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BODY SIZE AND PERCHING BEHAVIOR OF *ANOLIS SABANUS*, THE SOLITARY ANOLE OF SABA, NETHERLANDS ANTILLES

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Abstract. The body size and perching behavior (location, body temperature, posture) are reported for *Anolis sabanus*, the only anole present on Saba, Netherlands Antilles (= solitary species). Snout–vent length (SVL) was at the lower end of the range for other solitary anoles as was sexual dimorphism in SVL. Body shape (characterized by the constant in the equation Mass = $cSVL^{3}$) was similar to that of other *Anolis*. The perching substrate of *A. sabanus* included tree trunks, rocks, branches and twigs, and walls and buildings in direct sun, sun/shade, and deep shade. Mean body temperature was 29.2°C. Injured tails were common in both males and females, with larger animals more likely to have suffered an injury. Perching height was primarily within 2 m of the ground. Males perched higher than females; otherwise, perching sites did not differ by gender. Perching posture was unusual for anoles; most often only the head was raised off the substrate. Otherwise, the body size and shape, perching locations, and body temperature distribution were similar to those of other solitary anoles in the Lesser Antilles.

Key Words: *Anolis*; Perch site; Body size, Saba, Netherlands Antilles.

Anolis lizards have long intrigued ecologists because of their systematic diversity, large geographic distribution, and occurrence in a broad range of habitat types (for reviews see Losos 1994; Roughgarden 1995). The approximately 150 species on the islands of the Caribbean basin exist in three types of communities. On the Greater Antilles six or more species often coexist at a site. The anoles at such sites differ in body size and shape as well as perching location. On the Lesser Antilles, only one or two species are found on each island. On islands with two species, the anoles typically differ substantially in body size; in contrast, *Anolis* species that are solitary on an island have a similar body size that is intermediate to those of *Anolis* on the two-species islands. Solitary *Anolis* on the Lesser Antilles tend toward a maximal body size (snout–vent length = SVL) of ~84 mm for males and ~60 mm for females (Roughgarden 1995; Schoener 1969). SVL tends to be sexually dimorphic with males substantially larger than females (largest male approximately 1.4× the size of the largest female) (Roughgarden 1995).

These trends in perching location and body size and shape can be explained if competition in complex anole assemblages results in partitioning of resources, such that each species becomes a relative specialist in its perching location and evolves a body size suitable for its perching location and diet selection. Williams (1983) proposed that each of the Greater Antilles has witnessed an independent evolution of assemblages of "ecomorphs" that partition resources within a complex forest habitat. A recent phylogenetic analysis (Losos 1992) suggests that among islands, a particular

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ecomorph can have independent evolutionary origins, thus supporting Williams' hypothesis.

The SVL of solitary anoles may represent the ancestral condition for *Anolis* (Losos 1990) which has been retained because solitary anoles have not experienced selection for specialization to reduce competition. The overall natural history of solitary anoles (perching location, diet, times of activity, etc.) might also resemble the ancestral state. Alternatively, solitary anoles may have responded to the absence of competition with congeners by exploiting a broader range of perching locations and microhabitats. Testing these ideas is difficult because habitat structure on the small Lesser Antilles can differ substantially from those in the larger islands. Also, the details of the natural history of only a small proportion of *Anolis* species are known (Lister and Garcia Aguayo 1992).

Here we examine some aspects of the natural history of a poorly known solitary anole, *Anolis sabanus* of the small eastern Caribbean island of Saba. Lazell (1972) noted that the extreme degree of sexual dimorphism in squamation and other characters argue that *A. sabanus* has had a long, independent evolutionary history from other anoles in the Caribbean. We present data on perching location and body size and shape of *A. sabanus*. Because thermoregulatory behavior may be an important corollary to use of perching location (e.g., Hertz 1983), we present data on body temperatures of *A. sabanus*. Although competition is usually regarded as the selective force shaping perching behavior in anoles (above), Lister and Garcia Aguayo (1992) and Scott, et al. (1976) suggest predation can likewise influence microhabitat choice by *Anolis*. Therefore, we also present information on tail injuries as a probable indication of predation pressure.

MATERIALS AND METHODS

Saba is located at 17°42' N latitude in the northeastern Caribbean, 52 km SW of St. Martin. The 13 km^2 island rises 887 m above the sea and the terrain is steep, with few extensive horizontal areas. Lower elevation areas tend to be more xeric; the cooler and wetter valleys and peaks support rain forest and cloud forest. Vegetation varies from scrub forest (trees and shrubs to about 4 m tall) to rain forest/cloud forest. Average monthly temperature varies little (26–28°C), but rainfall is very variable among years, with a wetter season from late August–December ($\bar{x}$ = 125–150 mm of rain per month in the rainy period, and 50–80 mm in the dry season) (Meteorological Service of the Netherlands Antilles data).

We observed and collected *Anolis sabanus* at 50 sites during the dry season (15 May–19 August 1992, July 1993, January 1994, 1995, and 1996). Lizards were collected by hand or noosed, placed into mesh bags and in the evening each lizard was sexed, its SVL taken in nearest mm, and tail condition noted as injured (broken or regenerated) or intact. We weighed a sample of lizards with a Pesola spring scale that had been calibrated against an electronic balance. A drop of blood was taken from a toe clip and used to make a blood smear as part of a study of malarial parasites in the Saban anole (Staats and Schall 1996*a*). All lizards were returned to their point of capture within 24 h.

Perching location and behavior were observed for a sample of adult lizards. The perching substrates were scored as rock wall, tree trunk, free standing rock, ground (combining bare surface or on litter), dead branches or twigs on ground, or wall of building or other structure. Body position of each lizard was noted as horizontal to the ground or vertical (head up or down). The position of the head was scored as either elevated above the substrate or flat against the substrate. For those lizards perching with the head elevated off the substrate, we classed their position as "head only elevated" or "entire forebody elevated with forelegs extended." The lighting condition of the perching site was noted as direct sun, mix of sun and shade, or complete shade (observations were not make on rainy days). Perching height was measured to the nearest cm. Body temperature of a sample of lizards was measured with a Schultheis® rapid reading thermometer, taking precautions during the procedure to touch the lizard while still on the noose only by its toes. Perching location of the lizards sampled for body temperature was not recorded, but we assume the distribution of locations is similar to that measured above.

Mean SVLs are reported for the entire sample and for the largest third of the sample of lizards. A standard way to determine sexual dimorphism in anoles is to examine the ratio of maximum body size for males vs. females (Roughgarden 1995). Body shape is here described as the nonlinear relationship between SVL and mass; we fit the data to the equation of Schoener and Schoener (1978), mass = $cSLV^3$, where c is a species specific constant (only animals with intact tails were used in the analysis). The c value for *Anolis sabanus* is compared to the values of c reported for other species. For all statistical comparisons, nonparametric tests were used; P values are reported for two-tailed tests.

RESULTS

Males were larger than females (Males: $\bar{x}$ = 54.0, *SD* = 6.62, *n* = 1,420; females: $\bar{x}$ = 44.8, *SD* = 4.27, *n* = 666, Mann-Whitney U-test, $P < 0.0001$). The largest third of the sample reveals a similar sexual dimorphism in body size (largest third, males: $\bar{x}$ = 61.0, *SD* = 2.78, *n* = 459; females: $\bar{x}$ = 49.0, *SD* = 1.85, *n* = 228, U-test, $P < 0.0001$). The maximum SVL was 72 mm for males and 55 mm for females; males were thus 1.3× the size of females. Males are more common in the sample because they are larger, more obvious on perches, and were easier to collect. For males, c = 2.5×10^{-5} ($n = 200$); for females, c = 2.3×10^{-5} ($n = 96$).

The majority of perching locations for 371 lizards (Table 1) were on trees or rocks, but in towns and other developed areas lizards were commonly seen on walls and buildings. Few anoles were seen on the ground or on twigs. Males and females perched on similar objects ($\chi^2 = 6.92$, $df = 5$, $P = 0.23$). Most lizards perched close to the ground; 79% of females and 67% of males were found within 1 m of the ground (Fig. 1). Males, though, tended to perch higher than females (U-test, $P < 0.05$); only 1 female was seen > 2 m above the ground, whereas 7% of males perched from 2–4 m high. Lizards were sighted perching equally in shade, partial sun, and full sun (Table 1). No significant difference existed for lighting condition of perches of males and females ($\chi^2 = 0.96$, $df = 2$, $P = 0.62$).

Most *Anolis sabanus* held their heads off the substrate (78% overall), but those with a raised head often did not extend the forelegs in the fully erect position that is common for other anoles on Caribbean islands (Lazell, 1972). Only 20% of the females perching with the head off the substrate stood fully erect under extended forelegs, and 42% of the males held this posture. However, no difference was found for body position (horizontal or vertical) or head position (raised or lowered off the substrate) for males and females ($\chi^2 = 0.01$, $df = 1$, $P = 0.91$; Table 1).

The distribution of body temperatures was not normally distributed (Fig. 2), but is skewed (skew = –0.20) such that the modal temperature lies above the mean of 29.2°C. Means for males (29.2°C; *n* = 128) and females (29.1°C; *n* = 38) did not differ (Mann-Whitney U-test; $P > 0.05$).

Overall, a significantly higher proportion of males had injured tails (broken or regenerated) than females ($\chi^2 = 19.0$, $df = 1$, $P = 0.0001$). Larger animals were more likely to have an injured tail (Fig. 3; χ^2 for females = 33.36, $df = 3$, $P = 0.0001$, for males $\chi^2 = 62.76$, $df = 6$, $P = 0.0001$).

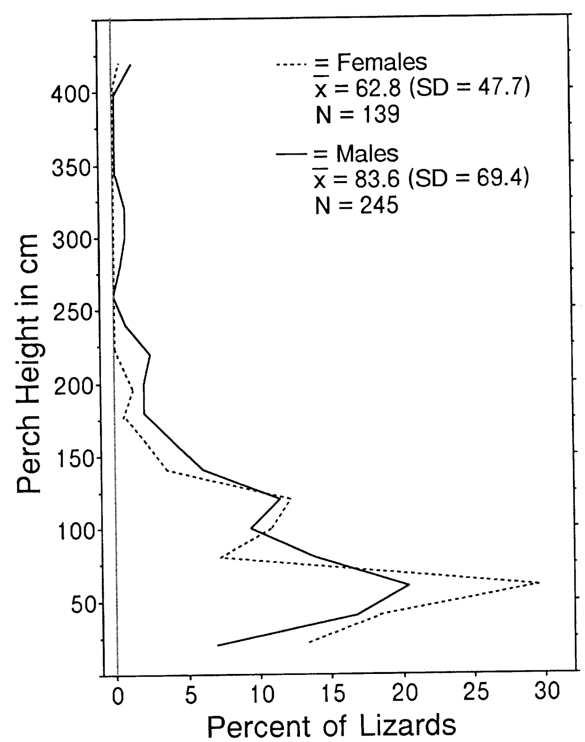

Figure 1. Distribution of perching heights of male and female *Anolis sabanus*.

Table 1. Perching location and behavior for *Anolis sabanus*.

	Males (*n* = 237)	**Females** (*n* = 134)
Rock Wall	0.09	0.13
Tree Trunk	0.41	0.45
Lone Rock	0.29	0.31
Ground	0.03	0.01
Branches/Twigs	0.10	0.07
Buildings	0.08	0.03
Direct sun	0.31	0.27
Sun/shade	0.34	0.33
Shade	0.35	0.40
Horizontal	0.49	0.50
Vertical	0.51	0.50
Head raised	0.80	0.73
Head down	0.20	0.27

The higher proportion of injured tails in males vanishes when body size classes are examined; a gender difference exists only for the 50–54 mm size class for which females have a higher injury proportion (χ^2= 7.23, *df* = 1, *P* = 0.0072). The largest males and females had a high proportion of injuries (38–47%).

DISCUSSION

Previous data on *Anolis sabanus* are scant. Lazell (1972) presented some notes on the natural history of the Saban anole; Dobson et al. (1992) reported on the gut helminth parasites of *A. sabanus*; and Staats and Schall (1996*a,b*) examined the ecology of its malarial parasites. We found that the distribution of body temperatures ($\bar{x}$ and SD) of *A. sabanus* is similar to those of other solitary anoles, such as *A. marmoratus* on Guadaloupe (Huey and Webster 1975), *A. occultatus* on Dominica (Brooks 1968), and *A. roquet* on Martinique (Hertz 1983). *Anolis sabanus* is among the smallest of the solitary anoles, just within the range of other species (Fig. 4). The same is true for the degree of sexual size dimorphism (Fig. 4). This is not surprising because sexual dimorphism in SVL tends to be less pronounced in smaller species (r = 0.61, *n* = 33, *P* < 0.01 for male SVL by male SVL/female SVL (data extracted from Roughgarden 1995).

The body shape of a lizard is characterized in part by the value of c in the Schoener and Schoener (1978) equation; higher values indicate a more stocky body form. For example, c ($\times 10^{-5}$) for *Sceloporus occidentalis* is about 3.5 (genders combined), but lower for *Anolis aeneus* of Grenada (3.0, genders combined; Roughgarden 1995), *A. gundlachi* of Puerto Rico (males = 2.4, *n* = 117; females = 2.6, *n* = 55; Schall, unpubl. data), and *A. gingivinus* (males = 2.4, *n* = 28; Schall, unpubl. data.) The value of 2.5 (males) and 2.3 (females) for *A. sabanus* is thus similar to that for other anoles. We conclude that body size and shape of *A. sabanus* are that of typical solitary anoles.

Although primarily arboreal, *Anolis sabanus* also was commonly seen on rocks. Given the steep topography over most of the island, rocks provide perches with wide views of the area below. The

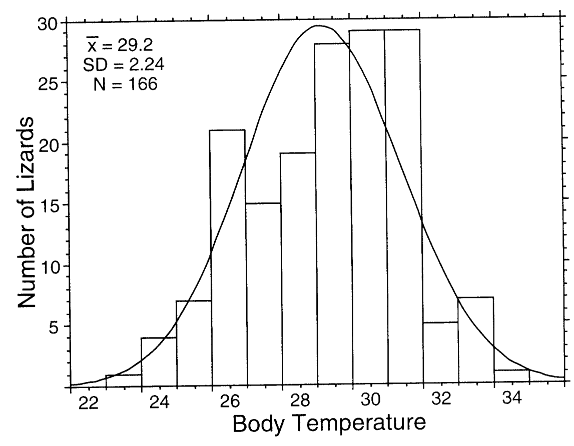

Figure 2. Distribution of body temperatures of *Anolis sabanus*. A normal curve fit to the mean and standard deviation is also shown.

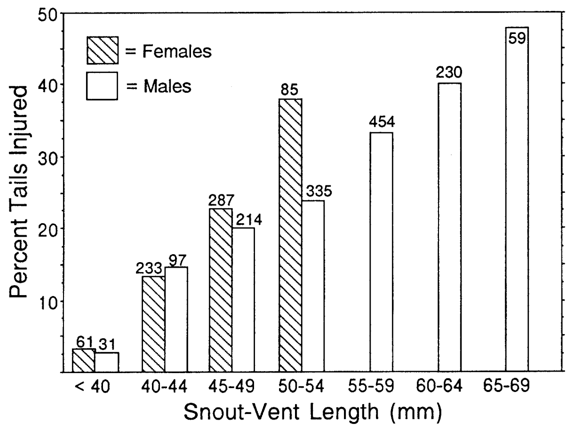

Figure 3. Proportion of tails of *Anolis sabanus* that were injured (broken or regenerated) for different body size classes. Male and female lizards are shown separately.

Saban anole uses more diverse perching substrates than many anoles in the Greater Antilles (Schoener and Schoener, 1971a, 1971b), but direct comparisons are not meaningful because a large rock surface may be functionally identical to that of a large tree at any elevation above the ground and large rocks or walls may be simply absent or rare from some sites in the Greater Antilles.

In complex anole faunas, such as on Puerto Rico and Jamaica, the overall use of perch heights is much broader than on Saba (Schoener and Schoener 1971*a,b*). Perch height of *Anolis sabanus* resembles that of a single species at each of the sites in the Greater Antilles, *A. lineatopus* on Jamaica (Schoener and Schoener 1971*a*) and *A. cristatellus* on Puerto Rico (Schoener and Schoener 1971*b*). Thus, *A. sabanus*, although released from competition with other *Anolis*, does not exploit the entire range of available perching heights. Few *A. sabanus* were seen above 2 m in trees, and few lizards were on the ground surface although potential perching locations > 2 m high were common at some of our study sites. On nearby St. Martin, where two species of *Anolis* coexist, the perch height distribution of *A. gingivinus* at sites where it is the solitary anole is very similar to that of *A. sabanus* (Roughgarden et al. 1983), but *A. gingivinus* does use higher perches at sites where it coexists with *A. pogus* (Roughgarden et al. 1983). This suggests that some factor other than competition or availability of perching sites keeps *A. sabanus* from using higher perches.

The restriction of perching heights might be a result of predation or distribution of food prey. Perhaps predation pressure is more severe on the ground from the common snake, *Alsophis rufiventris*, or in trees higher than 2 m from the very common pearly-eyed thrasher (*Margarops fuscatus*) (Adolph and Roughgarden 1983; Schwartz and Henderson 1991; Voous 1983). We often saw *Alsophis* and thrashers attempting to attack caged *Anolis sabanus*. Losos (1994) discounted the importance of predation in the origin of anole perching location and proposed that the overall ecology of solitary anoles on small

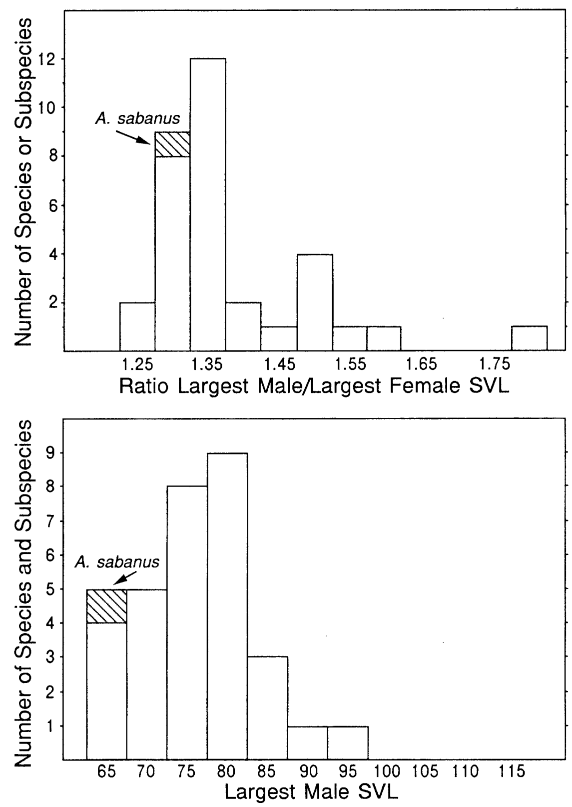

Figure 4. Distribution of body sizes for solitary species and subspecies of *Anolis* on Caribbean islands. Data, excluding those for *A. sabanus*, from Roughgarden (1995). Data are for preserved specimens, so results from sizes of live animals on Saba are corrected for normal shrinkage in preservative fluid (live SVL × 0.91 = size of preserved animal). Top: Distribution of size ratio between males and females. Bottom: Distribution of size of males.

Caribbean islands represents the ancestral state for *Anolis*. This hypothesis suggests that *A. sabanus* has not been pushed by competition with other species to evolve away from this ancestral ecology. Indeed, the high proportion of injured tails in the Saban anole could simply mean that predators are inefficient or intraspecific fights are common (Arnold 1988). Alternatively, the density of arthropod prey may simply be higher in the zone frequented by the Saban anole. Lister and Garcia Aguayo (1992) and Scott et al. (1976) concluded that changing prey density and predation levels influence perch site selection by anoles at two mainland sites.

We found that *Anolis sabanus* tends to keep its body close to the substrate more often than other anoles we have observed in the Caribbean in agreement with Lazell's (1972) observations. In the typical perching posture for *A. sabanus*, only the head and neck are raised above the substrate. Other than its unusual perching posture, the Saban anole is a typical solitary species in body size, sexual dimorphism in body size, and body shape. Its perching location is similar to at least one other Lesser Antillean anole (*A. gingivinus*) when it is the solitary species at a site.

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