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Distribution of Malaria in *Anolis* Lizards of the Luquillo Forest, Puerto Rico: Implications for Host Community Ecology[1]

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ABSTRACT

Five species of *Anolis* lizards of the Luquillo forest, Puerto Rico were surveyed for infection with malarial parasites. Two species of parasite, *Plasmodium floridense* and *P. azurophilum,* commonly infect *Anolis gundlachi. P. azurophilum* also very rarely infects *A. stratulus, A. krugi, A. evermanni,* and *A. cristatellus.* For *A. gundlachi,* males are more often infected, and percent of animals infected increases with body size, but percent infected decreases for the very largest body size class in males. *P. azurophilum* is far more common than *P. floridense,* and the two parasite species appear to associate randomly into mixed infections with no evidence for interspecific competition between malaria species. Infected *A. gundlachi* have a greater prevalence of injured tails. The five anole species differ by body size (three large and two small species) and habitat used (shady cool places vs sunny warmer locations). *A. gundlachi* and *A. evermanni* are the only species that are similar in size that are often found in the same locations. Malarial infection may mediate competition between these two species of lizards.

RESUMEN

Cinco especies de lagartijos del género *Anolis* de la Sierra de Luquillo, Puerto Rico, fueron examinados para detectar infección con malaria. Dos especies de este parásito, *Plasmodium floridense* y *P. azurophilum,* comunmente infectan a *Anolis gundlachi,* mientras que sólo *P. azurophilum* rara vez infecta a *A. stratulus, A. krugi, A. evermanni,* y *A. cristatellus.* Para *A. gundlachi,* donde los machos están infectados con major frecuencia, el porciento de animales infectados aumenta con el tamaño del cuerpo, pero disminuye para la clase con el mayor tamaño de cuerpo en machos. Las dos especies de parásitos parecen asociarse al azar en infecciones mezcladas sin evidencia de competencia interespecífica entre las especies de malaria. Infectados de *A. gundlachi* tienen una major incidencia de colas heridas. Las cinco especies de *Anolis* se diferencian por el tamaño del cuerpo (tres especies grandes y dos pequeñas) y el hábitat donde viven (sitios fríos y con sombra vs sitios soleados y más calientes). *A. gundlachi* y *A. evermanni* son las únicas especies de tamaño similar que son frecuentemente encontradas en los mismos habitáculos. La infección con malaria podría estar mediando la competencia entre estas dos especies de lagartijos.

Key words: Anolis; *infection; malaria; parasitism;* Plasmodium; *Puerto Rico; reptile; tropics.*

Anolis lizards are a common and conspicuous component of the faunas of all terrestrial environments of the Caribbean islands. Their taxonomic and ecological diversity has made them important models in studies on population and community ecology, behavioral biology, and environmental physiology (Stamps 1978, Hertz 1981, Williams 1983, Roughgarden & Pacala 1989, Losos 1992). For example, some of the best examples of resource partitioning and ongoing competition in closely related vertebrates are the studies of Antillean islands with two or more species of *Anolis* (Schoener 1968, Roughgarden *et al.* 1983, Pacala & Roughgarden 1985). Despite long-standing interest in anole biology among ecologists, one important phenomenon remains virtually unexplored—the role of parasites in the natural history of these lizards. This is not surprising because parasite–host ecology remains one of the most poorly developed topics in tropical biology.

Malarial parasites (*Plasmodium* spp.) are widespread in Caribbean anoles, and are known from all the Greater Antilles except Cuba, and many Lesser Antillean islands (Saba, St. Maarten, St. Eustatius, St. Bartelemy, San Andres, St. Lucia, Martinique), but appear absent from dry small islands (Aruba, Bonaire, St. John) (Ayala 1975, Telford 1975, Ayala & Hertz 1981, Guerrero & Pickering 1984, Schall 1992, J. Schall, pers. obs.). Studies over the past decade have demonstrated that malaria can have substantial impact on the biology of lizard hosts in both temperate and tropical environments (reviews in Schall 1990a, b). The parasite initiates a cascade of effects beginning with hematological upset that leads to physiological, reproductive, and behavioral changes in its host.

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Information on the ecological impact of malaria on *Anolis* is scant, but a malarial parasite, *Plasmodium azurophilum,* causes substantial hematological pathology in its host *A. gingivinus* on St. Maarten island (Schall 1992). Also, the parasite appears to influence the distribution of the two-species anole community on the island (Schall 1992). *A. gingivinus* is found throughout the island; whereas, *A. wattsi* occurs in a patchy distribution in the central hills. Malaria is common in *A. gingivinus,* but rare in *A. wattsi.* The parasite also has a spatially patchy distribution on the island and the two species of *Anolis* coexist only where the parasite is present. This suggests that infection reduces the competitive ability of *A. gingivinus* and allows the otherwise competitively inferior *A. wattsi* to persist where the parasite occurs. These facts suggest that malarial infection may well play a previously unsuspected role in the biology of *Anolis,* including the mediation of competition among species. Such parasite-mediated competition is currently of substantial interest for both theoretical and empirical community ecologists (Price *et al.* 1986, 1988; Minchella & Scott 1991; Schall 1992).

We have studied the distribution of malaria in five species of *Anolis* of the Luquillo rain forest of eastern Puerto Rico. Our research was limited to species that perch within 3.5 m of the ground; species of *Anolis* that are restricted to the canopy were excluded from study. Our goals were to identify the species of *Plasmodium* infecting anoles in the Luquillo forest; to determine the specificity of the parasites for different species of *Anolis*; and, to examine differences in body size and habitat use among anole species. The distribution of *Plasmodium* in Puerto Rican *Anolis* has not previously been properly described. The general ecology of the *Anolis* assemblage has been well studied, but there is still some minor controversy concerning the niche relations of the El Verde species. The ultimate purpose of this paper is to highlight systems for future study of possible parasite-mediated competition between species of *Anolis.*

METHODS

Between 16 May and 16 August 1990 and 2 January and 18 January 1991, we surveyed *Anolis* from 12 sites in the vicinity of the Center for Energy and Environmental Research (University of Puerto Rico) El Verde Field Station in the Luquillo Mountains of eastern Puerto Rico. Nine of the sites were within a 1.2 km radius of the field station buildings located 2.2 km southeast of the town of El Verde (elev. range 250–500 m); one was 2.8 km north of the field station (elev. 150 m); one was in the Bisley Drainage study site of the U.S. Forest Service 7.0 km northeast of the station (elev. 150 m); and the last was on El Yunque Mountain (elev. 1000 m). The sites varied from about 0.1 ha to 1.0 ha in area. The habitat is lower montane and montane rain forest as described by Odum and Pigeon (1970) and Weaver and Murphy (1990). We placed each site into one of three types of habitat. In "Closed forest" much of the canopy remained, despite substantial damage to the forest by Hurricane Hugo (September 1989); understory growth was substantial. "Open forest" lacked much canopy and was clearly sunnier and warmer. "Mixed forest" was intermediate in structure.

Anolis were located by slowly searching tree trunks, logs, twigs, branches, rocks, and the ground. Lizards were collected by hand and noosing with a small loop of fishing line on the end of a 1.5 m fishing pole. Thus, we collected perching lizards from ground level to approximately 3.5 m above ground. Attempts to collect lizards were random by species, but some species were more difficult to capture than others. Therefore, collection data give only an approximation of relative abundances. In the evening lizards were identified to species, sexed, snout to vent length (SVL) taken to the nearest mm, and tail condition scored as intact or injured (= broken or regenerated). Blood smears were made from a tiny drop of blood taken from a toe clip. All lizards were returned to their point of capture the next morning.

After microscope slides were dipped in absolute methanol, the slides were stored for one to two months until stained in Giemsa 1:10 at pH 7.1 for 50 minutes. Each slide was scanned at 1000× at least once for six minutes; >10,000 erythrocytes can be examined during a six minute scan. Parasites were identified by reference to original species descriptions (Thompson & Huff 1944, Telford 1975) and the review of Telford (1984).

RESULTS

Five species of *Anolis* occurred in our sample of 2456 lizards; these species varied substantially in body size (Table 1). The species group by size; three are large (*A. gundlachi, A. evermanni,* and *A. cristatellus*), and two are small (*A. stratulus* and *A. krugi*). There was clear separation of species by habitat type (Table 2). *A. gundlachi,* and to a lesser extent *A. evermanni,* were species of closed forest, *A. cristatellus* and *A. krugi* were found in more

TABLE 1. *Snout to vent lengths of five species of* Anolis *lizards from the Luquillo forest. Mann-Whitney tests for all male-female comparisons,* P < *.001, except for* A. krugi *for which* P < *.01.*

	Males			Females		
	$\bar{x}$ (SD)	*N*	Range	$\bar{x}$ (SD)	*N*	Range
A. gundlachi	57.8 (7.8)	1027	32–76	43.0 (3.5)	494	32–51
A. evermanni	58.3 (6.0)	225	37–69	47.2 (4.1)	178	35–56
A. stratulus	44.9 (3.6)	152	30–61	40.3 (2.5)	107	33–50
A. cristatellus	62.6 (7.9)	147	37–77	45.7 (3.6)	69	34–54
A. krugi	45.9 (5.6)	38	34–53	39.0 (2.8)	8	35–44

open and sunny locations. *A. stratulus* was found in all types of habitat. *A. krugi* was seen primarily within one meter of the ground, the others were more arboreal. We frequently found *A. evermanni, A. gundlachi,* and *A. stratulus* in the same microhabitat. The two larger species were often seen perching on the same tree trunk, and *A. gundlachi* was occasionally seen chasing *A. evermanni.*

Two species of malarial parasite infect the anoles of El Verde, *Plasmodium floridense* and *P. azurophilum. P. azurophilum* was detected in all five *Anolis,* but *P. floridense* was restricted to *Anolis gundlachi*. Malaria was common only in *A. gundlachi* (Table 3) and only a single infected animal was found in each of the other species. Percent of *A. gundlachi* infected with malaria differed between males and females and among body size classes (Fig. 1, *G*-tests, *P* < .05). Overall, 26.2 percent of 1017 males and 14.2 percent of 484 females were infected (*G*-tests, *P* < .01).

The percentage of *A. gundlachi* infected did not differ substantially among sites (24–36% infected), except for the most open, sunny, and warm site (Bisley Drainage area) where only 7 percent of 29 lizards were infected (*G*-test, *P* < .05). There was no significant difference in percent of *A. gundlachi* infected by month during the summer dry season (22–28%, *G*-test, *P* > .05), but infections were less common during the January wet season sampling (14%, *G*-test, *P* < .05).

Frequency of injured tails is a measure of attack by conspecifics, other anole species, or predators (Table 4). Both infected male and female *A. gundlachi* were more likely to have an injured tail compared with noninfected lizards, but this was significant only for females (30.2% of infected males had injured tails, 22.8% of noninfected males, *N* = 868, *G*-test, *P* > .05; 29.8% of infected females had injured tails, 18.0% of noninfected females, *N* = 407, *G*-test, *P* < .05).

We identified the species of malarial parasite in infected animals in the first 406 smears from *A. gundlachi* in our collection. Of 77 infections, 70 contained *P. azurophilum* (17.2% of total sample) and 11 contained *P. floridense* (2.7% of total sample); 66 were solitary *P. azurophilum* infections, 7 were solitary *P. floridense* infections, and 4 were mixed infections. If the two malarial species associated randomly among hosts, 1.9 mixed infections would be expected ([.172] [.027] [406] = 1.9).

TABLE 2. *Relative abundance of the anoles in three habitat types estimated from numbers collected. The description of these habitat types is given in Methods.*

	Closed forest	Mixed forest	Open
A. gundlachi	1267	285	0
A. evermanni	328	63	12
A. stratulus	151	59	24
A. cristatellus	2	49	134
A. krugi	8	31	8
Total	1756	487	178

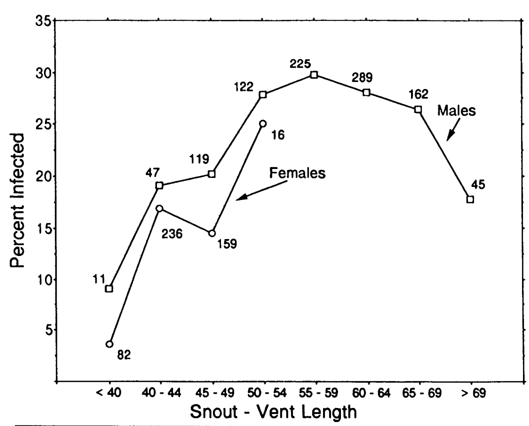

FIGURE 1. Percent of *Anolis gundlachi* infected with the malarial parasites *Plasmodium azurophilum* and *P. floridense* by body size in mm. Numbers next to points are sample sizes.

TABLE 3. *Percent of each species of* Anolis *infected with malaria.*

A. gundlachi	22.1%	(N = 1516)
A. evermanni	0.2%	(N = 386)
A. stratulus	0.4%	(N = 256)
A. cristatellus	0.5%	(N = 216)
A. krugi	2.1%	(N = 47)
Total		2421

This number of expected mixed infections and the number actually seen did not differ significantly (binomial test, P = .103).

TABLE 4. *Tail condition of* A. gundlachi *either infected or not infected with malaria. Also given are sample sizes for each sex and results of* G*-tests comparing infected and noninfected samples.*

	Males % Injured	Females % Injured
Infected	30.2	29.8
Not infected	22.8	18.0
N =	868	407
G =	2.64	3.97
P	>.05	<.05

DISCUSSION

The malarial parasites of El Verde anoles appear to have a strong predilection for only one of the lizard species studied, *Anolis gundlachi*. Infections in the other species were rare. The only previous survey for lizard malaria in Puerto Rico was by Guerrero and Pickering (1984); in a small sample from the El Verde area they found only *A. gundlachi* infected. (Future researchers on malaria in Puerto Rican anoles should be aware that the data in Table 1 of Guerrero and Pickering's note were severely miscast [S. Guerrero, pers. comm.]; the corrected table should be obtained from the authors.)

The origin of the vertebrate host specificity of malaria in Puerto Rican anoles is unknown, and perplexing. The five anoles of El Verde are closely related, all falling into two species series of the cristatellus species group of *Anolis* (Roughgarden & Pacala 1989). *A. gundlachi* is found in the same habitat as three of the other species, suggesting they would all be subject to attack by the biting insects that are the likely vectors of the parasites. The insect hosts of only two lizard malaria species are known: the vectors of *P. mexicanum* in fence lizards of California are two species of psychodid fly, and the vector of *A. floridense* in Florida is most likely a mosquito (Ayala & Lee 1970, Klein *et al.* 1987). These kinds of insects do not seem to be particularly host specific in their blood feeding behavior, at least in the laboratory (J. Schall, pers. obs., J. Anderson, pers. comm.). The apparently random association of *P. floridense* and *P. azurophilum* suggests the two parasites share the same vector(s) and are not interspecifically competitive. The rareness of *P. floridense* (*P. azurophilum* is over six times more common) also presents a puzzle. Perhaps this species of parasite is primarily a lowland form that is at its distributional periphery in the upland rain forest. The primary host of malaria at El Verde, *A. gundlachi,* has a considerable elevational range (Hertz 1981), suggesting a survey for malaria in this species in areas below El Verde would be interesting.

Evidence for any effect of malaria on *A. gundlachi* is scant. The apparent increase in frequency of broken tails in infected animals suggests they may be hindered by the parasite. However, use of tail injury frequencies as a measure of predator attack or intraspecific or interspecific fights is problematic (Schoener 1979, but see Schall & Pianka [1980] who correlate abundance of predators with injury frequencies of a desert-dwelling lizard). Figure 1 shows male anoles are more often infected, the percentage of animals infected increases with body size, and the percentage infected decreases for the very largest size class. This pattern has been seen in other lizard malaria systems (*P. mexicanum* in California fence lizards, *P. azurophilum* in the *Anolis* of St. Maarten island, *P. agamae* in west African *Agama agama,* and *P. colombiense* in *Anolis auratus* of Colombia [Ayala and Spain 1976; Schall 1983a, 1992; J. Schall, pers. obs.]). Body size in lizards may be crudely correlated with age, with older animals having had a longer time to be exposed to the parasite. A drop in percentage infected would occur if lizards are cured of malaria as they age. However, we have never observed a cure in any lizard infected with *Plasmodium,* including free-ranging lizards followed in mark-recapture studies as well as those observed in the laboratory. The other more likely possibility is that infection causes increased mortality in the oldest animals.

Studies on other lizards argue that malaria could be harmful to *A. gundlachi. Plasmodium azurophilum* in *Anolis gingivinus* of St. Maarten causes an increase in immature red blood cells and decreased hemoglobin concentration in the blood when the parasite is found primarily in erythrocytes. In some infections *P. azurophilum* occurs primarily in white blood cells (monocytes and neutrophils), and when in these cells appears to alter production of an enzyme important in their functioning as part of the immune system (Schall 1992). Malaria in *Sceloporus occidentalis* in California reduces reproductive output of females, reduces testis size in males, and alters blood hormonal balance in males (Schall 1983b, K. Dunlap and J. Schall, pers. obs.). Infected males are less active socially than noninfected males, have difficulty in maintaining a territory and having access to females, and show altered ventral color patterns (reviewed in Schall 1990a, b). Physiological consequences of malaria infection, including reduced ability to deliver oxygen to tissues and reduced locomotive stamina, are similar in *Sceloporus* from California and *Agama agama* from west Africa (Schall 1990a).

As only one of the El Verde *Anolis* species, *A. gundlachi*, is commonly infected with malaria, could this have consequences for interspecific interactions among the anoles? Resource partitioning in *Anolis* is driven by differences in body size (= differences in sizes of arthropods eaten) and perching location (Roughgarden & Pacala 1989, Roughgarden 1992). Based on body size and habitat used, only *A. evermanni* is likely to be a competitor of *A. gundlachi*, and it is only interactions between this pair of species that might be influenced by the parasite. *A. stratulus* and *A. krugi* are both much smaller than *A. gundlachi*. In addition, *A. krugi* is rarely found in the same locations as *A. gundlachi*, and *A. stratulus*, although often perching within 4 m of the ground, uses perches with smaller diameters and is primarily a lizard of the canopy (Reagan 1992). The other three species are similar in size, but we found *A. cristatellus* only in more sunny locations, rarely nearby *A. gundlachi*. This is in agreement with Schoener and Schoener (1971) and Huey and Webster (1976).

A. gundlachi and *A. evermanni* in our sample were similar in body length (Table 1), although *A. gundlachi* has a larger head and thus can appear more stocky in build. Other authors declare *A. gundlachi* to be larger than *A. evermanni* (Lister 1981, Reagan 1992), but provide no data on actual measurements. Williams (1983) states *A. gundlachi* is a "stocky" species, but substantially shorter than *A. evermanni* (maximum male length of 72 vs 78 mm). Our sample sizes are quite large (1027 male *A. gundlachi* and 225 male *A. evermanni*), and we conclude that, although *A. gundlachi* may reach larger sizes than *A. evermanni*, they overlap greatly in body length and are likely to eat the same size foods. This is confirmed by the data reported by Lister (1981). We often found the two species in the same locations (Table 2), often perching on the same branches or trunks. In contrast, Williams (1983) regards *A. evermanni* to be primarily a lower crown species and Schoener and Schoener (1971) state the two species use different perch locations. An examination of the raw data in Schoener and Schoener's paper, however, reveals little difference between the two species. Lister (1981), Hertz (1983), and Reagan (1992) also report considerable overlap in perching location of *A. gundlachi* and *A. evermanni*. *A. gundlachi* appears to be an aggressive species, occasionally chasing other species. Such interspecific aggression appears common in many *Anolis* including the larger species found in the Luquillo Mountains (Hess & Losos 1991). Hertz (1981) also noted that *A. gundlachi* and *A. evermanni* differ in their peak time of activity, suggesting these species are potentially strong competitors.

We conclude that malarial infection could play a role in the population biology and behavior of *A. gundlachi*. Also, the parasite might well mediate competition between *A. gundlachi* and *A. evermanni* at locations where the two species coexist. Some of the advantage *A. gundlachi* might have where its population size is large (lower part of the shady forest: Table 2, Reagan [1992]) might be offset by the effects of the parasite. The role of disease in altering the outcome of competition between human populations has been well-established (Crosby 1986), but has seldom been explored in studies of interspecific competition in wildlife populations (reviewed in Price *et al.* 1988 and Schall 1992). Such an effect in the very well-studied populations of anoles in Puerto Rico would be an important and previously unsuspected finding. Thus, future studies on anole community ecology and possible competition between species of *Anolis* should consider the effect of malaria, a common parasite of these lizards.

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