more than 1 minute before their application. A plexiglass cover was placed on the sucrose gap chamber to completely enclose the compartment containing the spinal cord. Even with these precautions, some loss of anesthetic may well have occurred. Hence the minimum effective concentration would, if anything, be lower than the values reported.

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Lizards Infected with Malaria: Physiological and Behavioral Consequences

Abstract. *In northern California, western fence lizards,* Sceloporus occidentalis, *are frequently parasitized by* Plasmodium mexicanum, *which causes malaria. Animals with this naturally occurring malarial infection are anemic; immature erythrocytes in peripheral blood become abundant (1 to 30 percent), and blood hemoglobin concentration decreases 25 percent. Maximal oxygen consumption decreases 15 percent and aerobic scope drops 29 percent in infected lizards; both correlate with blood hemoglobin concentration. Running stamina, but not burst running speed, is reduced in malarious lizards. There is a hierarchical relation between infection with malaria and effects on hematology, physiological function, and behavioral capacity. The results suggest that malarial infection may have significant effects on the ecology of lizard hosts.*

Over the past several decades, lizard models have played a central role in development of modern concepts in population, community, physiological, and behavioral ecology. However, lizard ecologists almost never consider the impact of parasites on individual lizards or lizard populations. This is curious since lizards are hosts of a wide range of parasite taxa (*1*) and parasites frequently have considerable effects on the biology of hosts (*2*). One common group of lizard parasites consists of the malarial organisms (genus *Plasmodium*); indeed, half of the 120 (more or less) described *Plasmodium* species are lizard parasites (*3*). The diversity of lizard malaria parasite-host associations make them ideal systems in which to examine the impact of parasitic infection on physiology and ecology of host organisms.

Although lizard malaria is considered a relatively benign parasitic infection (*1*), several lizard malaria species produce anemia, tissue damage, and even mortality in their hosts (*3–5*). Here we report physiological and behavioral effects of a lizard malaria, produced by *P. mexicanum*, on the host, the western fence lizard, *Sceloporus occidentalis*. Our data demonstrate that hematological alterations resulting from malarial infection are correlated with ecologically important effects on activity metabolism and behavior of the host.

Since 1977 a wild population of *Sceloporus* infected with malaria has been under study at the University of California Hopland Field Station, a tract of foothill oak woodland in southern Mendocino County (*5*). Fence lizards are abundant there and approximately 25 percent of wild adult lizards are infected with malaria at any given time.

As *Plasmodium* infects and reproduces in vertebrate erythrocytes, hematological effects of infection could be an important source of pathology to lizard hosts. Hematological and parasitological variables of field-caught lizards were measured by standard techniques. Blood was drawn from a toe clip and a smear was made for Giemsa staining and examination for parasites (*5, 6*). Parasitemia, expressed as parasites per 10,000 red blood cells (RBC), and the percentage of immature red blood cells (iRBC) were determined by scoring 2000 to 3000 RBC (*7*). Also measured were erythrocyte abundance (RBC per cubic millimeter of blood), hematocrit, and hemoglobin concentration in postorbital sinus blood (*8*).

Lizards infected with malaria respond by rapid production of iRBC (*6, 9, 10*). This response serves to replace cells destroyed by the parasite and possibly to reduce parasite population growth (*5, 11*). Infected *Sceloporus occidentalis* show a marked increase in circulating iRBC (Table 1). Abundance of iRBC ranged from 0 to 2 percent for noninfected and 1 to 30 percent for infected fence lizards. Abundance of iRBC for lizards with very low parasitemia (< 25 per 10,000 RBC) ranged from < 1 to 30 percent. For lizards in which the number of parasites was substantially greater (400 to 2800 per 10,000 RBC), the proportion of iRBC was about 5 to 30 percent. This weak relation between parasitemia levels and percentage of iRBC may be a result of time lags between changes in parasitemia levels and the hemopoietic response. Therefore, the percentage of iRBC appears more likely than parasitemia to be correlated with other physiological effects.

Hemoglobin concentration in blood of parasitized lizards is lower (~ 25 percent less) than in noninfected lizards, but hematocrit and RBC counts do not differ between groups (Table 1). The percentage of iRBC and hemoglobin concentration are negatively correlated ($r = -.51$, $P < .01$, $N = 49$). Thus, hemoglobin deficiency in infected lizards seems to be a result of reduced hemoglobin in iRBC rather than of a decrease in RBC number per volume of blood (*12*).

A 25 percent deficit in blood hemoglobin in malarious lizards should result in a reduction in the ability of the blood to deliver oxygen to tissues. Resting and maximal oxygen consumption were measured (*13*) in adult male *Sceloporus* at 35°C, the preferred body temperature for this species. Blood hemoglobin concentrations were measured within several hours after metabolic measurements. Infected and noninfected lizards do not differ in resting oxygen consumption. However, maximal oxygen consumption and aerobic scope, the increment between resting and maximal oxygen consumption (*14*), differ significantly between groups (Table 1). There is a strong positive relationship between hemoglobin concentration and both maximal oxygen consumption (Fig. 1) and aerobic scope. The fact that data for both infected and noninfected lizards fall on the same regression line shown in Fig. 1

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suggests that the difference in maximal oxygen consumption between groups is strictly a result of differences in blood hemoglobin concentration.

Because aerobic scope is reduced in malarious lizards, their capacity for aerobically supporting behavior activity should also be reduced. Very short bursts of activity in lizards are supported principally by anaerobic metabolism, while longer efforts also involve a significant aerobic component (*13, 15*). We measured burst speed and running stamina as measures of behavioral performance capacity in infected and noninfected lizards (*16*). If malaria primarily influences oxygen transport capacity, we would anticipate that very short term, anaerobically supported burst activity would be little affected by infection. More sustained exertion involving maximal oxygen consumption should, however, be reduced. Results show that, although burst running speed (1 to 2 seconds duration) for noninfected lizards was slightly greater compared to malaria-infected animals, the difference is not significant (Table 1). Running stamina, measured as the distance covered during 30 seconds and 2 minutes of running, is significantly greater in the noninfected group, as predicted. These data show that burst speed is independent of infection, and parasitized animals retain a capacity for rapid escape and avoidance. However, the decrement in aerobic scope as a result of infection is accompanied by a decline in stamina. The ecological consequences of these physiological and behavioral effects of infection are difficult to decipher. These lizards may seldom need to run for more than a few seconds, even when fleeing a predator. In fact, malarious lizards are not more likely to have an injured tail, an indicator of a predator's attack, than are noninfected animals (*17*).

The influence of malarial infection in these lizards is pervasive through many functional systems. The following scenario emerges from our results: After infection, the host liberates immature erythrocytes into peripheral circulation, producing a 25 percent deficit in blood hemoglobin concentration. This in turn results in a 29 percent decrease in oxygen transport capacity with a resultant 20 percent reduction in aerobically sustainable activity performance; in free-living *Sceloporus*, malarial infection also results in decreased fat storage, in reduced clutch size in females, and reduced testis size in males (*5*). Decrements in all these physiological and reproductive factors are approximately 20 to 25 percent. This is a significant detriment, but infection apparently does not result in complete incapacitation and failure of functional systems, except during periods of stress (*5*).

Although the biology of *Plasmodium* has been intensively studied for the past 100 years, understanding of the costs of natural infection on the great majority of nonhuman hosts is poor. This novel study on the effects of natural malarial infection on western fence lizards suggests that malaria can have an important impact on lizard hosts. By investigating the influence of parasite-induced pathology on physiology, reproduction, and behavior, we may cast light on the real ecological consequences of natural parasitism. Such studies will also assist in development of theory concerning the evolution of the host-parasite relationship.

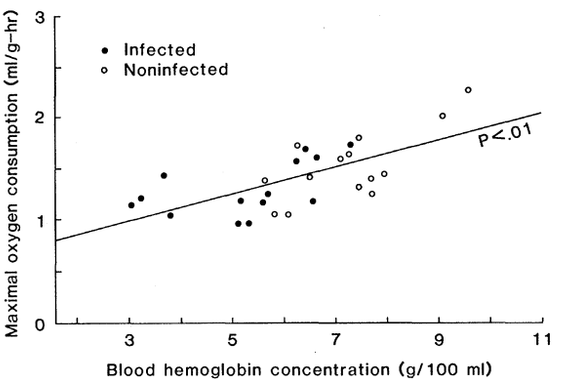

Fig. 1. Relation between blood hemoglobin concentration and maximal oxygen consumption for malarious and noninfected *S. occidentalis*. No significant difference exists for regressions for the two groups (analysis of covariance, $P > .05$). Data are combined to yield the regression: maximal O_2 consumption = .557 + .136 hemoglobin concentration. A similar pattern emerges for aerobic scope plotted as a function of hemoglobin concentration.

Table 1. Comparison of hematological parameters, oxygen consumption, and behavioral performance of *Sceloporus occidentalis* infected and not infected with the malarial parasite *Plasmodium mexicanum*. Mean values are reported followed by standard deviations and sample sizes in parentheses. Significance levels are determined by Mann-Whitney *U* tests. Hematological variables were measured as follows: (i) Hematocrit. Within 8 hours of the animal's capture, blood was drawn into a capillary tube and centrifuged. Data are pooled for both sexes since no difference was apparent between them ($P > .5$). (ii) Erythrocytes per cubic millimeter of blood. One month after the animals were captured, hemocytometer counts were made on blood of male lizards. (iii) Hemoglobin concentration. Blood from male lizards used in the physiological experiments was assayed by Drabkin's colorimetric method (*8*).

	Group		
	Infected	Noninfected	*P*
Hematological parameters			
iRBC (percent)	9.5 (7.3; 68)	2.6 (4.1; 25)	⩽.001
Hemoglobin (g per 100 ml of blood)	5.5 (1.3; 27)	7.3 (1.4; 22)	<.001
Hematocrit (percent)	33.4 (6.5; 17)	32.3 (5.1; 21)	>.25
RBC ($\times 10^3$ per mm^3 of blood)	972.1 (245.1; 12)	843.4 (251.2; 15)	>.05
Oxygen consumption [ml/(g.h)]			
Resting	0.59 (.105; 14)	0.54 (.131; 15)	>.10
Active	1.30 (.252; 14)	1.53 (.351; 14)	<.05
Aerobic scope	.71 (.247; 14)	1.00 (.336; 14)	<.01
Behavioral performance			
Burst speed (m/sec)	1.28 (.41; 15)	1.44 (.38; 15)	=.1
Running stamina*	17.0 (3.68; 14)	21.3 (5.82; 15)	<.01
Running stamina†	26.9 (6.81; 15)	32.2 (8.1; 15)	<.05

*Meters run in 30 seconds. †Meters run in 2 minutes.

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Scorza (*10*), who found an increase in percent iRBC but also a decrease in hematocrit and RBC counts in the lizard *Tropidurus torquatus* when infected with *P. tropiduri*. The infections studied by Scorza were experimentally induced by inoculation with whole blood from malarious donors and reached very high parasitemia (up to 7800 per 10,000 RBC). Such massive infections are rarely observed in *Sceloporus* with natural infections (observed range: 25 to 4000 per 10,000 RBC) but are frequently observed in experimental infections in this species.

13. Oxygen consumption was measured according to the methods of A. F. Bennett and T. T. Gleeson, *Physiol. Zool.* **49**, 65 (1976). Animals were held in captivity for approximately 1 month before measurement; infected and noninfected lizards were size-matched.
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17. Broken tail frequencies: males = 49 percent for infected, 42 percent for noninfected (N, 731; $\chi^2 = 3.44$, $P > .05$); females = 36 percent for infected and 33 percent for noninfected (N, 628; $\chi^2 = .36$, $P > .05$). As larger *S. occidentalis* are more likely to be infected as well as to have broken tails, only animals in a restricted size range (61 to 70 mm body length) were used in this analysis.
18. We thank R. W. Schall for assistance in fieldwork and figure preparation; J. E. Simmons for advice and facilities at the University of California, Berkeley; the staff of the Hopland Field Station; and T. J. Bradley, J. M. Herbers, B. Heinrich, and R. Huey for comments on the manuscript. Work was supported by an NIH postdoctoral fellowship to J.J.S. and NSF grant PCM77-24208 and NIH grant K-04 AM00351 to A.F.B.

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Obligate Necrophagy in a Social Bee

Abstract. *The social bee* Trigona hypogea *uses carrion instead of pollen as a protein source. Nests lack stored pollen, pollen is absent in larval provisions, and corbiculae for pollen transport on worker hind legs are reduced. Glandular secretions of 20 percent protein content appear to replace stored pollen. Toothed mandibles, pheromonal recruitment to resources, and aggressive foraging behavior facilitated evolution of necrophagy in this tropical forest bee lineage.*

Highly social bees are anomalous among bees and Hymenoptera. All are native to tropical forest, and all but four species (Apinae) lack a functional sting. The remainder are the Meliponinae, a pantropical group of at least 400 species (*1–7*). Stingless bees display immense diversity in resource use. In addition to nectar, pollen, spores, homopteran exudates, sap and resin, also used by apines, they collect mud, feces and carrion (*1–9*). Necrophagy by stingless bees had not been studied carefully, and this behavior was thought to involve collection of nest construction material or liquid exudates from carcasses (*1, 6, 10*). Study of *Trigona (Trigona) hypogea* Silvestri in the wet lowland forest of eastern Panama shows that this species partly digests animal flesh, then transports it to the nest, where it is regurgitated to other bees. No other protein sources are used by *T. hypogea*, and pollen transporting structures have been lost, making this species an obligate necrophage.

Nests of *T. hypogea* lack stored pollen. In four dissected nests, I found abundant stored honey but no indication of pollen (*11*). Microscopic analysis of brood provisions from cells containing eggs revealed the absence of pollen grains, the primary brood food of normal bees. Other highly social bees provide a mixture of hypopharyngeal gland secretions, honey, and pollen for the brood (*1*). Brood provisions of *T. hypogea* appear to be largely glandular. Some storage pots in nests contained a substance that was approximately 20 percent protein, comparable in color and quality to larval cell provisions (*12*). Furthermore, colorimetric protein assay of these substances gave identical results to that of worker hypopharyngeal secretions of *Apis mellifera* (*12*). Pollen carried by foragers to nests of stingless bees is first placed in storage pots, from which it is taken by workers to provision brood cells prior to deposition of an egg. Newly emerged adult bees consume stored pollen, necessary for glandular development (*1*). Stored glandular secretions have probably taken the place of pollen as food for brood and young adult bees.

Trigona hypogea is not unique among *Trigona* in rending and visiting animal flesh, and several other species, primarily of the subgenus *Trigona*, are known to do so (*1, 6, 10*). However, these species maintain colony stores of pollen, used as the primary protein source (*1, 13*). *Trigona hypogea* and its subgenus differ significantly from all other *Trigona* in possessing five large, pointed teeth on each mandible (Fig. 1A). This structural adaptation has led to many unique behavioral and ecological attributes, often associated with the propensity of these species to rob flowers and attack competitors for food and nest sites (*2, 14, 15*). Toothed mandibles and associated aggressive foraging behavior probably preadapted this lineage to the harvest and defense of large, compact nonfloral protein sources.

Trigona sensu stricto combines the advantages of toothed mandibles with massive recruitment and communication behavior, features that are analogous with social mammalian carnivores that dominate resources by aggression and sheer number (*16*). The subgenus *Trigona* deposits a pheromone trail between resources and the nest; bees arrive at resources rapidly and in large numbers, sufficient to displace competitors (*1, 15*). I watched *T. hypogea* deposit trail pheromones on plants between the nest and animal resources; it recruited rapidly and aggressively deterred dipteran competitors while foraging at animal carcasses.

In Panama, observation colonies recruited several hundred foragers in 2 hours to freshly killed large lizards (*Amyva* species) and toads (*Bufo marinus*). A large dead lizard placed 15 meters from one nest was located by bees within 8 hours. Groups of 60 to 80 bees

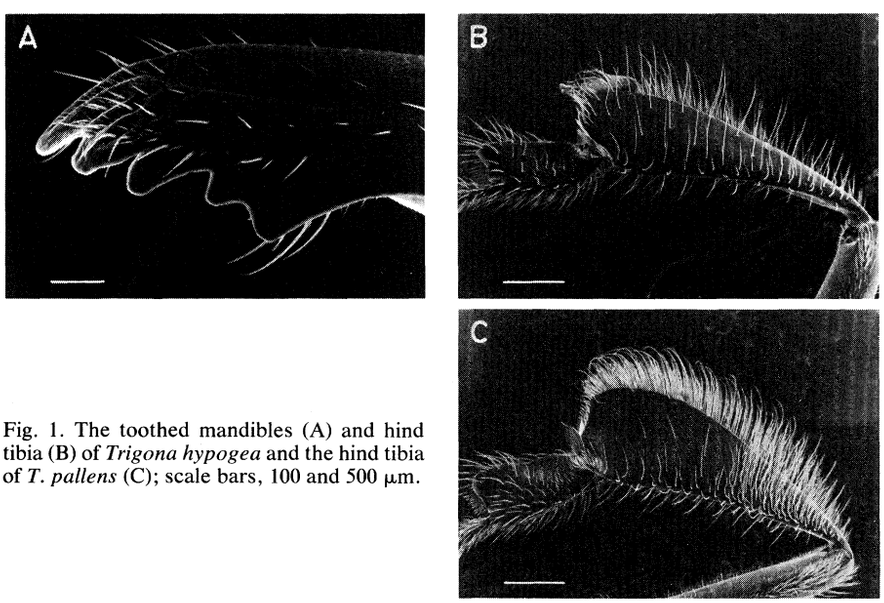

Fig. 1. The toothed mandibles (A) and hind tibia (B) of *Trigona hypogea* and the hind tibia of *T. pallens* (C); scale bars, 100 and 500 μm.

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