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Malarial Parasites (*Plasmodium*) of *Anolis* Lizards: Biogeography in the Lesser Antilles[1]

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ABSTRACT

Anolis lizards (Iguanidae) were surveyed for malarial parasites on 14 islands in the eastern Lesser Antilles, St. John in the Virgin Islands, and Curaçao and Aruba in the southern Caribbean. Two species of malaria were identified in 4859 lizards sampled from the 17 islands, *Plasmodium floridense* and *P. azurophilum*. There was no relationship between island size, elevation, or rainfall and the presence or absence of malaria. Some of the largest islands had no malaria, some large and small islands had one species, and some, including tiny Saba, had both species of *Plasmodium*. *P. azurophilum* was found throughout the Lesser Antilles from St. Martin to Grenada; *P. floridense* was restricted to the northern islands, not further south than Montserrat. Our results, combined with surveys from other areas of the Caribbean basin, show both species of malaria infect anoles from distantly related taxonomic groups, suggesting that the parasites have had an ancient association with their lizard hosts.

Key words: Anolis; *Antilles; biogeography; Caribbean; lizards; malaria;* Plasmodium.

Approximately 150 species of *Anolis* lizards (Iguanidae) occur in the Caribbean islands. Many, and perhaps all, of the Caribbean *Anolis* populations are exploited by assemblages of helminth and protozoan parasites (Dobson *et al.* 1992, Schall 1992, Schall & Vogt 1993). A common parasite in Caribbean anoles is malaria (*Plasmodium*) which infects the vertebrate host's blood and is transmitted by an insect vector. Vector-borne parasites such as lizard malaria suggest challenging questions in biogeography: How does malaria reach the islands? Is the distribution of malaria explained by the phylogenetic history of the lizards; by the islands' present geographic position, size, topography, or climate; or by strictly random events when the parasite travels from island to island in windblown vectors? Ayala and Hutchings (1974) suggested that blood parasites such as *Plasmodium* could be used as "zoogeographical tracers" to reconstruct the history of island populations of lizards.

We have surveyed the distribution of malarial parasites in anoles of the Lesser Antilles. Combining our results with previous findings on malaria in *Anolis* elsewhere in the Caribbean basin shows that two species of *Plasmodium* infect anoles in the Lesser Antilles: *P. floridense* and *P. azurophilum* (Telford 1974, Ayala & Hertz 1981, Schall 1992). Our goal was to understand the relative importance of island location, size, topographic relief, and rainfall in determining the presence of lizard malaria and the number of species of *Plasmodium* infecting the lizards on each island. Once ecological effects are partitioned out (island area, relief, rainfall), we can determine if patterns in malaria distribution mirror the phylogenetic relationships of the anoles.

METHODS

We surveyed 14 islands in the eastern Lesser Antilles. Also sampled were St. John, Virgin Islands, on the greater Puerto Rico Bank, and two islands off the coast of Venezuela (Curaçao and Aruba). We scanned the literature for records of lizard malaria from the Caribbean and found results for several of the Greater Antilles (Puerto Rico, Jamaica, and the Dominican Republic) and another small island (San Andrés) in the western Caribbean (Ayala 1975, Telford 1975, Ayala & Hertz 1981, Telford *et al.* 1989).

We visited islands for one to six days typically and collected lizards at several sites on each island (Table 1). Collecting sites were chosen where lizards were common and the habitat was well-vegetated and moist, qualities that our previous experience indicated are more likely to be suitable for the parasite. Island area, highest elevation, and annual rainfall were obtained from numerous literature citations and maps. Lizards were captured by noose or hand, a toe was clipped to obtain a drop of blood, and a blood smear made for later staining. The smears were stained with Giemsa using standard techniques (Schall & Bromwich 1994). Blood

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TABLE 1. *Islands sampled for malaria in* Anolis *lizards. Malaria species are* P. floridense *(Fl) and* P. azurophilum *(Az).*

Island	Area (km^2)	Elevation (m)	Rainfall (mm)	*Anolis* species	Sample size	Number of sites sampled	*Plasmodium* species
St. John	41	389	1016	*cristatellus*	13	5	—
Anquilla	90	65	914	*gingivinus*	97	4	Fl
St. Martin	89	392	1143	*gingivinus*	828	17	Az & Fl
				wattsi	206	10	Az
St. Barthélémy	21	300	No data	*gingivinus*	133	5	Fl
Saba	13	860	1066	*sabanus*	2271	50	Az & Fl
St. Eustatius	20	600	1067	*bimaculatus*	78	6	—
				wattsi	48	4	—
St. Kitts	174	1156	1267	*bimaculatus*	290	5	Az & Fl
				wattsi	16	5	—
Antigua	280	402	1143	*bimaculatus*	8	4	—
				wattsi	22	4	—
Montserrat	100	914	1575	*lividus*	63	3	Fl
Dominica	781	1147	1981	*oculatus*	260	8	Az
Martinique	1100	1397	2118	*roquet*	161	6	Az
St. Lucia	609	959	1829	*luciae*	119	3	—
St. Vincent	348	1231	2311	*trinitatis*	79	4	Az
Barbados	430	340	1290	*extremus*	28	2	—
Grenada	344	840	1775	*richardi*	20	3	Az
				aeneus	26	3	Az
Curaçao	448	372	520	*lineatus*	15	2	—
Aruba	184	189	423	*lineatus*	83	3	—

smears were examined under 1000× for a minimum of six minutes, sufficient time to examine at least 10,000 blood cells. Presence or absence of malaria was noted. The blood smears from islands apparently free of lizard malaria were reexamined for false negatives. Infected smears were examined for up to one hour to determine the species of *Plasmodium* present. The literature on the systematics of *Plasmodium* of lizards is marred by a lack of consistency in identifying blood cell types infected, and by the questionable biological significance of some morphological traits used to identify species. Molecular techniques will eventually allow clear definition of taxa in *Plasmodium*; for this report we use morphological traits of lizard malaria species (Telford 1974, 1975, 1984, Ayala & Hertz 1981). These characteristics allow ready discrimination between the two taxa in the eastern Caribbean, now named *P. azurophilum* and *P. floridense.*

RESULTS

We sampled 4859 anoles from 17 islands; *P. floridense* was found on six islands and *P. azurophilum* on seven (Table 1; Fig. 1). Sample size varied greatly among islands and could well bias the likelihood of observing malaria on islands where it occurs. This problem would be particularly acute for any islands where the parasite is rare. Malaria prevalence in the anoles among islands ranged from about 10 percent to 40 percent of lizards infected. Grouping islands by number of detected malaria species showed a significant difference in sample sizes for islands with 0, 1, or 2 species (Kruskal-Wallis test, $P < 0.05$). For example, the three islands with largest samples had two species of *Plasmodium* detected, and the four islands with smallest samples had no detected malaria. This result, though, is questionable because we collected most heavily on the three islands with both malaria species (St. Christopher, Saba, St. Martin), because preliminary sampling showed the presence of malaria in the anoles. For example, in the first survey on Saba, only 43 lizards were collected, but two species of *Plasmodium* were detected. Two samples were taken on St. Christopher, approximately two years apart, that differed in sample size. There was no difference in percent of *A. bimaculatus* on that island that were infected in the two samples (20% of 79 vs. 14% of 211, *G*-test, $P > 0.05$). The habitat quality measures (island area, maximum elevation, and rainfall) were not correlated with sample size (Spearman correlations, $P > 0.05$); this indicates that there would be little bias in our analysis of these measures and presence or absence

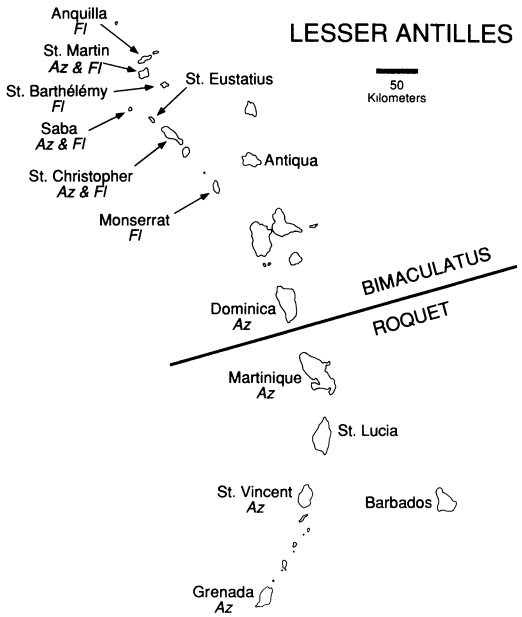

FIGURE 1. Distribution of malaria in *Anolis* lizards of the Lesser Antilles. Islands surveyed in this study are indicated with names, presence of malaria is shown with abbreviation of species names (Az = *Plasmodium azurophilum* and Fl = *P. floridense*). Islands where malaria was not detected are indicated with the island name only. Distributional limit of the Bimaculatus and Roquet groups of anoles is shown.

of malaria. Therefore, any conclusions drawn from islands with small samples can only be considered preliminary, but broad trends observed are more robust.

There was no relationship between island size, elevation or annual rainfall and the presence or absence of *P. floridense, P. azurophilum,* or any malaria (*i.e.,* either species). Wald-Wolfowitz runs tests were used for island size and elevation ($P > 0.05$). Rainfall varies greatly at different sites on the larger islands, so islands were cast into two groups (914–1290 vs. 1575–2311 mm/yr) and Fisher Exact tests applied ($P > 0.05$). In all of these analyses, Bonaire and Aruba were excluded because they are outliers geographically. Malaria was not more or less likely to occur on the large, high, wet islands than the lower, dry, and small islands. Some of the largest islands we surveyed had no malaria (St. Lucia, Antigua, Barbados, and Curaçao, although sample size was large only for St. Lucia); whereas, anoles on Saba, the smallest island, were infected by both *P. azurophilum* and *P. floridense.*

P. azurophilum was found on islands throughout the Lesser Antilles from St. Martin to Grenada; *P. floridense* was restricted to the northern part of the archipelago, reaching no further south than Montserrat (Fig. 1).

DISCUSSION

Lizard malaria is widespread throughout the Caribbean region. *P. azurophilum* was previously known from Martinique (Ayala & Hertz 1981) and St. Martin (Schall 1992) in the eastern Caribbean, and Puerto Rico (Schall & Vogt 1993), Hispaniola, and Jamaica (Telford 1975) in the Greater Antilles. *P. floridense* was known to have an even wider range, from Panama and Florida on the mainland (Telford 1974, 1984), North Bimini in the Bahamas, and Grand Cayman in the northwestern Caribbean, San Andrés in the Central Caribbean, and Jamaica, Hispaniola, and Puerto Rico in the Greater Antilles (Ayala & Hertz 1981, Schall & Vogt 1993). We extend the known distribution of these parasites to many islands of the Lesser Antilles. In the Lesser Antilles, *P. floridense* is restricted to islands in the north; whereas, *P. azurophilum* occurs throughout the islands.

What determines the distribution of lizard malaria in the Lesser Antilles? The distribution could not be explained by ecological factors that intuitively seemed likely to influence a vector-borne parasite (island topography, rainfall, and size). Thus, long-term historical factors apparently have influenced the distribution of the two *Plasmodium* species more than the continuing influence of habitat quality.

Malaria could have moved to new islands either in infected vectors as they were blown about in storms or prevailing wind currents, or in the lizards as they either dispersed over water (Lazell 1972) or via vicariance followed by dispersal and speciation (Roughgarden 1990). In the first case, the presence of malaria on an island could be relatively recent, and the time of establishment could have varied greatly among islands. In the second case, the anole-malaria associations would be very ancient and were established at the very origin of each species of *Anolis* on the islands.

Parasitological lore argues that malaria is more likely to disperse in its vertebrate host. Very few individuals in a population of malaria vectors are infected, typically far less than 1 percent, and the likelihood of an infected insect living long enough to take another blood meal once it arrives on an island is very low (Lehane 1991, Fialho & Schall 1995). In contrast, 10–50% of anoles in a malarious

region can be infected (Schall 1992, Schall & Vogt 1993) and an infected lizard may live for months or years and readily carry malaria to a new island. Up to half of the lizards moving between islands could be infected with the parasite. Also, malarial parasites of humans and lizards show that presence or absence of the parasite, and even particular strains within a species of *Plasmodium,* often have a patchy distribution. Even nearby sites can differ in presence of the parasite or a strain (Forsyth *et al.* 1989, Schall & Marghoob 1995). This suggests that the apparently mobile vectors seldom move malarial parasites between sites. At least five species of lizard malaria occur on Hispaniola, making the malaria fauna there more diverse than nearby Puerto Rico (where two species infect lizards). Telford *et al.* (1989) suggest that the greater taxonomic diversity of anoles on Hispaniola accounts for the larger number of lizard malaria species there, including some plasmodia that are very similar to species in Panama. Again this argues for dispersal of the parasites in their vertebrate host.

We were surprised that no malaria was detected on St. Lucia despite *P. azurophilum* being found on both Martinique to the north and St. Vincent to the south. Also, no malaria was found in *A. bimaculatus* on St. Eustatius despite both parasite species occurring in *A. bimaculatus* on St. Christopher which was connected to St. Eustatius only approximately 15,000 years ago (Roughgarden & Pacala 1989). It is possible that St. Lucia and St. Eustatius are false negatives, especially if the parasite's prevalence is very low. Sample size, though, for these islands was substantial (120 and 119). Windblown vectors, if they are carrying the parasite between islands, should have reached both St. Lucia and St. Eustatius. The endemic anole of St. Lucia, *A. luciae,* is most closely related to *A. bonairensis* on Bonaire island just off the Venezuelan coast (Lazell 1972, Roughgarden 1990). Roughgarden (1990) proposed that St. Lucia and Bonaire originated in the western Caribbean and traveled to their present position; therefore, *A. luciae* arrived in the eastern Caribbean by vicariance and this might explain the absence of malaria on the island. Lazell (1972) presents a more accepted view, that *A. luciae* and *A. bonairensis* arrived on their islands by dispersal. It is likely that malaria once existed on St. Eustatius, no matter how it arrived there, and has since either become extinct or has a patchy distribution that was not sampled during our visit to the island.

This model of dispersal of malaria in its lizard hosts becomes strained when the distribution of *P. floridense* and *P. azurophilum* are compared with the phylogeny of Caribbean anoles. The phylogenetic history of the enormous radiation of anolines has drawn contentious discussion (Guyer & Savage 1986, Cannatella & de Queiroz 1989, Williams 1989). Relationships of the major groups in the eastern Antilles, however, are relatively clear and uncontested. *Anolis* of the Bimaculatus group inhabit islands from Dominica north, while the Roquet group includes lizards south of Dominica. The Bimaculatus group is likely to be of Greater Antillean origin, and is a sister group to the Cristatellus group of Puerto Rico (Lazell 1972). The Roquet group had an independent origin in South America (Gorman & Atkins 1969), and species on most islands in the southern Caribbean are members of that group (the *Anolis* of Curacao and Aruba are placed in another taxon).

P. floridense has been found in the Bimaculatus group in the Lesser Antilles and sister groups in the Greater Antilles. This parasite could be an ancient malarial species that traveled from Central America with the ancestral stock of anoles into the Greater Antilles and then dispersed with the anoles onto the eastern islands. *P. azurophilum* appears to have had a South American origin. This malarial parasite infects both erythrocytes and several classes of white blood cells (Telford 1975, Schall 1992). Other similar plasmodia exist in some South American iguanid lizards (Lainson *et al.* 1974, 1975). Thus, *P. azurophilum* could have been brought into the Caribbean in the ancestor of the Roquet group. *P. azurophilum,* though, is also found in the northern Lesser Antilles in the Bimaculatus group as well as lizards in several other Caribbean species groups (Cristatellus, for example). Such a distribution could be explained if *P. azurophilum* is an even more ancient parasite of *Anolis* than *P. floridense,* having existed in the ancestor of all the Caribbean anoline lizards; but, if so, its apparent absence from Central America and St. Lucia is perplexing.

In summary, the known distribution of lizard malaria in the Caribbean does not strongly support either the vector-transported or lizard-dispersed models. A more clear picture should emerge from a study of the systematics of *P. azurophilum.* If *P. azurophilum* is an ancient species that arrived in the *Anolis* of the Lesser Antilles in phylogenetically distinct ancestors from both the north and south (Bimaculatus and Roquet groups), this would suggest that the parasite should be distinct on islands from Dominica and north and on islands from Martinique and to the south. The taxon described as *P. azurophilum* could actually be several species with a

complex and long history. Morphological traits may be unreliable to distinguish species of *Plasmodium,* so molecular data are required to determine the relationships of the parasites in the Caribbean. Molecular data for the parasites could then be compared with phylogenies for anoles to determine congruence of the two data sets. The results would cast new light on the evolutionary history of malaria in its lizard hosts as was achieved for crocodilians and their helminth parasites by Brooks (1980).

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