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The Ecology of Lizard Malaria

J.J. Schall

The lizard malarias are a taxonomically and ecologically diverse group of parasites that offer excellent models for research on the ecology of malaria in free-ranging non-human vertebrate hosts. Studies over the past decade show that plasmodia of lizards can play an important role in the ecology and behavior of their hosts. The behavior of malarial infections in lizards also reveals unsuspected variation in the life history of Plasmodium.

An enormous amount of research has been conducted on the biology of *Plasmodium*, yet our understanding of the effects of malarial infection on non-human natural hosts, the ecological consequences of malaria for host populations, and the range of life histories in the genus *Plasmodium* is surprisingly scanty. The plasmodia of lizards, however, present a superior opportunity to study the ecology of malaria in nature ie. in free-ranging, natural hosts as opposed to experimental hosts in the laboratory. Lizards are often easy to observe and capture, typically remain in a limited area (making mark–recapture studies possible), and sometimes occur in very dense populations. As ectotherms, their body temperatures can be readily manipulated in laboratory experiments. Most important, lizard malaria systems are diverse, both taxonomically and ecologically.

The Diversity of Lizard Malarias

Laveran's epochal description of the organism that causes human malaria was followed by the discovery that related parasites exploit a diversity of vertebrate hosts. In 1909, Wenyon named the first known *Plasmodium* species of reptiles from the rainbow lizard of the Sudan, *Agama agama*[1]. Since then, 76 species of lizard malarial parasites have been described, approximately half of the 169 known plasmodia (Table 1). The malarias of lizards seem fairly host specific, and since there are approximately 3000 species of lizards, there

may still be hundreds of species of lizard malaria to be discovered. Ecologically-oriented parasitologists can therefore study malaria in the wild without the need to travel extensively – I have collected malarious lizards within sight of San Francisco's skyscrapers and Golden Gate Bridge! Many lizard malaria species have been described recently through the tireless efforts of a single researcher, S.R. Telford, and our knowledge of the genus is curiously skewed by Telford's

Fig. 1. Species of Plasmodium *discussed in this article. (a)* Immature schizont of P. giganteum; *(b)* mature schizont of P. giganteum *with about 100 merozoites; (c)* mature schizont of P. agamae, *which typically produces about eight or nine merozoites; (d)* mature schizont of P. mexicanum, *which usually yields about 14 merozoites; (e)* mature schizont of P. azurophilum *in a heterophil; this species infects both red and white blood cells and the number of merozoites produced is quite variable (about 12–90).* P. azurophilum *is also unusual because it stores no malarial pigment. Scale bar = 10 μm.*

location during his career with the WHO[2].

Lizard malaria has been found on all the warm continents except Europe, where there have not been adequate surveys. Most of the important families of lizards are exploited by plasmodia (Table 1) and infected lizard populations have been found in many kinds of habitats, including seasonal temperate woodland, tropical rain forest and cool upland tropical habitats. The distributions of only a few species of lizard malaria are well known, but they suggest that at least some lizard malarias are ancient parasite–host associations. For example, *P. mexicanum* of fence lizards (*Sceloporus*) in North America is found in a disjunct distribution, including northern California, Wyoming, and south-central Mexico. These wooded areas, now separated by vast deserts, were contiguous during the Pleistocene[3].

Particularly intriguing is the great range in reproductive characteristics seen among the lizard-infecting plasmodia[4]. Some species produce only four daughter cells per mother cell (merozoites per schizont), whereas others produce over 100 (Fig. 1) and this range in fecundity should have consequences for the population biology of the parasite within hosts. Although merozoite number has long been used as a taxonomic character in malaria studies, its ecological and evolutionary significance has not been explored. Indeed, reproductive output may not be a natural systematic character at all; species with similar merozoite numbers may simply have converged under similar ecological constraints. Since 1977, my students and I have used several lizard malaria systems to explore a variety of issues in the evolutionary ecology of malaria.
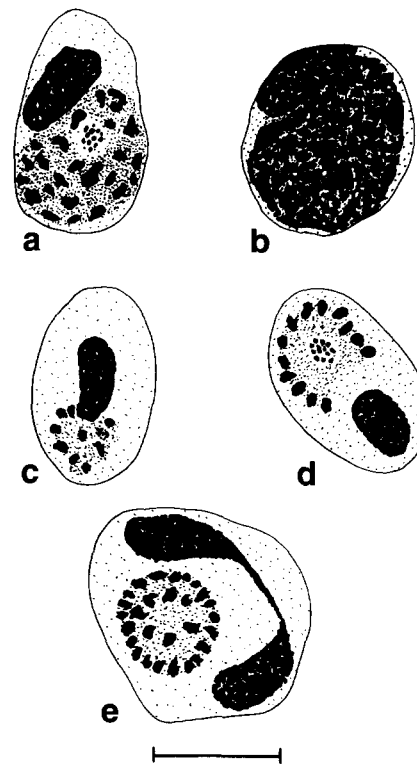
Course of Infection and Gametocyte Sex Ratio

We conducted a large mark–recapture program to follow the course

of infection of *P. mexicanum* in a population of fence lizards (*Sceloporus occidentalis*) in northern California (Fig. 2)[5]. The classic pattern of malarial infection is an exponential rise followed by a crisis (if the host survives), a crash of parasite density, which is sometimes followed by a chronic low-level blood infection. However, *P. mexicanum* infection usually rises exponentially and levels off at a chronic condition, with parasite load varying greatly among host individuals (Fig. 3a and b). Parasitemia drops during winter dormancy of infected lizards but rebounds very rapidly early the next spring. The parasite is thus challenged by a strongly seasonal environment; few lizards in our mark–recapture study lived more than two years and winter mortality was substantial. We expected to find that infections followed an optimal course to prepare for transmission by the end of the summer, but no typical course of infection was apparent. Chronic parasite load varied over two orders of magnitude (examples in Fig. 3a) and no relationship between host sex or starting date of the infection and ultimate parasite load was observed. However, there was a trend for older animals to maintain lower chronic parasitemia. Reliable estimates of the growth rate of infection were available for 18 lizards; growth rate varied four-fold, with a weak, but non-significant, trend for infections starting late in the season to grow more rapidly.

Almost all infections in lizards brought into the laboratory crashed quickly to a very low-level chronic condition. This phenomenon not only deserves scrutiny for its intrinsic interest, but also illustrates the danger of assuming laboratory kept animals reflect events in natural conditions.

Timing of gametocyte production is clearly of paramount importance for malaria parasites in a seasonal environment. However, the production of sex cells was unpredictable, occurring early or late in the infection, and the relative production of gametocytes differed greatly among chronic infections (Fig. 4). For 11 initial infections, gametocytes first appeared in the blood from 0 to 78 days after asexual stages became patent; the timing to first gametocyte production was not related to the starting date of the infection, nor to host age or sex.

Examination of gametocyte sex ratios also revealed an unexpected result[6]. Modern evolutionary theory predicts that natural selection acting on individuals will result in an equilibrium sex ratio that is adaptive, and usually 1:1. Many authors have stated that macrogameto-

Table 1. *Plasmodium* species infecting lizards

| Species	Host	Known distribution
achiotense	Basiliscus	Panama
acuminatum	Chamaeleo	East Africa
agamae	Agama	Tropical Africa
arachniformis	Chamaeleo	Tanzania
archiotensis	Basiliscus	Panama
attenuatum	Ameiva	Venezuela
audaciosum	Plica	Brazil
aurulentum	Thecadactylus	Venezuela
australis	Amphibolurus	E. Australia
azurophilum	Anolis	Caribbean Islands
balli	Anolis	Panama
basilisci	Basiliscus	Panama
beebei	Gonatodes	Venezuela
beltrani	Sceloporus	Mexico
brumpti	Sceloporus	Mexico
brygooi	Chamaeleo	Madagascar
chiricahuae	Sceloporus	N. America
clelandi	Varanus	Sri Lanka
colombiense	Anolis	Colombia
cordyli	Cordylus	E. Africa
cnemaspi	Cnemaspis	Tanzania
cnemidophori	Cnemidophorus	Brazil
diploglossi	Diploglossus	Brazil
diminutivum	Ameiva	Panama
effusum	Neùsticurus	Brazil
egerniae	Egernia	E. Australia
fischeri	Chamaeleo	E. Africa
floridense	Anolis	Caribbean etc.
giganteum	Agama	Tropical Africa
gologoloense	Chamaeleo	Tanzania
gonatodi	Gonatodes	Panama
guyannense	Plica	Guyana
heischi	Mabuya	Kenya
holapsi	Holapsis	Tanzania
iguanae	Iguana	Venezuela
josephinae	Ameiva	Mexico
lacertiliae	Carlia	Goodenough Island
lainsoni	Phyllodactylus	Venezuela
lionatum	Ptychozoon	Thailand
loveridgei	Lygodactulus	Tanzania
lygosomae	Leilopisma	New Zealand
mabuiae	Mabuya	Sudan
mabuyi	Mabuya	Brazil
mackerrasae	Egernia	Australia
maculilabre	Mabuya	Congo
marginatum	Anolis	Panama
mexicanum	Sceloporus	N. America
michikoa	Chamaeleo	Tanzania
minasense	Ameiva	Venezuela
modestum	Tropidurus	Brazil
multiformis	Plica	Brazil
morulum	Mabuya	Panama, Brazil
pifanoi	Ameiva	Venezuela
pitmani	Mabuya	E. Africa
rhadinurum	Iguana	Mexico
robinsoni	Chamaeleo	Madagascar
saurocaudatum	Mabuya	Thailand
scelopori	Sceloporus	Belize
sasai	Takydromus	Japan
siamense	Draco	Thailand
simplex	Plica	Brazil
scorzai	Phyllodactylus	Venezuela
tanzaniae	Chamaeleo	Tanzania
telfordi	Ameiva	Venezuela
torrealbai	Anolis	Venezuela
tropiduri	Anolis	Panama
tubinambi	Tupinambus	Brazil
uluguruense	Hemidactylus	Tanzania
uncinatum	Plica	Guyana
uranoscodoni	Uranoscondon	Brazil
utingensis	Anolis	Brazil
uzungwiense	Chamaeleo	Tanzania
vastator	Draco	Malaysia
vacuolatum	Plica	Brazil
vautieri	Urostrophus	Brazil
zonuriae	Cordylus	S. Africa
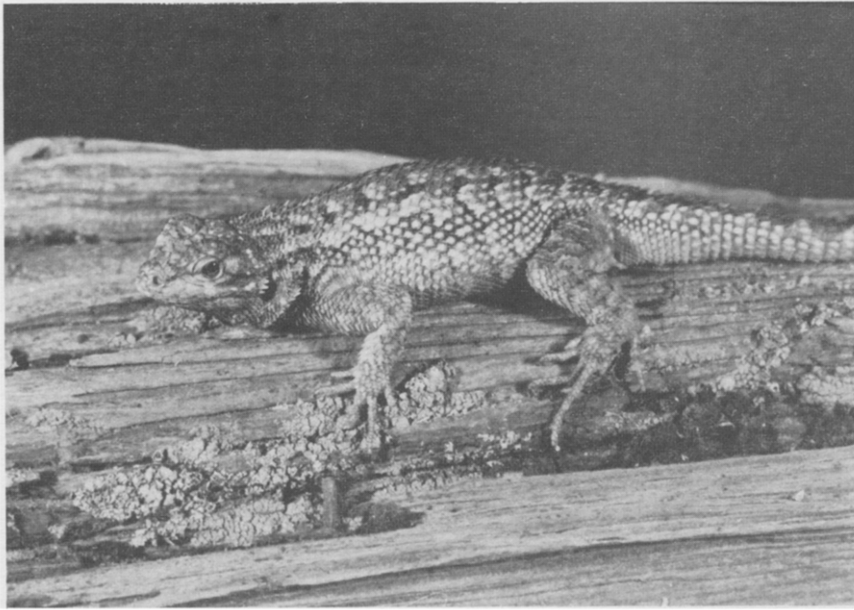
Fig. 2. Western fence lizard from California. These small lizards (adult male snout-vent length about 65 mm) are common in oak woodland habitat and are frequently exploited by P. mexicanum.

course of infection in *P. mexicanum*. To place this into perspective, we began a study of the population biology of the insect vectors and transmission success of the parasite from lizard to insect. Two phlebotomine flies appear to be the vectors of *P. mexicanum*: *Lutzomyia vexator* and the much less common *L. stewarti*. Although apparently new infections of *P. mexicanum* appear in the lizards at any time during the warm season, the flies are quite rare until July, becoming common only in late summer. We are currently attempting to determine if natural variation in the character of malaria infections (parasite density and gametocyte sex ratio) has any effect on transmission success to the fly. Perhaps the variation observed in the course of infections is not mirrored by variation in transmission success to the vector, which would be surprising, but would explain the lack of an 'optimal' behavior by the parasite. Alternatively,
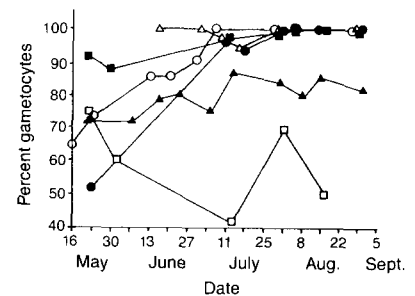
cytes ('females') typically outnumber microgametocytes ('males') in malaria infections. However, very few actual counts have been published. The sex ratio of gametocytes in *P. mexicanum* appears to be constant, even when the infection is growing, but the equilibrium proportion varies considerably among infections (Fig. 5). In free-ranging lizards, stable sex ratios varied from 36% to 50% microgametocytes. I also followed gametocyte sex ratios in lizards maintained in the laboratory (*P. mexicanum* and two African species, *P. agamae* and *P. giganteum*, all in the rainbow lizard). The results were similar to those described above except for a substantially greater variation in sex ratios. Male and female gametocytes are readily distinguishable in many lizard malaria species (unlike the plasmodia of mammals and birds), so I compared the sex ratios of *P. mexicanum*, *P. agamae*, and *P.*

giganteum. Sex ratios differed significantly between these species, with a maximum proportion of 0.474 microgametocytes for *P. mexicanum* and 0.371 for *P. giganteum*.

These results, while certainly preliminary, indicate that the study of sex ratios of malarial gametocytes presents an unexplored and important avenue for research in evolutionary parasitology. The general theory of sex allocation predicts an equilibrium sex ratio that is uniform among infections and with equal investment in micro- and macrogametocytes[6]. However, some theory predicts 'extraordinary' sex ratios driven by unusual population structure, close genetic relatedness in a breeding group, or group selection. These ideas have so far been applied only to social insects, but may well be relevant in the study of malarial parasites.

In summary, there is no clear optimal

Fig. 4. Proportion of gametocytes in several representative infections of P. mexicanum with stable parasitemia. Note that percent gametocytes varies greatly between infections. (Redrawn from Ref. 5.)

there may be several equally successful strategies for parasite behavior in the vertebrate host, depending on variation in local conditions. No typical course of infection would therefore exist, a behavior termed 'hedge-betting' by ecologists.

Interspecific Relationships Between *Plasmodium* Species

Does interspecific competition shape the structure of parasite communities within host individuals and populations? Ecologists have long debated this question, some arguing that competition is a major force in parasite community ecology, others doubting that resources are ever limiting for *r*-selected parasites[7]. Many lizard populations are subject to infection by two or more species of *Plasmodium*, so the kind of interspecific relationship between coexisting malarial species can be determined.
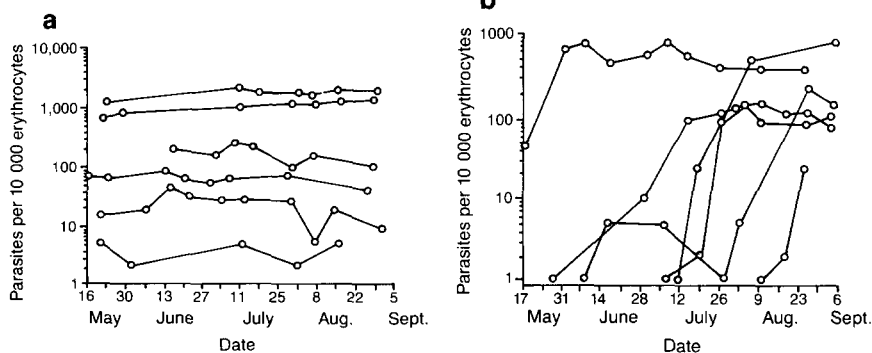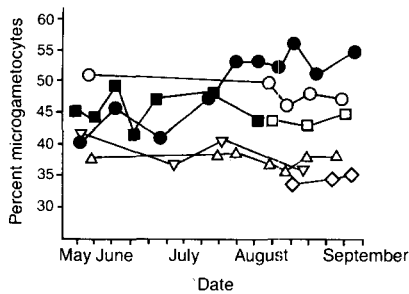

Fig. 3. (a) Parasite density for six representative fence lizards with stable infections of P. mexicanum. Note that parasitemia varied over two orders of magnitude between the infections. (b) Examples of rising infections, several of which leveled off to a stable condition. (Redrawn from Ref. 5.)

Fig. 5. Proportion of microgametocytes among gametocytes of several representative infections of P. mexicanum *in free-ranging fence lizards. The sex ratio frequently remains constant for each infection, but differs between infections. (Redrawn from Ref. 6.)*

We studied the coexistence of *P. agamae* and *P. giganteum* in the rainbow lizard in Sierra Leone. If competition is important, mixed infections should be less common than if the parasites associated in individual hosts by chance, and parasitemia of each species in mixed infections should be lower than that in single infections. The results of this project have not yet been published, but our preliminary conclusions suggest that in lizards from over 20 scattered sites the parasitemia for each species in mixed infections was similar to that in single infections. Thus, total parasitemia in mixed infections was approximately equal to the sum of parasite loads in solitary infections. These results argue against the competition hypothesis and for a neutral relationship between the two species.

Prevalence data, though, provided an unexpected surprise: mixed infections were more common than expected by a chance association of the two species ie. the two species were positively associated. Mixed infections were 2.5-fold more abundant than expected by chance in male lizards and 3.5-fold in females. The two species of parasite may simply share the same vector, but dissimilar seasonal patterns in apparent transmission argue against this. Alternatively, the two species may exploit different blood cell classes, with *P. agamae* invading mature erythrocytes and *P. giganteum* immature cells. Immature erythrocytes are rare in the blood of lizards, but are produced copiously after infection with malaria[4]. *P. giganteum* may do best in individuals with blood already altered by *P. agamae*.
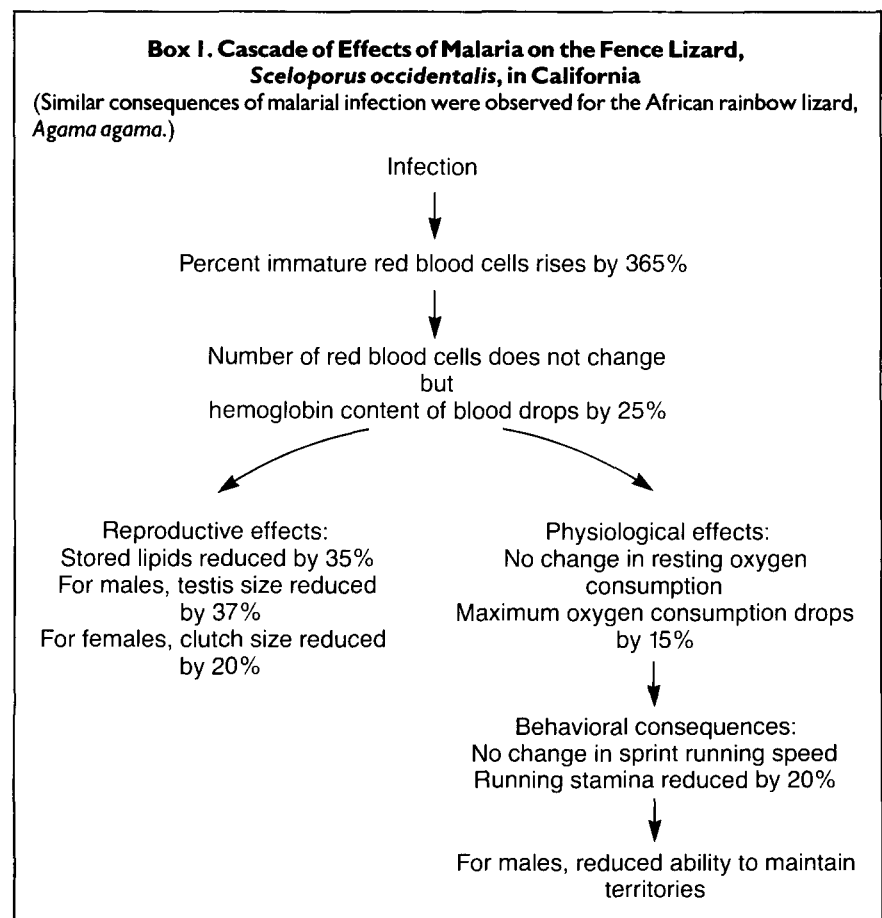
Effects of Malaria on Lizard Hosts

Infection with malaria initiates a cascade of effects on the lizard host[8]. Early in the infection, large numbers of immature erythrocytes appear in the blood, probably because the lizard's antiparasite tactic is to discard even slightly aberrant red cells. Immature erythrocytes contain less hemoglobin, so blood hemoglobin concentrations fall. In laboratory experiments, infected lizards have reduced ability to deliver oxygen to tissues (measured as oxygen consumption at maximal activity). The behavioral consequences are predictable: burst running, which is anaerobically supported in lizards, is not affected, but sustained locomotion, which requires significant aerobic support, suffers. Infected male lizards have smaller testes and females produce smaller clutches of eggs (Box 1). All the species of *Plasmodium* we examined cause similar levels of pathology in their hosts, despite the great range in merozoite numbers they produce (Fig. 1)[4].

All the lizards we studied are 'sit-and-wait' foragers, that catch food or escape from predators by short bursts of running. We studied the behavior of fence lizards in California to determine if malaria alters a lizard's behavior in nature[9]. Six hundred natural runs by fence lizards were observed, and then the length of each run measured; most were very short and must have taken less than one second, none could have lasted longer than four seconds. Recovery from such short bursts of activity, as measured in the laboratory, is rapid, suggesting that malaria would not interfere with foraging or escape from enemies (Box 2). The frequency of broken tails, an indication of predator attacks on the lizards, was measured and no difference between infected and non-infected individuals was found.

Social interactions between fence lizards, however, are often physically vigorous and can last for several minutes. Such activity must therefore require substantial aerobic support. We staged contests between males, one infected and the other uninfected, in large outdoor pens[10]. Infected males were much less likely to win; the noninfected male almost always forced the other individual to leave its perch and hide. This result was also observed in lizards in their natural home range. Lizards were also captured, marked, a blood smear made and the animals released at the point of capture. These lizards were scored as dominant or submissive over a six week observation period, without knowledge of the infection status of the animals. The result was clear; almost all submissive animals were infected, all dominant ones were not (Box 3). Malarial infection may therefore prevent a male lizard from

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Box 1. Cascade of Effects of Malaria on the Fence Lizard, *Sceloporus occidentalis*, in California

(Similar consequences of malarial infection were observed for the African rainbow lizard, *Agama agama*.)

Infection

↓

Percent immature red blood cells rises by 365%

↓

Number of red blood cells does not change
but
hemoglobin content of blood drops by 25%

Reproductive effects:
Stored lipids reduced by 35%
For males, testis size reduced by 37%
For females, clutch size reduced by 20%

Physiological effects:
No change in resting oxygen consumption
Maximum oxygen consumption drops by 15%

↓

Behavioral consequences:
No change in sprint running speed
Running stamina reduced by 20%

↓

For males, reduced ability to maintain territories

maintaining a territory and wooing mates.

We also found that ventral color pattern, a sexually dimorphic trait in the fence lizards, was altered by malarial infection[11]. Female lizards may use the appearance of the ventral colors as an aid in choosing mates. Hamilton and Zuk have proposed that parasites may alter the appearance of extravagant features of male hosts and thus allow females to determine the infection status of prospective mates[12]. Their hypothesis suggests a reduction in attractiveness of


S. Ressel

Fig. 6. Three male fence lizards of the same body size and approximate age. Ventral surface colored with two lateral blue stripes (lighter areas) outlined with black on a buff background. As seen, ventral color varies greatly among males. Infected lizards tend to show more black (lower photograph). 827 males were collected and photographed. The proportion of ventral colors were then determined with a digitizing planimeter. Because lizards with the same proportion of each color might vary in actual color arrangement, a series of photographs showing a range of pattern classes were made, then 500 additional males were captured and scored for color pattern. Both of these studies revealed that infected males display more black, on the average, than non-infected males. This effect remained when the data were corrected for lizard age.

Box 2. Time Budget of Infected and Non-infected Lizards

Marked California fence lizards were observed for 1202, five minute periods. The infection condition of the lizards was unknown to the observer. (a) This graph shows that these sit-and-wait foragers spend over 90% of their time 'inactive': alert, but still. (M = adult males; F = adult females; J = juveniles.) (b) They only rarely run, for food, in response to intruding fence lizards, or away from predators, and (c) these runs are usually very short. However, during social interactions, vigorous activity can last for several minutes and this aerobically supported behavior seems affected by malarial infection. The only significant difference between the time budgets of infected and non-infected lizards is in the amount of time spent by adult males in social activity.

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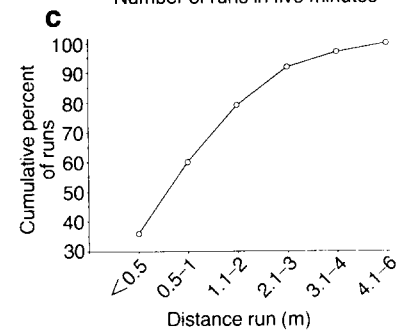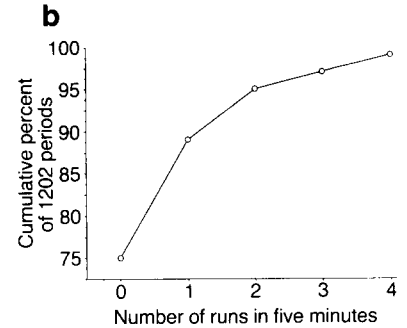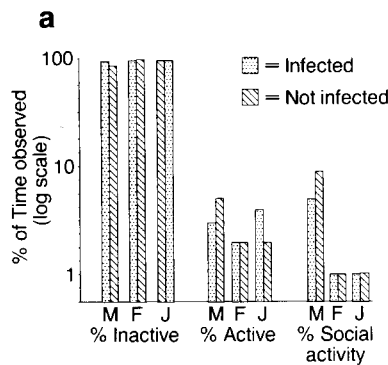
infected males, but in our study, infected lizards were more extravagantly colored (Figs 6 and 7). This was mirrored in another study[13], in which brightly colored males of a tropical teiid lizard were found to be infected with a haemogregarine parasite more frequently than duller individuals. These results suggest that, in at least some parasite–host associations, females may prefer the appearance of infected males.

It is conceivable that the conclusion that malaria is severely virulent for lizards actually reverses the true cause-and-effect relationship, ie. sickly animals may simply be more prone to infection with malaria, or submissive males may be bitten more frequently by the insect vector. I have no data that would support either possibility, despite examining the effects that would logically result from infection with a parasite that causes erythrocyte destruction. Clearly, though, this remains an important unresolved issue.

Finally, perhaps malaria causes an infected lizard to alter its behaviorally-maintained body temperature. Infected lizards may develop a behavioral fever, as they do when infected with some bacterial pathogens. This would alter their use of habitat and the period of time for which they are active. However, no such fevers were observed for either fence lizards in California or rainbow lizards in Africa[4]. In laboratory experiments, *P. mexicanum* was shown to have a broad thermal buffering ability and thermal tolerance. Infection growth rate seems unaffected by temperatures ranging from 20°C to 35°C, and the parasite can survive temperatures lethal to the lizard. Lizards may therefore not develop behavioral fevers because the parasite's thermal tolerance is broader than their own.

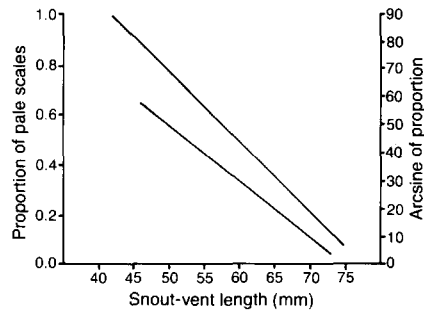## Parasite-Mediated Competition Among Host Species

In 1948, Park showed that a parasite could mediate the outcome of competition between two species of *Tribolium* beetles in laboratory experiments[14]. The possibility that parasites may alter the competitive ability of their hosts has intrigued generations of ecologists, but evidence for the phenomenon is scanty. On the Caribbean island of St Maarten, two species of small arboreal lizards, *Anolis gingivinus* and *A. wattsi*, are strong competitors[15]. *A. gingivinus* is clearly superior in competition and occurs throughout the island. *A. wattsi*, in manipulative experiments, proved to be an inferior competitor and is restricted to a

limited area of the island. What allows A. wattsi to persist in those areas?

I found that A. gingivinus is susceptible to infection with Plasmodium azurophilum, but A. wattsi appears almost immune. The parasite has many of the effects on A. gingivinus described for other lizard malarias, but it also invades white blood cells and appears to alter production of acid phosphatase by these cells. At every location where both Anolis species were found, malaria was common in A. gingivinus (typically 40% of lizards were infected), but where only A. gingivinus occurred, very few or none of the lizards was parasitized. These results strongly suggest that the distribution of malaria on the island is patchy, infects only the competitively dominant lizard species, and thus mediates competition between the two species.

Prospects

The work described here shows that lizard malaria is an ideal system in which to examine a broad range of topics in ecology, evolution, and animal behavior. Other possibilities abound. The rela-

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Box 3. Male–Male Interactions and Malarial Parasitism

In many species of lizards, males compete vigorously for access to females. This is especially true for territorial species, including the California fence lizard, African rainbow lizard, and the Caribbean anoles used in these studies on malaria. In the fence lizard, for example, males perform a stereotyped "pushup" display, raising the body off the substrate while compressing the body laterally. This reveals the brightly colored ventral surface. Males may circle each other, chase, and even grapple in fierce biting matches. To a human observer, the winner in such interactions is usually clear, and the submissive male flees the dominant animal's perching location. Female lizards appear to take great interest in these matches; strangely, females may follow the submissive male, perching nearby and thus precipitating another attack by the dominant male. David Crews[16] has shown that seeing such male–male interactions initiates ovarian activity in female lizards. Intense activity by males must have a significant aerobic component, which may explain why in our experiments with penned lizards, in infected versus non-infected pairs, the non-infected male was dominant in 90% of cases, and in observations on free-ranging animals, all of the dominant lizards were non-infected.

Fig. 7. The changes in ventral color with age in California fence lizards (body size is correlated with age). For male lizards, the proportion of pale scales declines as the lizards age because additional black, blue, and yellow pigment is added. The lower regression line (correlation coefficient $r = -0.59$, $n = 119$) represents infected animals that are more colored than uninfected animals, shown above ($r = -0.71$, $n = 708$). Infection does not alter growth rate, but these data suggest that it alters color. This result probably stems from the parasite's impact on the hormonal picture of the lizards, and this is currently being investigated by the author and colleagues. (Redrawn from Ref. 11.)

tively simple reptilian immune system and the ease in working with wild lizard populations would allow immunoparasitologists to develop studies in ecological immunology. Developmental biologists might become intrigued by the gametocyte sex ratio data. The relationship between hormone levels and malarial infection in the lizards could be studied in wild animals by mark–recapture programs. Population ecologists could study the population consequences for the host of a harmful parasite; for example, does the parasite control the host population size? The vectors of malaria in California are rela-

tively easy to capture in the wild and culture in the laboratory, allowing medical entomologists to compare results from studies on human malaria with another ancient group of Plasmodium species. Indeed, the large number of lizard malaria systems allows use of the comparative approach that has been so productive in biology.

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