determined by placing adult lizards at the bottom of a 2.5 m track angled at 37° and inducing them to run toward a dark bag at the top of the track. Running lizards interrupted light beams stationed every 0.25 m; photocells were connected to a Compaq portable computer which calculated sprint speed over each interval. The fastest interval during five trials, conducted at hourly intervals, was considered the maximal speed for each individual. Animals that did not appear to run maximally during at least two trials were excluded. Jumping ability was measured by placing lizards on a flat surface 28 cm above the ground and inducing them to jump, by a tap to the tail, toward a dark corner. The longest of three jumps, conducted at hourly intervals, was considered maximal for that individual. Individuals that did not appear to jump at maximum capability on any of three trials were excluded. Jumping and sprinting measurements were conducted on consecutive days. For each lizard, testing began the day after capture. All performance measurements were made at a body temperature of 30°C.

### *Diet*

The stomach contents of 16 lizards (eight of each sex) were removed and stored in alcohol in January–February 1973 (the size, but not prey composition, of these items was reported in Scott et al. [1976]). Fecal samples from ten freshly collected captive animals (four male, six female) were collected and stored in alcohol in November–December 1988. Prey from both stomach and fecal samples were identified to family if possible. No obvious differences in prey type were noted between samples; conse-

quently, the data are combined for our analyses.

### RESULTS

Between May 1976 and July 1977, 30 lizards were seen at one site (“Lutz”) during 152 person-hours of searching. During the same period and approximately the same amount of search time, only three *A. frenatus* were seen at another site (“AVA”) about 3 km away. During December 1983–1986, 11 sites were censused on Barro Colorado Island. Six *A. frenatus* were seen during 113 person-hours of search, including 19 person-hours of searching at the Lutz site, which yielded no *A. frenatus*.

The home ranges of males ( $\bar{x}$  804.6 ± 164.4 [SE] m<sup>2</sup>,  $n$  = 3) were larger than those of females ( $\bar{x}$  = 438.6 ± 171.9 m<sup>2</sup>,  $n$  = 5). Juveniles, which are most abundant in April and May (Fig. 1), had the smallest home ranges ( $\bar{x}$  = 176.9 ± 103.5 m<sup>2</sup>;  $n$  = 4).

Males perch higher than females (males:  $\bar{x}$  = 2.56 ± 0.44 [SE] m, range = 0.95–6.0,  $n$  = 11; females  $\bar{x}$  = 1.67 ± 0.13, range = 0.75–2.0,  $n$  = 11; Mann-Whitney U-test, one-tailed because male > female is the expectation [see below],  $P$  < 0.05). Most lizards were observed perched on vertical tree trunks (82.4%) facing head downward (81.3%). No difference existed between males and females or between adults and juveniles in use of vertical trunks or perch posture.

During a two-week period, the locality in which a small adult male had previously been found was visited 53 times. The lizard was observed in 51 (96.2%) of these visits. The lizard was observed on the same tree trunk 51% of the time, and on an adjacent trunk 31.4% of the time. The other sightings were on nearby trees and once on a vine. The lizard was perched head-downward 82.3% of the time at a mean height of 0.81 ± 0.07 m. On one occasion, the lizard was observed feeding. It was perched 1.83 m high facing down when it saw a katydid on the ground. It ran down the tree, stopping twice, then jumped to the ground, caught the insect, climbed back up the tree 0.61 m and ate it.

Lizards were extremely inactive; only six lizards moved at all, and none moved more

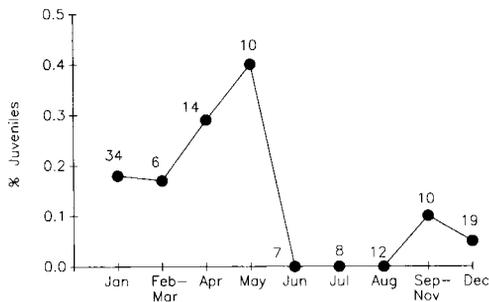


FIG. 1. Proportion of juveniles in the population during the year. Each point represents the proportion of all lizards caught that were <50 mm svl. Numbers above the points are the sample sizes for each month.

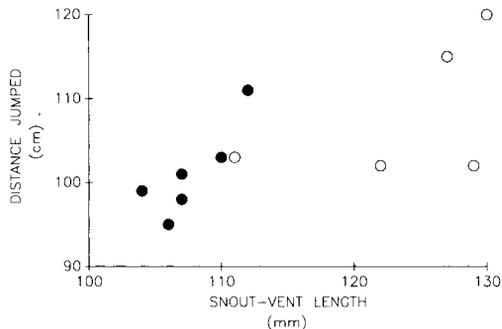


FIG. 2. Distance jumped by *A. frenatus*. Filled circles are females, open circles are males.

than twice. All movements were brief (<10 cm). Mean movement rate was 0.050 cm/min (or 2.6 km/decade!). Of the nine males observed, four exhibited display behavior. Two males displayed frequently, exhibiting display behavior for 16.0% and 8.5% of the time observed, whereas the other two males displayed infrequently (3.5% and 1.6% of observation time).

Jumping ( $r^2 = 0.28$ ,  $P < 0.05$ ), but not sprinting ( $r^2 = 0.01$ ), ability is correlated with svl when all data are considered; within each sex, neither performance ability is correlated to svl (Figs. 2, 3). Males have greater sprinting ( $2.80 \pm 0.18$  m/sec) and jumping capability ( $108.4 \pm 4.3$  cm) than females (sprint speed:  $2.64 \pm 0.20$  m/sec; jump distance:  $101.4 \pm 2.1$  cm), but the differences are not significant (analysis of covariance, differences in slopes and intercepts all  $P > 0.35$ ; Mann-Whitney U-test,  $P > 0.10$  for both sprinting and jumping).

*Anolis frenatus* eats a wide variety of arthropods; beetles and orthopterans are the most common prey (Table 1). In addition, Ballinger (pers. comm.) found three insect larvae and a grasshopper femur in the stomach of one adult *A. frenatus* (svl = 104 mm, sex unknown) and has observed juvenile *A. frenatus* eating flies and insect larvae.

## DISCUSSION

A remarkable pattern exists in the Greater Antilles: on each island (Cuba, Hispaniola, Jamaica, and Puerto Rico), a set of ecologically and morphologically different species (termed "ecomorphs" [Williams,

1972]) occurs. These patterns result from minimally three essentially independent radiations (Williams, 1972, 1983). Similar patterns are not apparent among the mainland anole faunas. Where possible in the discussion below, we will highlight how the biology of *A. frenatus* compares to that of the large "crown-giant" ecomorphs of the West Indies (the crown-giants, however, are the most poorly known of the ecomorphs). Further, interspecific variation in physiology and ecology often can be explained by differences in body size (Peters, 1983; Calder, 1984). We will assess to what extent the large size of *A. frenatus* can account for differences between it and other *Anolis*.

## Behavior

Focal animal observations suggest that *A. frenatus* is extraordinarily sedentary and/or extremely wary in the presence of humans, even though the observer often watched from behind trees or vegetation. Other Central American anoles are wary and seem not to behave normally when observed (J. A. Pounds, pers. comm.; Losos, unpubl.). By contrast, most West Indian *Anolis*, including the giant *A. garmani* Stejneger, will behave seemingly normally when observed under similar circumstances (Losos, 1990a). Some large West Indian species (*A. reconditus* Underwood and Williams and members of the *A. ricardii* Duméril and Bibron complex), however, also move infrequently when observed (Losos, unpubl.; also see Hicks, 1973).

The general difference in behavior be-

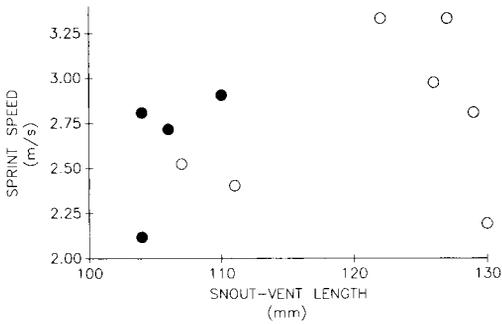


FIG. 3. Sprint speed of *A. frenatus*. Symbols as in Fig. 2. Sample size; are different from those in Fig. 2 because some animals would jump but not sprint or vice-versa.

tween mainland and island species may relate to the greater predation pressure in the more diverse Central American fauna (Greene, 1988). For example, a variety of animals prey on *A. frenatus*, including snakes (Myers, 1982), monkeys (Mitchell, 1989), and, probably, forest raptors (Scott et al., 1976; H. W. Greene, pers. comm.). Among-island comparisons also suggest a relationship between risk of predation and wariness. Anoles on Hispaniola seemed warier and moved less when observed than anoles on Puerto Rico and Jamaica (Losos, unpubl.); Hispaniola contains a number of snakes whose diet is composed primarily of *Anolis* (Henderson et al., 1988), whereas Puerto Rico and Jamaica have few saurophagous snakes (Henderson and Crother, 1989).

The average proportion of time spent displaying by the four males which displayed was 7.4%, which is greater than 17 of 21 West Indian *Anolis*, including the only other giant (*A. garmani*) for which display data are available (Losos 1990a, unpubl.). However, means for West Indian species include animals that were active but did not display. No data on display rates of other mainland anoles are available.

Only the Puerto Rico crown-giant *A. cuvieri* Merrem has a home range (325.8 m<sup>2</sup>) comparable to that of *A. frenatus* (Losos et al., 1990). The home range of juvenile *A. frenatus* is larger than home ranges for the other ten *Anolis* (none large) for which data are available (Schoener and Schoener, 1982).

TABLE 1. Diet of *A. frenatus*, based on stomach content analysis of 16 specimens (8 male: 8 female) collected in January-February, 1973 and fecal analysis of 10 adult animals (4 male: 6 female) captured in November-December, 1988. Numbers in the columns are the number of that prey type. Except where noted by asterisks, each individual contained only one item of that type.

Prey item	Males	Females
Arachnida	5	0
Diplopoda	3	1
Chilopoda	0	1
Isopoda	0	3*
Insects		
Odonata		
Anisoptera	1	0
Orthoptera		
Tettigoniidae	3	1
Gryllidae	0	1
Unidentified	4	0
Blattidae	2	2
Coleoptera		
Scarabeidae	9†	0
Curculionidae	0	4**
Larvae	1	0
Unidentified	1	8††
Homoptera		
Cicadidae	0	1
Unidentified	2	0
Neuroptera		
Myrmeleontidae		
Larvae	1	0
Hymenopteran		
Formicidae		
Ponerinae	2*	1
Unidentified	1	0
Lepidoptera		
Larvae	1	3*
Unidentified larvae	0	1

\* One individual contained two prey of this type.

\*\* Two individuals each contained two curculionid beetles.

† One individual contained seven scarabeid beetles; another contained two.

†† One individual contained three beetles; two others each contained two beetles.

### Reproductive Cycle

Based on the frequency of occurrence of juveniles at different times of the year, oviposition, incubation of eggs and early growth of hatchlings appear to be concentrated during the dry season (Mid-December to late-April). This conclusion follows from our data because: 1. Juveniles less than 50 mm svl are probably at most two months old, given a mean juvenile growth rate of 0.3 mm/day (Andrews, unpubl.); and 2. Incubation is probably at least as long as the six-week incubation period of a smaller sympatric species, *A. limifrons* (Andrews and Sexton, 1981). Our only records of oviposition occur at this time as well: nest construction and oviposition was observed in the field on 19 December 1971 and another female laid two eggs shortly after capture on 22 December 1972.

The reproductive cycle of *A. frenatus* is very different from that of sympatric *A. limifrons* (Andrews and Rand, 1982). Most eggs of *A. limifrons* are laid during the early wet season (May–September) so that incubation and early growth of hatchlings occur during wet season months (May to mid-December). One potential explanation for this difference in the reproductive cycles of these species is that the eggs of *A. frenatus* are more resistant to desiccation because they are relatively large and placed in sub-surface nests. In contrast, the relatively small eggs of *A. limifrons* are placed on the surface of the ground just below the litter (Andrews, 1988).

### Relative Density

The density of *A. frenatus* varies both spatially and temporally on Barro Colorado Island. In 1976–1977, *A. frenatus* was ten times more abundant at one site (Lutz) than at another (AVA). Densities were much lower at both sites in the 1983–1986 censuses. Based on the observation rate from 1976–1977 (averaging the rates at the two sites in 1976–1977 to calculate the island-wide rate), in 1983–1986, 11 *A. frenatus* would have been expected islandwide (six were observed) and four individuals at the Lutz site (none observed). High temporal

variation in density is also observed in sympatric *A. limifrons* (Andrews and Rand, 1982; Andrews, unpubl.). In contrast, populations of West Indian anoles appear to be more temporally stable (Schoener, 1985; McLaughlin and Roughgarden, 1989; Roughgarden and Pacala, 1989).

### Microhabitat Use

Scott et al. (1976) found that males perch higher than females, but the differences were not statistically distinguishable. Our data yield a significant difference as does combination of the two data sets. The perch heights we report are also significantly higher than those documented by Scott et al. (1976) for both males and females. The discrepancy may result either from spatial or temporal variation in microhabitat use by *A. frenatus* or from differences in lizard censusing protocols; the data herein were collected during censuses specifically devoted to finding *A. frenatus*.

Males also use larger diameter perches than females (Scott et al., 1976; Losos, unpubl.; Sexton, unpubl.; values from these three studies are in close agreement). Similar sexual dimorphism in perch height and diameter is displayed by most *Anolis* (e.g., Andrews, 1971b; Schoener, 1974; Pounds, 1988).

Microhabitat use of *A. frenatus* is more similar to that of some smaller species of *Anolis* than it is to the West Indian giant anoles. The mean male height (above) and perch diameter ( $\bar{x} = 20.8 \pm 2.4$  cm,  $n = 19$ , data from our observations and those of Scott et al. [1976], but excluding two individuals on the buttresses of large trees) differs from West Indian crown-giants, which usually are found higher, but is similar to the “trunk-ground,” “trunk,” and “trunk-crown” ecomorph categories (generally 45–75 mm svl), which often are found on the trunk 0–3 m above the ground (Rand, 1964, 1967; Schoener and Schoener, 1971a, b; Losos 1990a, unpubl.). While perched, *A. frenatus* often uses the head-down posture (Scott et al., [1976] and above) which is typical of most anoles, but is most common among “trunk-ground” species (Losos, unpubl.).

### Jumping and Sprinting Ability

Sprint speed and jumping ability are closely related to *svl* among species of *Anolis* (Losos, 1990b). *Anolis frenatus*, the second largest species for which performance data are available, can run faster and jump farther than any *Anolis* species measured. Based on its *svl* ( $\bar{x} = 115.7$ , calculated using only individuals for which performance data are available) and regression slopes based on 15 species (14 for sprinting [Losos, 1990b]), *A. frenatus* is predicted to be able to run 2.32 m/sec and jump 93.0 cm. Observed mean values, with data for the sexes combined, are substantially greater (sprint speed: 2.74 m/sec; jump distance: 104.3 cm). Hindlimb length is also an important determinant of sprinting and jumping performance (Losos, 1990b). Multiple regressions for 15 species using *svl* and hindlimb length as independent variables yield predictions closer to the observed values for *A. frenatus* (sprint speed: 2.50 m/sec; jump distance: 102.4). Thus, the great performance capabilities of *A. frenatus* result from both its large body size (as represented by *svl*) and relatively long hindlimbs. Further work may clarify why *A. frenatus* sprints 10% faster than predicted based on its *svl* and hindlimb length.

### Diet

Most other anoles exhibit similar dietary breadth to that of *A. frenatus*, although ants predominate by number in some species (e.g., Andrews, 1971a; Talbot, 1979; Dalrymple, 1980; Losos et al., 1990; see also references in Schwartz and Henderson, 1991). A number of giant anoles are known to prey on vertebrates (*A. cuvieri*: Rand and Andrews, 1975; Perez-Rivera, 1985; *A. equestris* Merrem: Dalrymple, 1980; *A. garmani* Stejneger: G. C. Mayer, pers. comm.). Although we report no data, it is likely that *A. frenatus* will prey on vertebrates as well. Royce Ballinger (pers. comm.) observed a female *A. frenatus* (*svl* = 110 mm) jump from the base of a large tree trunk, grab a female *A. limifrons* (*svl* = 45 mm) behind the neck, and return to the tree. He also reports that an adult *A. frenatus* (*svl* = 102 mm) ate an *A. lemurinus* Cope (*svl* = 48 mm) contained in the same collecting bag.

### CONCLUSIONS

Although much remains to be learned about the biology of *A. frenatus*, what little is known indicates that it is in some ways similar to the crown-giants of the West Indies, but these similarities probably result solely from the large body size of these species. In terms of microhabitat use and behavior, *A. frenatus* is not particularly similar to the crown-giants, nor to any of the other "ecomorph" types, of the West Indies. The paucity of information on Central American anoles precludes comparison to these species (but see Pounds, 1988). To fully understand and appreciate the radiation of *Anolis* will require considerably more research.

*Acknowledgments.* — The senior author was supported by a Smithsonian Tropical Research Institution Pre-Doctoral Fellowship. The second author was supported by grants from the Smithsonian Tropical Research Institution, Post-Doctoral and Environmental Sciences Programs. We thank A. S. Rand and the staff of the Barro Colorado Island facility for advice and assistance. Professor R. E. Ballinger kindly provided data on prey of *A. frenatus*.

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