Parasite-mediated competition in *Anolis* lizards

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Summary. On many small Caribbean islands, two species of *Anolis* lizard coexist, but the two are typically very different in body size. The two *Anolis* of St. Maarten, however, are exceptional because they are similar in size and are known to be strongly competitive. One species, *A. gingivinus*, appears the stronger competitor and occurs throughout the island; the other, *A. wattsi*, is found only in the central hills. The malarial parasite *Plasmodium azurophilum* very rarely infects *A. wattsi*, but in some locations is very common in *A. gingivinus*. Wherever malaria infects *A. gingivinus*, *A. wattsi* is present, but wherever malaria is absent, only *A. gingivinus* occurs. This pattern of coincidence of malaria and coexistence of both *Anolis* is observed over distances of only a few hundred meters. The parasite infects both red and white blood cells of *A. gingivinus* and causes important pathology: immature erythrocytes increase in abundance, blood hemoglobin decreases, monocytes and neutrophils increase, and infected white cells are less likely to produce acid phosphatase. These results argue that malaria mediates competition between the two species and determines the present distribution of the lizards on St. Maarten. This kind of parasite-mediated competition could be common if susceptibility to parasitic infection varies among competitors. The distribution of malaria in the *Anolis* of Caribbean islands suggests this parasite can play an important role in *Anolis* community ecology.

Key words: Parasite – Competition – Malaria – *Anolis* – Lizards – Caribbean

In the 1940's Thomas Park and his associates conducted a series of laboratory experiments on the competitive interactions between two species of *Tribolium* beetles (Park 1948). These studies were influential at the time in helping ecologists imagine how interspecific competition might function in nature, and they are still widely discussed in general ecology textbooks as model experiments on competition (for example, Pianka 1988). However, an important and intriguing outcome of Park's work was almost ignored by ecologists for many years: He found that a protozoan parasite (*Adelina tribolii*) could alter competitive relations between the two species of *Tribolium*. In some environmental conditions, the competitively superior beetle was prone to infection by *Adelina*, allowing the competitively inferior species to survive or even dominate in mixed-species experiments.

Such parasite-mediated competition has recently provoked considerable renewed interest. Several synthetic reviews have been produced (Freeland 1983; Price et al. 1986; Price et al. 1988), as well as some new theoretical treatments (Holt 1984; Holt and Pickering 1985; Price et al. 1988; Minchella and Scott 1991). The idea has considerable intuitive appeal because parasites are enormously diverse (perhaps half of all animal species are parasites [Dogiel 1966]), and they often cause at least moderate harm to their hosts. It is easy to visualize how an introduced pathogen could cause epidemic disease in only one or a few host species, causing their local extinction, and reducing the complexity of the community. In some cases the pathogen could be brought into a community by an invading species that acts as an unharmed reservoir host. This is the theme introduced by Haldane (1949) when he argued, "A non-specific parasite to which partial immunity has been acquired, is a powerful competitive weapon." Price more recently suggested that this "natural biological warfare" may play a major role in determining the outcome of migrations into new habitats (Price 1980). A tragic example of natural biological warfare was the near extermination of indigenous human populations over vast regions by epidemics of disease brought by European colonists (Crosby 1986).

Park's experiments, though, suggest an alternative situation in which parasite-mediated competition might increase the diversity of species that coexist in a biological community when normally competitively superior species are hindered by infection. This would occur when the competitive ability or carrying capacity of the dominant species is reduced, perhaps even slightly, to allow the coexistence of other species. The image of a pathogen mediating competition recalls the influence of the predacious starfish *Pisaster* on the community structure of

sessile animal species (Paine 1977) and of parasitoid flies on competitive interactions between ant species (Feener 1981).

Despite the plausibility of this reasoning, documented examples of parasite-mediated competition are surprisingly few. Two points are clear from a perusal of the examples presented in reviews on the subject (cited above). First, many of the most often discussed examples are based on few data or are simply interesting speculation (for example, Barbehenn 1969; Wheatley 1980). Second, most of the published cases of parasite-mediated competition describe epidemic disease with severe, and obvious, consequences for the infected hosts, and in which the pathogen eliminates one or more host species (for example, bird malaria and the native Hawaiian land birds; van Riper et al. 1986). Thus, parasites are viewed as reducing potential biological diversity within the host's trophic level. Only a very few published examples argue parasites may allow coexistence of competitors and consequently increase biological diversity (Barbehenn 1969; Price 1980; Ayling 1981).

Why are examples of parasite-mediated competition so uncommon? Perhaps the elimination of species by pathogens, although spectacular when it occurs, is rare. The more typical situation may be parasites with subtle effects on their hosts, that is, low to moderate virulence (Dogiel 1964). These parasites could alter the outcome of competition among host species by reducing their host's carrying capacities or competitive abilities.

I present here a new case of parasite-mediated competition in which a malarial parasite appears to allow the coexistence of two species of Anolis lizards on the Caribbean island of St. Maarten. Anolis are small, predominantly arboreal lizards that are often extremely abundant on Caribbean islands. A large literature on Caribbean Anolis has built a strong case for the importance of interspecific competition in anole 'biology (Roughgarden et al. 1983). Thus, mediation of competition in these Anolis is not a trivial special case in ecology because anoles have served as important models in studies on competition and resource partitioning (Schoener 1968). Most studies on parasite alteration of interspecific interactions center on epidemic disease with lethal effects on the host. The example pursued here may be closer to the rule in such situations; that is, the parasite is endemic in its host population, has moderate impact on its host, but seems to influence the outcome of competition between the two species of Anolis.

Caribbean Anolis

Each of the Greater Antilles supports a complex fauna of Anolis species; at a single site as many as six species may coexist (Williams 1983). These assemblages provide one of the classic examples of supposed resource partitioning to reduce the intensity of competition: the species vary in their normal perching and foraging location as well as size. Size is important because head dimensions are correlated with the size of insect prey consumed. Each island of the Lesser Antilles supports either one or two Anolis species (excluding very recent introductions) (Roughgarden et al.

1983). These islands range in size from 1 to 1500 km^2, but island area is not related to number of species of anole. Many of the islands are very similar in climate, habitat structure, and vegetation (pers. obser.). The Anolis of single-species islands are all of about the same body size, suggesting there is an optimal size for solitary species (Roughgarden et al. 1983; Schoener 1969). On islands with two anoles, however, body size of the two species is usually very different (Fig. 1). These results suggest that when two anoles coexist on a small island, they must be substantially different in body size and thus eat different foods.

On St. Maarten in the northeastern Caribbean, however, two coexisting Anolis species are much more similar in body size than typically seen (Fig. 1). Roughgarden and his colleagues (Roughgarden et al. 1984) have demonstrated that there is ongoing competition between the St. Maarten anoles. Perch height, growth rates, reproductive output, and prey taken are influenced by the presence of the other species. Indeed, these studies have provided some of the best evidence that competition is a real, present force in nature (Pacala and Roughgarden 1985).

The distributions of the St. Maarten Anolis are peculiar (Fig. 2). The larger species, Anolis gingivinus, is distributed throughout the island in almost every habitat, whereas the smaller species, A. wattsi, is found only in a patchy distribution in the wooded hills in the island's center. The hills tend to be more vegetated and more mesic, but the restricted range of A. wattsi cannot be a result simply of its inability to exist in drier habitats. On other nearby islands (for example St. Eustatius where it coexists with the much larger A. bimaculatus) I have found A. wattsi throughout the island in a broad range of habitats, including dry scrubby zones. Also, in experimental manipulations, A. wattsi can survive and reproduce in the lower, drier habitats of St. Maarten provided A. gingivinus has been removed (Roughgarden et al. 1984).

Anolis gingivinus appears to be the competitively superior species and seems to have eliminated the competitively inferior A. wattsi from lower elevations. But why do
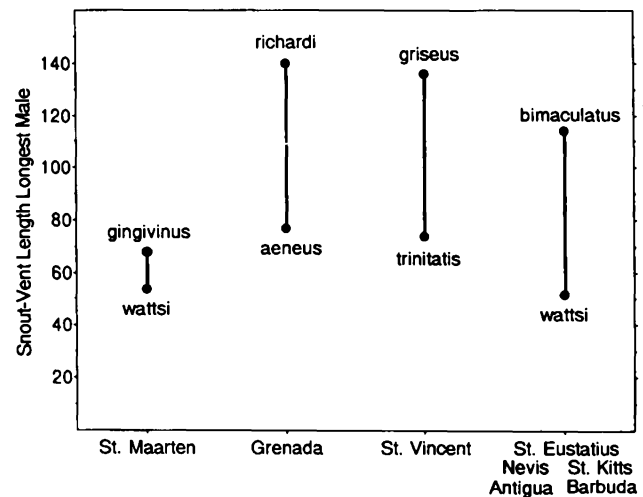

Fig. 1. Body size, given as maximum snout to vent length, for largest male lizards of each species from Caribbean islands with two anole species. Data for St. Maarten and St. Eustatius from author's unpublished data, and other data from Lazell (1972)

the two species coexist in higher elevations? Habitat quality cannot be the determining factor, because there are wetter locations where *A. gingivinus* exists alone, sometimes only a few hundred meters from places where *A. wattsi* is very abundant (below). Perhaps elimination of *A. wattsi* is in progress, driven by coevolution of the two species (Roughgarden and Pacala 1989). I propose another interpretation, that a malarial parasite mediates competition between the two anoles on St. Maarten and explains the present distributions of the two anoles on St. Maarten.

Methods

Anolis were collected from 17 sites scattered throughout the island of St. Maarten (Fig. 2) during four periods: March 1987, July 1988, January 1989, and January 1990. These periods included both wet and dry seasons on the island. One series of sites (Sites 2–8) was a 1.7 km transect from locations where *A. wattsi* was common to where it was absent. Because a long-term population study of anoles on St. Maarten is in progress (Roughgarden, pers. comm.), I carefully chose sites to avoid disturbance of locations used in those studies.

Determined for each lizard were: species, snout to vent length in mm, sex, and tail condition (intact or injured – broken or regenerated). A blood smear was made from a tiny drop of blood taken from a toe clip. Animals were returned to the point of capture usually within 12 h. Smears were fixed in absolute methanol, stained with Giemsa, and later viewed to detect blood parasites. Identification of parasites was made by reference to original species descriptions and the review of Telford (1984).

Four hematological measures were compared for malaria infected and noninfected lizards. Percent immature erythrocytes was determined by counting 1000 red blood cells on the smears and noting immature cells by their characteristic color and nuclear size (Schall 1990a). Hemoglobin content of the blood was determined by taking blood from the postorbital sinus, mixing with cyanmethemoglobin reagent, and reading absorbance at 540 nm (done within six hours of capture) (Schall 1986). The ratio of red to white blood cell classes was determined by counting the number of monocytes and neutrophils compared to a count of 1000 erythrocytes on the blood smears. Acid phosphatase presence in monocytes and neutrophils was visualized as dye deposits after cells on a fresh smear were treated with naphthol
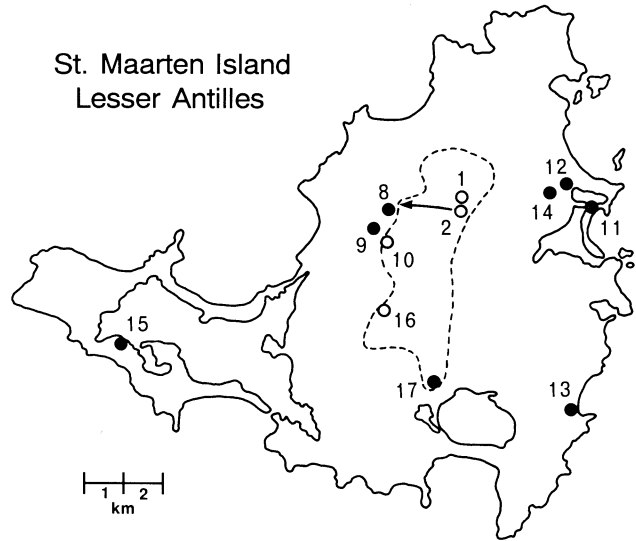

Fig. 2. Caribbean island of St. Maarten, showing collection sites. *Anolis gingivinus* is found throughout the island, but *A. wattsi* occurs only in the central hills approximately indicated by the dashed line. *Arrow* indicates a 1.7 km transect down from a wooded hill. Open points show sites where malaria is present in lizards, closed where malaria is absent. Site numbers match those in Table 1

AS-BI phosphate and fast garnet GBC salt, a diaszo compound (Goldberg and Barka 1962).

Results

The location of 17 study sites is shown on Fig. 2 and data given in Table 1. Both anole species were infected with the malarial parasite *Plasmodium azurophilum*, a common parasite of *Anolis* on Caribbean islands (Telford 1975; Schall, unpubl. data for many islands). *A. wattsi* was only

Table 1. Sample sites on St. Maarten island as shown in Fig. 2. Percentage of lizards infected with malaria and sample sizes are shown. Relative abundance of *A. wattsi* also given. Data for four sampling periods, in both wet and dry season, are combined

Site	Site Location	Elevation	*Anolis gingivinus*	*Anolis wattsi*	
1	Pic du Paradis	414	44% (124)	4% (68)	Very common
2	South Peak	370	37% (155)	1% (79)	Very common
3	Peak Road	340	40% (25)	13% (15)	Very common
4	"	300	46% (52)	0% (12)	Very common
5	"	200	30% (40)	0% (7)	Very common
6	"	140	32% (25)	–	Common
7	"	120	23% (35)	0% (3)	Rare
8	Ponderosa	100	5% (79)	–	None seen
9	Colombier	45	0% (58)	–	None seen
10	Colombier Hills	80	30% (47)	0% (17)	Very common
11	Le Galion	5	0% (17)	–	None seen
12	Orient Beach Woods	10	0% (13)	–	None seen
13	Guana Bay Woods	10	0% (26)	–	None seen
14	Jones Gut	20	0% (31)	–	None seen
15	Simpson Baai	10	0% (40)	–	None seen
16	Marigot Hill East	315	31% (35)	0% (3)	Very common
17	Mary's Fancy	150	0% (26)	0% (2)	Rare
	Totals		25% (828)	3% (206)	

rarely parasitized with malaria; overall only 3% of adults were infected ($N = 206$). These rare infections were always weak, often barely detectable in scanning many thousands of cells. In contrast, *A. gingivinus* was frequently infected (overall 25%, $N = 828$), and infections were often severe, with high parasitemia. Malarial infections were more common in higher elevations (Spearman correlations for percent infected by elevation were 0.85 for *A. gingivinus* [$P < .01$] and 0.78 for *A. wattsi* [$P > .05$]), suggesting the insect vector is more common in higher elevations.

There was a strong association between presence of the parasite and coexistence of the two species of *Anolis* (Table 1, Fig. 2). At every site where *A. gingivinus* occurred alone, malaria was either absent in the species or very rare. At every site (except Site 17 discussed below) where the two species of lizards coexisted, malaria was present in *A. gingivinus*. Where it occurred, the abundance of *A. wattsi* varied from very rare to extremely abundant; the more common malaria was in *A. gingivinus*, the more abundant was *A. wattsi* (Table 1). For those sites where I collected *A. wattsi*, the number collected can serve as a crude index of the abundance of this species; Spearman correlation between number of *A. wattsi* collected and percent of *A. gingivinus* infected was significant (0.84, $P < .01$).

Two examples will illustrate this trend. First, two sites near the town of Colombier (Sites 9 and 10) are within a few hundred meters and are very similar in habitat structure. At site 9 *A. wattsi* was absent and the abundant *A. gingivinus* was not infected with malaria. At nearby Site 10 *A. wattsi* was extremely abundant, *A. gingivinus* was less common than at Site 9, and it was frequently infected with *Plasmodium azurophilum*. Second, a transect from Site 2 to Site 8 is shown by an arrow on Fig. 2. At sites 2–6 *A. wattsi* was very abundant and *A. gingivinus* was often attacked by malaria (approximately 40% of lizards were infected), lower on the hill at Site 7 malaria was less common and *A. wattsi* was also uncommon, and lower still at Site 8 malaria was rare and *A. wattsi* was either absent or very rare.

Site 17 is the only location where I found both species of anoles, but no malaria in either. This was a severely disturbed site where the woods were being destroyed to build new houses in a residential area. *A. wattsi* was rare here, but *A. gingivinus* was common. Most likely this was a site in transition and *A. wattsi* was being eliminated.

Plasmodium azurophilum is an unusual malarial parasite because it infects both red and white blood cells (most plasmodia infect only erythrocytes) (Telford 1975). In 24 of 31 infections (77%) studied from *A. gingivinus* on St. Maarten, the parasite was seen only in either erythrocytes or two types of white cells, monocytes and neutrophils (terminology from Sypek and Borysenko 1988). The relatively few infections in which both red and white cell classes were infected may have represented cases when the parasite was moving from one cell class to the other, but confirmation of the course of infection of *P. azurophilum* requires further study. However, these results indicated the parasite may have two kinds of costs to the host, depending on which cell class is infected. Table 2 confirms this; infections in red cells result in anemia (production of immature red cells to replace lost erythrocytes) and re-

duced hemoglobin concentration. As expected from these results, percent of immature erythrocytes and hemoglobin concentration are negatively correlated (ARCSIN transformed percentages, $r = -0.72$, $P < .01$).

The relationship between *P. azurophilum* and the lizard's white blood cells is intriguing. Infected animals seem to produce more of the white cell classes exploited by the parasite than noninfected lizards (Table 2), and the abundance of white cells increases as the parasite population grows (parasitemia vs. RBC/WBC, Spearman correlation $= -0.54$, $P < .001$). Perhaps the parasite first enters erythrocytes, then manipulates the host to produce abundant white cells which may provide the later habitat for the parasite. I have not seen an increase in white blood cells in other lizard malaria species I have studied (*P. mexicanum, P. agamae, P. giganteum, P. floridense*; Schall, 1990a and unpublished). In any case, the parasite appears to alter the function of infected white cells because production of acid phosphatase, an important product of healthy white cells, is reduced (Table 3). This may indicate that when these cells are infected with malaria, they no longer fully function as elements of the lizard's immune response and cannot respond to infection with other pathogens.

Two weak lines of evidence suggest infected *A. gingivinus* may suffer increased mortality. Figure 3 shows the relationship between body size (a rough indication of age) and the percent of *A. gingivinus* infected. As might be

Table 2. Effects of *Plasmodium azurophilum* on the lizard *Anolis gingivinus*. The parasite can enter either red or white blood cells. Comparison is made between uninfected lizards, lizards having only white blood cells infected, and lizards having only erythrocytes infected. Compared are percent of immature erythrocytes, hemoglobin concentration in g/dl, and ratio of red to white cells on a blood smear. Means given followed by SD in parentheses and sample sizes. P value for Kruskal-Wallis test also presented. Results indicate the parasite has different effects on the host depending on which cell class is infected

	Not Infected	WBC Infected	RBC Infected	P
% iRBC	2.2 (1.27) 17	2.8 (2.82) 31	5.9 (5.87) 31	.011
[Hb]	6.66 (1.02) 53	6.24 (0.937) 10	5.94 (1.169) 29	.016
RBC/WBC ratio	143.8 (115.9) 17	95.7 (74.4) 34	213.2 (213.2) 29	.015

Table 3. Acid phosphatase activity in white blood cells (monocytes and neutrophils) of *Anolis gingivinus*, comparing cells infected and not infected with the malarial parasite *Plasmodium azurophilum*. Labeled cells were those assumed to contain the enzyme. A total of 300 cells were examined from three infected lizards (no significant difference among lizards)

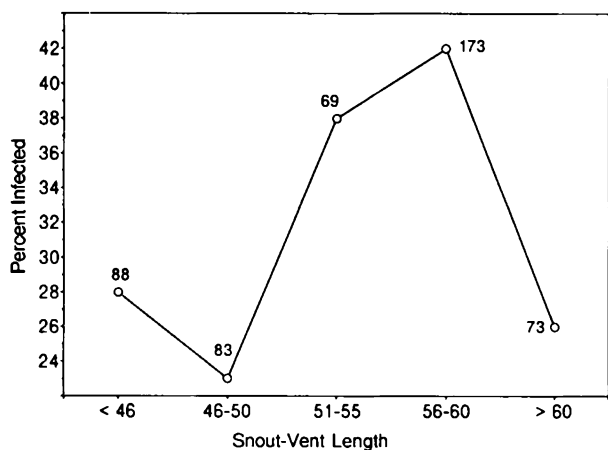|	Infected Cell	Cell Not Infected
Labeled	87	46
Not Labeled	145	22
	38% labeled	68% labeled

G-test, $G = 19.45$, $P < .01$

Fig. 3. Percent of *Anolis gingivinus* infected with the malarial parasite *Plasmodium azurophilum* for different body size classes of lizards. Sample sizes are given by data points

expected, older animals are more likely to be infected because they have been exposed to the possibility of transmission from a biting insect vector for a longer period of time. However, there is a sharp decline in percent infected for the very largest animals compared to smaller lizards. This could result if animals are cured of malaria as they age, but I have never observed such a cure in any lizard infected with *Plasmodium*, including dozens of malarious *A. gingivinus* followed in the laboratory (unpubl. data). The only other possibility is that infected older lizards suffer increased mortality compared to noninfected lizards. Infected adult male lizards (> 55 mm SVL) also are more likely to have an injured tail than noninfected lizards (45% of infected male lizards [$N=91$] vs. 26% of noninfected males [$N=147$]; G-test, $P<.05$). Tail injuries most likely result from encounters with predators or fights with other males. There is no difference in percent injured tails for infected vs. noninfected females or juveniles (G tests, $P>.05$). If injured tails result from attacks of predators, an increase in frequency of injured tails suggests predation intensity is higher on infected lizards or predator efficiency is lower (Schoener 1979). This suggests infected adult males are injured more often during male-male aggressive interactions or are subject to greater predation intensity because they may perch on less desirable locations while visually scanning their territories.

Discussion

Two kinds of evidence support the conclusion that *Plasmodium azurophilum*, a malarial parasite, mediates the outcome of competition between the two *Anolis* species of St. Maarten. The first is distributional. Only the presumed competitively superior species, *Anolis gingivinus*, is frequently infected and the spatial distribution of the parasite on the island mirrors the distribution of *A. wattsi*. *A. wattsi* is essentially limited to areas where *A. gingivinus* is infected with malaria, and both species of anole are found wherever malaria is found. This pattern of coincidence of malaria and coexistence of both *Anolis* is observed over distances of only a few hundred meters.

The second kind of evidence is the demonstration of harmful effects of the parasite on *A. gingivinus*: immature erythrocytes increase in circulating blood, blood hemoglobin is reduced when the parasite exploits red cells, certain classes of white blood cells increase in abundance, and when infected are less likely to produce an enzyme important in their functioning as immune system cells. The increase in broken tails in infected males suggests malaria might hinder lizards when they compete for territories. Last, there is weak evidence that malaria might increase mortality among the largest (=oldest?) animals. These data on the virulence of *P. azurophilum* are incomplete but the impact of malaria on *A. gingivinus* is similar to that seen in much better known lizard malaria systems, *P. mexicanum* in the California western fence lizard, *Sceloporus mexicanum*, and *P. giganteum* and *P. agamae* in African rainbow lizards, *Agama agama* (Schall 1990a, 1990b). In *Sceloporus* infected with malaria there are the same hematological effects seen in *A. gingivinus* when that species' erythrocytes are infected with *P. azurophilum*, and these effects in *Sceloporus* initiate a cascade of physiological, behavioral, and reproductive costs.

Several of the effects of malaria seen in *Sceloporus*, if also present in *A. gingivinus*, could result in a reduction in this species' competitive ability or carrying capacity, both of which could alter the outcome of interspecific competition with *A. wattsi*. Reproductive output by females is reduced in infected fence lizards, and testis size of males is smaller (Schall 1983a, 1983b). The latter effect could indicate fewer sperm are being produced, but more likely there would be a shift in hormonal titres. Hormonal balance of infected male fence lizards is in fact altered with significant reduction in testosterone production by infected males (Dunlap and Schall, unpubl. data). Infected males are also socially active less often (Schall and Sarni 1987), and less able to maintain territories, travel over their home range, and defend access to females (Schall and Dearing 1987; Schall and Houle 1992). Infection with malaria also appears to alter the ventral color pattern of fence lizards, an important sexual signal in these lizards (Ressel and Schall, 1989). If *Anolis* have similar behavioral and reproductive consequences of infection with *P. azurophilum*, then *A. gingivinus* in malarious areas should suffer reduced ability to compete during interspecific contests with *A. wattsi* for territories and may produce fewer offspring while infected.

Data on the California lizard malaria system also suggest an explanation for the patchy distribution of malaria in *A. gingivinus*. *P. mexicanum* in fence lizards also has a patchy distribution, even over a scale of a few hundred meters in apparently uniform habitat in northern California. The cause seems to be the heterogeneous distribution of the vectors, two species of psychodid flies, which need well established rodent burrows as hiding and breeding sites (Schall and A. Marghoob, unpubl. data). Thus, the distributions of the *Anolis* of St. Maarten may ultimately depend on the microhabitat requirements of the vector of *P. azurophilum*.

The evidence presented here for parasite-mediated competition in the anoles of St. Maarten is, of course, circumstantial, but the kind of evidence – distribution pattern of parasite and hosts and demonstration of harm to only one of the hosts – is the same evidence available for all other

studies on the phenomenon in nature (Price et al. 1986) Manipulative experiments, in which the parasite is introduced into new locations, would be unethical. But, natural experiments could often occur, in which the parasite prevalence waxes and wanes. Thus, the parasite-mediation of competition hypothesis predicts that any long term establishment of *A. wattsi* in areas where it has long been absent should be correlated with a natural increase in the malarial parasite in *A. wattsi*.

Is malaria important in the ecology of anoles on other Caribbean islands? Malaria in *Anolis* is found in a patchy distribution among and within other islands. For example, my surveys show it is absent on some dry islands (Aruba, Bonaire, Curacao). On St. Barthelemy, *P. azurophilum* shows a patchy distribution in *A. gingivinus*, the only species of anole on the island. I predict *A. wattsi* could successfully invade this one species anole community and survive in the malarious sites (a prediction that clearly should never be tested by human experiment!). This prediction contrasts to the coevolution model of Roughgarden and Pacala (1989). On St. Eustatius *A. wattsi* coexists with the much larger *A. bimaculatus*; malaria is present in *A. wattsi*, but *A. bimaculatus* appears immune. On tiny Saba island, *A. sabanus* frequently suffers heavy infection with malaria. *A. wattsi* should also be able to colonize this island despite its similarity in size with *A. sabanus*. It is interesting to note that *A. wattsi* is the most widespread anole in the eastern Caribbean. Price et al. (1988) proposed that widespread species should be most adept at using natural biological warfare because they would meet a complex mix of pathogen strains over their large range and would evolve partial resistance to at least some of them.

In the Luquillo Mountains of eastern Puerto Rico, we have found five syntopic anole species infected with two species of malarial parasite (including *P. azurophilum*), but only one species, *A. gundlachi*, is commonly infected. This species is strongly interspecifically territorial and coexists with a similarly sized anole that is only very rarely infected with malaria (*A. evermanni*) (Schall and Vogt unpubl. data). Perhaps malaria plays an important role in the structure of this more complex *Anolis* assemblage.

Mediation of interspecific competition by predation (Paine 1977) and parasitoids (Feener 1981) that leads to an increase in biotic diversity at a site has been well documented. Thus, predators, parasitoids, and parasites all could influence competitive interactions of their hosts, perhaps with responses that reverberate down through complex communities in ways previously unsuspected. Most likely, though, microparasites are most important: predators may present a spectacle as they attack prey, but mostly invisible parasites are much more abundant, and their action is relentless. The role of parasites in community ecology has almost been ignored by researchers. Lizards and birds are two taxa that have played a major role in the development of community ecology, yet this is the first report of a parasite altering the community composition of lizards, and a recent important volume on bird-parasite interactions (Loye and Zuk 1991) ignores the parasite-host community effect. I agree with Minchella and Scott (1991) who stated: "The extent to which parasite effects on host populations are translated into com-munity-level effects will be one of the questions of the 1990's."

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