

## Malarial Parasitism and the Behavior of the Lizard, *Sceloporus occidentalis*

JOS. J. SCHALL AND GAIL A. SARNI

The behavioral time budget of the western fence lizard, *Sceloporus occidentalis*, was recorded in northern California, where fence lizards are frequently infected by the malarial parasite, *Plasmodium mexicanum*. Because malarial infection results in pathologies that could affect the host's behavior in nature, time budgets of malarious and noninfected animals were compared. Malarious and noninfected lizards utilized the microhabitat in similar ways, except that infected animals perched more often in shade. Fully 94% of the time lizards were observed, they spent perched, unmoving and apparently visually scanning the local area. Although behavior patterns differed seasonally and between sexes and age classes, they were very similar in infected and noninfected lizards. Noninfected adult males, though, spent more time engaged in social behaviors than did malarious males. Social interactions appear strenuous, occasionally lasting several minutes. Such social activities by the lizard may depend on rapid oxygen consumption that is disrupted by *Plasmodium* infection. Number of burst runs and length of runs were similar for both infected and noninfected animals; most lasted less than 1 sec, and the longest covered 6 m. In laboratory experiments, recovery from burst runs was rapid (less than 1 min/sec of running), probably negating any ecological consequences of an effect of the parasite on rate of metabolic recovery by infected lizards. The behavior of malarious lizards, compared to noninfected animals, can be explained by the effects of *Plasmodium* infection on the host's energy metabolism, as measured in the laboratory. These results demonstrate that estimating the virulence of parasitic infection requires both laboratory studies and observation on the host in a natural setting.

PARASITES are enormously abundant, both in number of individuals and diversity of species, but the role they play in shaping behavioral variation in their hosts is rarely considered. For example, virtually every lizard population surveyed hosts a wide array of parasite taxa, yet knowledge of the effects of these parasites on the natural activities of their hosts is meager. Parasites sometimes alter, or even manipulate, the behavior of their hosts (Holmes and Bethel, 1972), so that a fraction of the behavioral variation observed within lizard populations might be a result of parasite-host interactions. This would be a significant result because lizard models have proven very useful in testing hypotheses dealing with social, feeding, and activity behavior of vertebrates.

Perhaps the best known lizard-parasite system is the western fence lizard (*Sceloporus occidentalis*) and its malarial parasite, *Plasmodium mexicanum*, in northern California (Ayala, 1970; Bromwich and Schall, 1986; Schall, 1983a). In

northern California, fence lizard populations often sustain malarial prevalence of 25% or more (Ayala, 1970; Schall, 1983a). *Plasmodium* infection disrupts lipid storage by the lizard host with a concomitant reduction in testis size for male lizards and clutch size of females (Schall, 1983b). Infection also results in erythrocyte destruction and host anemia. This initiates a cascade of effects: hemoglobin levels drop 25%, maximal oxygen consumption decreases, and aerobically supported running stamina declines about 20%. Sprint, or burst, running, which is anaerobically supported in lizards, is not affected by malarial infection (Schall et al., 1982; Schall, 1983a).

The disruptions of physiological processes and behavioral performance that are observed in the laboratory suggest that malarial infection may alter the activities of *S. occidentalis* under natural conditions. For example, any vigorous activity that is supported aerobically, such as sustained social interaction or lengthy flights from a predator's attack, could be affected det-

rimentially. Activity bursts are anaerobically supported, but recouping from such sprints requires an aerobic component in vertebrates. Sprints to food, away from predators, or in response to social stimuli could occur more often than the lizard's ability to recover aerobically. In that case, malarious lizards might make fewer short runs, gather less food, be more wary of predator attack, choose safer perch sites, and engage in social activity less frequently. Although there is no supporting evidence, the smaller testis size in infected males could result in lower hormonal titers and less aggressive social interaction. Clearly, all of these possible behavioral consequences of *Plasmodium* infection would have detrimental effects on the host's reproductive success or fitness.

Establishing a causative connection between the parasite-induced pathology that is observed in the laboratory, and ecologically important costs to the host, or virulence, requires observations on the lizard in a natural setting. We have quantified the behavioral time budget of free-ranging *S. occidentalis* to compare malaria-infected and noninfected lizards. We sought answers to three questions. First, do infected and noninfected lizards partition activity time in different ways? Second, how often do *Sceloporus* maintain vigorous activity for periods of time long enough for aerobic respiration to become important? Third, do sprint runs occur often enough so that the rate of recovery would become a limiting factor for malarious lizards? Estimates of recovery time following sprints by lizards have not been reported; we therefore needed to conduct laboratory measurements of recovery rate. To our knowledge, these data represent the first quantification of the effects of parasitism on the natural behavior pattern of any lizard.

#### METHODS

We observed fence lizard behavior from 23 May to 28 July 1982 at the Hopland Field Station of the University of California. The station is a 24 km<sup>2</sup> tract of oak savanna located 140 km north of San Francisco, California. The *Sceloporus-Plasmodium* system has been under study there for 8 yr. A more detailed discussion of the Hopland Field Station is given by Schall (1983a) and Bromwich and Schall (1986).

Eight study areas were used. Most of the adult and subadult lizards had been permanently marked by toe clipping and had a number paint-

ed on their dorsal surface with Liquid Paper® as part of a separate study on the course of malarial infection in the lizard hosts (Bromwich and Schall, 1986). Blood smears for each animal were later stained with Giemsa and examined for parasites. The identification number of each marked lizard was usually visible and recorded during the observations, but we did not learn which animals were infected with *Plasmodium* until the data analysis stage of the project when the blood smears were examined.

In making comparisons, we classify animals as either infected or not infected at the time observations were made; no reference is made to the level of infection. Although intuition suggests parasite load should be correlated with effects on the host, the relationship is in fact inconsistent (Schall, 1983a, 1983b), suggesting that the best objective comparison to make is between infected and noninfected lizards.

Upon entering a study area, we scanned all logs, rocks, tree trunks, fence posts, building walls, and the ground surface. When a lizard was seen, observations began and a tape recorded spoken record was continuously made while the animal was quietly observed with binoculars. Observation distance was generally 6–16 m, a distance that should have minimized observer effects on the lizards' behavior. Observation time was broken into 5 min intervals; after 3 consecutive intervals, observations were terminated and the habitat scanned for a new subject to observe. The following were recorded for each observation period: 1) date; 2) study site; 3) air temperature at about 1 m height; 4) time of day; 5) observation distance; 6) animal number; 7) sex (available from records kept during the mark-recapture program); and 8) age of lizard recorded as juvenile (<60 mm snout to vent length) or adult (>60 mm SVL). Almost all juvenile lizards observed were about 50–59 mm snout-vent length and were probably animals hatched the previous summer. The manner in which each lizard utilized microhabitats was classified as: Place (log, rock, fence, tree, ground); Sun Quality (sunny, shade, mixed sunshade, tree canopy-filtered sun, overcast); Body Position (relative to ground surface: horizontal, vertical with head up, vertical with head down, diagonal with head up, diagonal with head down, hanging with dorsal surface down); Relation to Substrate (entire body in contact with substrate, body in contact with substrate but with head up, entire body and head up). Place, body position, and relation to substrate were recorded

at the last second of each 5 min observation period.

Last, the activity of the subject was recorded as: 1) Not Moving; 2) Eat; 3) Defecate; 4) Lick substrate; 5) Bob, or "push-up" behavior; 6) Other Social behavior; 7) Walk; 8) Run to Food; 9) Other Run (nonsocial); 10) Pause during other active movements; 11) Fidget; and 12) Scratch. Most behavior regarded as "social" consisted of full body bobs or push ups, in which the entire head, trunk, and abdomen were suddenly thrust upward so that the lizard was standing on fully extended limbs. Other social interactions, mostly brief chases and mutual circling struts, are gathered into class 6. Class 9 behaviors are probably class 6 and 8 behaviors that we failed to discriminate. Class 11 consisted of wiggling, very brief walks, or repositioning of the body. Class 12 consisted primarily of scratches by the hind foot administered to the neck region.

Whenever a lizard ran, we noted topographical features located at the origin and terminal points of the run and recorded these features onto the spoken tape record. At the end of the 15 min observation period for that animal, a metal meter tape was used to measure the length of the run, using the spoken record to help in relocating the origin and final destination of the run.

In the laboratory, tapes were reviewed and data recorded as number of seconds within each 5 min observation period for each behavior class. Thus, we report the proportion of total seconds of observation that lizards spent performing each kind of activity. Such behavioral time budgets, or ethograms, are useful for gross inspection. However, statistical comparisons among classes of animals (infected vs noninfected) are precluded because each second of behavior was not an observation independent of all others. For comparisons between infected and noninfected fence lizards we use the proportion of observation periods that contained any time devoted to each behavior, and comparisons of mean duration of each activity class within the observation periods.

To determine recovery time after burst activity, uninfected adult male lizards were placed in a 232 ml airtight glass chamber within a lighted incubator set at 35 C, the modal body temperature of free-ranging *S. occidentalis* (Schall, unpubl.). Tubes entering and leaving the chamber were brought out of the incubator and fed into a peristaltic pump, then through a column

of drierite to remove water vapor and ascarite to remove CO<sub>2</sub>, then finally to a Beckman E2 Oxygen analyzer. A 400 ml volume of air was allowed to flow around this closed system while oxygen content of the air was monitored. (The exact volume of gas in the system depended on the volume of the contained lizard.) Pin electrodes were placed into the base of the lizard's tail and brought out of the chamber and incubator to a Harvard stimulator so that very small jolts of electric current could be administered to the lizard while it was in the closed chamber.

While fresh air was pumped in, the system remained open for 1 h to permit the enclosed lizard to recover from being handled, then closed to monitor oxygen consumption. Once oxygen consumption reached a constant rate (indicated by a tightly linear decline in the system O<sub>2</sub> content), a short jolt of current was administered to the lizard. While observing through an observation slit we could record the duration of rapid running performed by the lizard within the glass chamber. If a lizard suddenly initiated a second burst of activity, the observations were terminated and data discarded. The duration of running for any single experiment could not be controlled, but the duration varied among experiments from 1–10 sec and thus provided a range of sprint running comparable to what was observed in the field. Soon after the stimulation was applied, the O<sub>2</sub> consumption rate increased markedly. When oxygen consumption rate returned to the original level, we could quantify the time needed for recovery. We do not assert that the extra oxygen used by animals in such an experimental apparatus estimates the extra oxygen used to remove lactate from muscle, but it does estimate the extra oxygen used by a lizard under conditions simulating sprint runs in the wild.

## RESULTS

During the 2 mo period, 1203 five minute observation intervals were recorded, totaling almost exactly 100 h. For comparisons between *Sceloporus* that were either infected or not infected with *Plasmodium*, the sample is somewhat smaller because positive identification of some observed animals was not possible (sample sizes given in Tables 1 and 2 are converted to total time in hours). The number of observation periods varied from 1–28 among 146 identified lizards used in this analysis; however, distribution of observation periods among lizards with-

TABLE 1. TIME BUDGET FOR *Sceloporus occidentalis* GIVEN IN PROPORTION OF TOTAL TIME LIZARDS WERE OBSERVED. Each observation period on an individual lizard lasted 5 min. Total time spent watching all lizards is given in hours.

Behavior class	All lizards	Males		Females	
		Adults	Juveniles	Adults	Juveniles
1. Not moving	.93713	.88138	.96400	.97125	.96619
2. Eat	.00136	.00115	.00006	.00052	.00190
3. Defecate	.00038	.00029	—	.00023	—
4. Lick	.00062	.00113	.00063	.00027	.00040
5. Bob	.01386	.03608	.01441	.00229	.00386
6. Other social	.02593	.03872	.00283	.00588	.00258
7. Walk	.01218	.01762	.00679	.00816	.01146
8. Run to food	.00082	.00102	.00048	.00069	.00171
9. Other run	.01030	.01479	.00854	.00750	.01034
10. Pause	.00134	.00291	—	.00012	—
11. Fidget	.00312	.00462	.00251	.00296	.00153
12. Scratch	.00015	.00029	.00019	.00013	.00003
Total hours	99.98	28.06	8.75	33.89	8.92

in the infected and noninfected samples was very similar (Fig. 1). Thus, although some animals were observed more often than others, the patterns in number of observations were similar for infected and noninfected lizards.

Larger *S. occidentalis* are typically more likely to be infected with malaria than smaller lizards (Schall, 1983a), perhaps because they are generally older. This relationship would seriously bias comparisons of behavior of infected and noninfected lizards. However, in the lizards observed in this study, body size between infected

and noninfected animals did not differ (for example, for adult noninfected males,  $\bar{x}$  SVL = 65.9 mm, infected males  $\bar{x}$  = 66.1; adult noninfected females  $\bar{x}$  = 67.8, infected females  $\bar{x}$  = 67.0; U tests,  $P > .05$ ). We have no explanation for the discrepancy between these results and those in Schall (1983a), but we can assume that there is no systematic body size bias in our results on behavior.

Our eight study areas differed in structure and degree of shade cast by trees. Proportion of animals located on different structures (log,

TABLE 2. TIME BUDGET FOR *Sceloporus occidentalis*, COMPARING LIZARDS INFECTED AND NOT INFECTED WITH MALARIA (*Plasmodium mexicanum*). Proportions of total time are given as well as total time spent watching all lizards within each group.

Behavior	Infected with malaria			Not infected with malaria		
	Adult M	Adult F	Juveniles	Adult M	Adult F	Juveniles
1. Not moving	.92079	.98199	.95864	.86303	.97385	.96819
2. Eat	.00070	.00051	.00215	.00147	.00051	.00058
3. Defecate	.00081	—	—	—	.00027	—
4. Lick	.00084	.00019	.00051	.00136	.00029	.00053
5. Bob	.02260	.00296	.00220	.04455	.00210	.01115
6. Other social	.03026	.00194	.00266	.04335	.00366	.00257
7. Walk	.01333	.00370	.00226	.02113	.00724	.00747
8. Run to food	.00056	.00083	.00299	.00134	.00073	.00039
9. Other run	.00817	.00514	.01463	.01669	.00827	.00706
10. Pause	—	—	—	.00476	.00017	—
11. Fidget	.00185	.00269	.00237	.00196	.00274	.00192
12. Scratch	.00008	.00005	.00006	.00036	.00017	.00014
Total hours	17.16	23.96	12.01	9.90	6.00	4.92

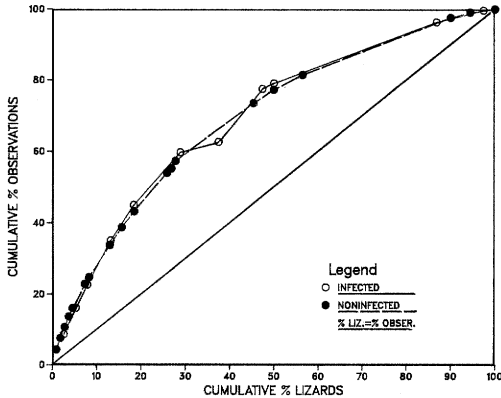


Fig. 1. Cumulative percent of total number of 5 min observation periods plotted against cumulative percent of total number of individual lizards observed for two samples, *Sceloporus occidentalis* infected with a malarial parasite and lizards not infected. The individual lizards were entered into the analysis in order of the number of observation periods for each animal; the most frequently seen lizard was entered first. If all individual lizards were seen an equal number of times, the points would fall on a straight line with slope of unity.

fence, etc.), and in different lighting conditions, differed among sites ( $\chi^2$  tests,  $P < .05$ ). As might be expected from these results, the proportion of animals in different body positions or their relation to the substrate also differed from site to site ( $\chi^2$  tests). Therefore, to prevent any bias, an approximately equal proportion of time was spent at each site. Lizards became difficult to find after 1400 h when air temperatures were high. Despite an increased effort during late afternoons to observe fence lizards, fully 80% of the observation time occurred before 1400 h. Proportion of animals infected with *P. mexicanum* was similar among sites ( $\chi^2$  test,  $P > .05$ ).

*Timed behaviors.*—Table 1 presents the proportion of time spent on each of 12 behavior classes. Data combined for all lizards observed reveal that fully 94% of time is spent not moving. Presumably, *S. occidentalis* is a sit-and-wait predator and spends this time visually patrolling the local area.

To determine the efficacy of our methods in differentiating behaviors, we compare adult males with females, and juveniles with adults. Proportion of time spent not moving appears similar for adult females (97%) and male and female juveniles (96%), but is somewhat lower for adult males (88%). When behavior classes 5

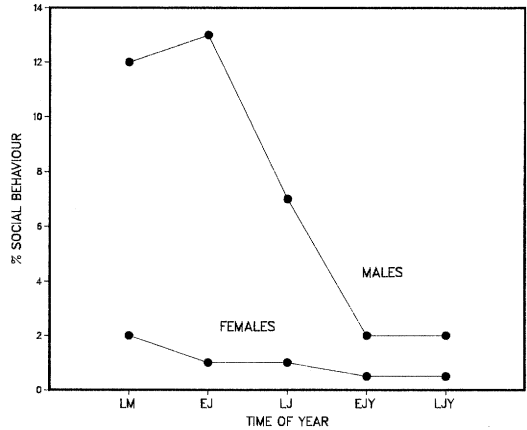


Fig. 2. Proportion of time spent on social interactions by male and female *Sceloporus occidentalis* over spring and summer. Time of year ranges from late May (LM) through late July (LJy).

and 6 are combined to represent social activities, adult males were socially active 7% of the observed time, whereas juvenile males (2%), adult females (<1%), and juvenile females (<1%) were socially active less often. Only 12% of observation periods of adult females included some social interaction, compared to 58% of the sample of males ( $\chi^2$  test,  $P < .001$ ). Social activity by adult males was observed more frequently early in the season when lizards were breeding (Fig. 2 and Kruskal-Wallis tests for mean duration of social activity within observation periods,  $P < .001$ ).

In Table 2 data are split to compare malarial and nonmalarial *S. occidentalis*. Both infected and noninfected *Sceloporus* spend most of their time not moving; therefore, possible effects of malarial infection must be sought in an examination of other behavior classes. For adult males, adult females, and juveniles, time spent in social behaviors (classes 5 and 6) are greater for noninfected animals (for example, 1.37% vs 0.49% for juveniles). This pattern remains when the juvenile age group is broken into males and females. Noninfected juvenile males spent 47% of their active behavior time (classes 2–12) on social interactions, whereas noninfected juvenile females spent 34%. For infected individuals, male juveniles spent 20% of active behavior on social activities and female juveniles spent 10%. Thus, male juveniles appear more social, but infected animals of both sexes spend less time on social interaction.

Duration of each behavior class within ob-

TABLE 3. MICROHABITAT LOCATION AND BODY POSITION OF *Sceloporus occidentalis* RECORDED AT LAST SECOND OF EACH 5 MIN OBSERVATION INTERVAL.

		Combined sample		Infected with malaria		Not infected with malaria	
		Number	%	Number	%	Number	%
Place	Log	548	45.6	138	55.2	269	42.1
	Rock	174	14.5	20	8.0	68	10.6
	Fence	276	23.0	62	24.8	167	26.1
	Tree	106	8.5	4	1.6	77	12.1
	Ground	101	8.4	26	10.4	58	9.1
Sun quality	Sunny	411	34.2	75	30.4	210	33.1
	Shade	258	21.5	73	29.2	122	19.1
	Sun/shade	298	24.8	56	22.4	164	25.6
	Filtered	148	12.3	21	8.4	94	14.7
	Overcast	87	7.2	24	9.6	48	7.5
Body position	Horizontal	450	37.4	105	42.0	241	37.7
	Vert (up)	175	14.6	17	6.8	106	16.6
	Vert (down)	159	13.2	34	13.6	85	13.3
	Diag (up)	334	27.8	57	22.8	179	28.0
	Diag (down)	70	5.8	31	12.4	25	3.9
	Hanging	14	1.2	6	2.4	3	0.5
Relation to substrate	Body flat	155	13.2	30	12.1	75	12.0
	Head up	291	24.8	65	26.3	167	26.8
	Body/head up	728	62.0	152	61.5	381	61.1

servation intervals was compared between infected and noninfected adult lizards, analyzing sexes separately (Mann-Whitney U tests). Only one comparison was significant; the mean period of social activity (classes 5 and 6) of noninfected males was significantly longer than for infected males (26.4 sec vs 15.8 sec for the entire season; 43.3 sec vs 25.6 sec for observations during May and June only). During the reproductive season in May and June, 74% of noninfected adult males were socially active during the observation period, but only 47% of infected males interacted socially ( $\chi^2$  test,  $P < .001$ ). Social interactions occasionally lasted for several minutes. The most time devoted to bobbing (class 5 behavior) that we observed was 90 sec and the longest uninterrupted social interaction was 494 sec (over 8 min!).

*Microhabitat and body position.*—Point observations of microhabitat use and body position made at the last second of each 5 min interval are summarized in Table 3. For a more complete picture of microhabitat use by *S. occidentalis*, the relationship of date, time of day, and sex and age of the lizard to Place, Sun Quality, Body Position, and Relation to Substrate were all compared with  $\chi^2$  tests. Not surprisingly, fence lizards are found significantly more often in the

sun early in the day before 1200 h (46% of animals) and in the shade during the hot afternoon period after 1400 h (28%). Earlier in the season (May and early June) *Sceloporus* are more likely to be positioned with their head and body off the substrate (72%), compared to only having their heads up (5%). The proportions became more similar by late July (45% vs 46%). Perhaps this represents more visual patrolling of the nearby habitat earlier in the season. Surprisingly, except for these two relationships, no other significant associations emerge from the analysis, including comparisons using lizard sex or age.

Place, Sun Quality, Body Position, and Relation to Substrate are all interrelated ( $\chi^2$  tests, all  $P < .05$ ), as might be expected. For example, lizards on logs and rocks were more often in the sun, whereas lizards on trees were more often in the shade. Most logs were the product of fallen trees and were in the open sun. During periods of time when overcast conditions existed, 51% of lizards had their body compressed against the substrate, and during other periods only 8–17% were so positioned. During overcast conditions lizards were most likely maintaining body temperature by receiving conductive heat from a warm substrate.

Table 3 also presents a comparison of infect-

TABLE 4. MOVEMENTS OF *Sceloporus occidentalis* OBSERVED DURING 1202 FIVE MINUTE OBSERVATION INTERVALS.

	Number of movements per five minute interval										
	0	1	2	3	4	5	6	7	8	9	10
Walk	72%	17%	5%	3%	1%	1%	<1%	—	—	<1%	<1%
Run to food	97%	3%	1%	—	—	<1%	—	—	—	—	—
Other run	75%	14%	6%	2%	2%	<1%	<1%	<1%	<1%	—	<1%

ed and noninfected lizards. Although the comparisons for Place and Body Position are significantly different for malarious and noninfected animals, the order of importance of each class was similar. Sun Quality at perching sites for infected and noninfected lizards also differed significantly. Data compressed into sunny (sun and sun/shade) and shady (shade, filtered sun, overcast) classes reveal that noninfected animals were more likely to be in sunny locations than malarious lizards (59.5% vs 49.6%;  $\chi^2$  test,  $P < .05$ ). Curiously, body temperature distributions of infected and noninfected animals do not differ (Schall, in prep.). Although there appears to be no clear trend in habitat use or body position that emerges from Table 3, perhaps infected *Sceloporus* spend more time out of the sun.

*Frequency and distance traveled during runs and walking.*—Table 4 summarizes the number of walks and runs made by lizards during the 5 min observation intervals, and demonstrates that fence lizards seldom run more than once during any 5 min period. During 100 h of observation, 599 runs (classes 8 and 9) were observed, an average of 6 runs each hour. Of 599 runs, only 419 could be accurately measured because animals occasionally ran out of the observer's line of sight. Table 5 shows that most walks and runs were quite short; the longest run seen was only 6 m in length. In the laboratory, *S. occidentalis* sprint at a mean velocity of 1.4 m/s (Schall et al., 1982). Most runs would therefore take un-

der a second to complete, with the longest consuming only about four seconds.

Number of runs and walks and distance traveled can be compared between infected and noninfected animals. When contingency tables are compressed to yield expected values of  $>5$  for all cells, none of the comparisons result in significant differences. Infected animals apparently are not more likely to avoid running and do not run shorter distances.

*Recovery from burst activity.*—Figure 3 shows a plot of oxygen consumption over time of an uninfected male *S. occidentalis*. In this example the slope of oxygen consumption did not return to the exact preexercise level. In a majority of experiments, however, the slopes before running and after recovery were indistinguishable, making the estimate of recovery time more precise. The rate of oxygen consumption increases dramatically after burst exercise. Recovery time generally increases with duration of the run (Fig. 4;  $r_s = .758$ ,  $P < .05$ ). Mean time to recovery was 0.93 min for each second of running (SD = 0.25). Thus, the longest run observed in our study (4 sec) would have taken about 4 min recovery time; the vast majority of runs would require far less than one minute of recovery.

## DISCUSSION

*Parasite pathogenesis and parasite virulence.*—Parasites make up a substantial portion of the world's animal species (Dogiel, 1966; Price,

TABLE 5. DISTANCE TRAVELLED DURING MOVEMENTS BY *Sceloporus occidentalis* OBSERVED DURING 1203 FIVE MINUTE INTERVALS.

	Distance traveled					
	<.5 m	.6-1.0 m	1.1-2.0 m	2.1-3.0 m	3.1-4.0 m	4.1-6.0 m
Walk (N = 348)	68%	17%	8%	5%	1%	1%
Runs to food (N = 37)	30%	30%	32%	8%	0	0
Other run (N = 382)	36%	24%	19%	13%	5%	3%

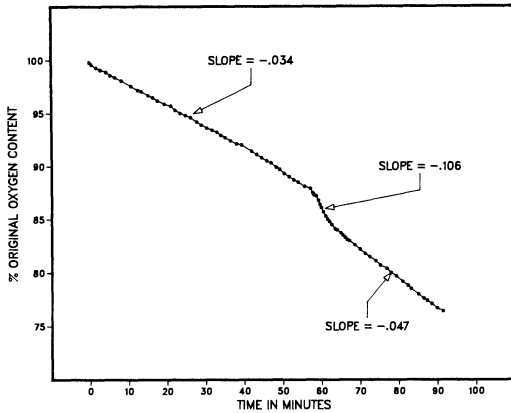


Fig. 3. Oxygen consumption of adult male *Sceloporus occidentalis* during rest and after a short burst of activity. Oxygen content of closed chamber given in percent oxygen at start of experiment. Oxygen content of chamber decreases gradually over time, but at a faster rate for period after a brief burst of activity. Duration of recovery period measured from end of activity burst to return of oxygen consumption curve to original slope.

1980), so it is not surprising that every carefully surveyed lizard population has been shown to support a rich parasite fauna. In a study of 26 lizard species from southern California, Telford (1970) found they supported 24 protozoan, 22 nematode; and 5 other helminth parasite species, for an average of 11 endoparasite species per lizard species. In Sierra Leone, West Africa, *Agama agama* hosts six protozoans in the blood alone, including two species of *Plasmodium* (Schall, in prep.). Some authors have suggested that these parasites are most often harmless to their hosts (Telford, 1971), but this view is supported only by anecdotal evidence. In fact, some of these parasites could affect their lizard hosts' ability to retain territories, secure mates, and obtain resources necessary to produce young, thus reducing host fitness. Likely candidates for parasites with a virulent nature would be the haemoproteozans which substantially disrupt the functioning of the host's blood tissue.

*P. mexicanum* is known to cause important pathology in its host, the western fence lizard (Ayala, 1970; Schall et al., 1982; Schall, 1983a, 1983b). Because the pathology induced in fence lizards by malaria is well described, this system is an ideal one in which to seek a link between pathology observed in the laboratory and the behavior of the host in the wild. Parasitologists frequently describe the pathogenic nature of

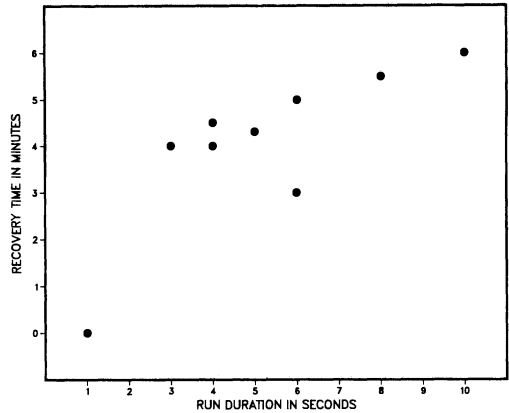


Fig. 4. Recovery time after short bursts of activity of *Sceloporus occidentalis* for various lengths of activity. Recovery time measured using graphs similar to one in Figure 3. Each point represents one observation; each observation was made on a different adult male lizard.

parasites. From the host's perspective, however, the only pathologies that are important are those that affect reproductive success. Thus, it is important to evaluate the impact of parasites in the proper ecological context. In the case of *S. occidentalis*, we proposed that the known physiological consequences of malarial infection could have an important impact during lengthy runs by infected lizards to catch food, escape predators, or engage in social interactions, all vital to final lifetime fitness. Burst activity, in contrast, is supported anaerobically and would be hindered by malarial parasitism only if recovery time from such bursts was lengthy compared to the time between sprint movements.

*Suitability of research methods.*—We first had to confirm the efficacy of our methods in detecting significant behavioral alterations in infected hosts. Time budget data reveal differences between males and females that are often observed in studies on lizard behavior (Andrews, 1971). Males are more often socially active than are females and the sexual difference is observed even in juvenile lizards. Frequency of social interaction also varies seasonally and is most intense early in the spring when animals establish territories. Fence lizards are more likely to be in the sun early in the day than they are in the hot afternoon and are more likely to be positioned flat against the substrate when overcast conditions prevail. These associations are not surprising, thus essentially calibrating



the data presented here. Our research methods should therefore be useful in comparisons of malarious and noninfected *Sceloporus*.

*Comparisons of Plasmodium-infected and noninfected lizards.*—No clear difference in microhabitat use emerges in a comparison of infected and noninfected fence lizards, except that infected animals may spend more time in the shade than noninfected individuals. This is surprising because body temperature distributions of the two groups do not differ either under natural conditions or in laboratory thermal gradients (Schall, in prep.). As discussed below, infected animals appear to be socially active less often, so it is possible that infected lizards are pushed into suboptimal parts of the habitat where there is relatively more shade.

In the laboratory lizards parasitized with *Plasmodium* exhibited reduced maximal oxygen consumption and running stamina (Schall et al., 1982; Schall, 1983a), suggesting locomotive behaviors would be likewise impaired in the wild. However, under field conditions malarious fence lizards ran just as often, and the distances run were not shorter than runs of noninfected animals. No *Sceloporus* were observed to run for longer than 6 sec, a sprint that would be primarily anaerobically supported. Sprint runs occur only about once every 10 min. As recovery time from burst activities is about 1 min for each second of running, and the duration of most runs was only a second or less, it would be a very rare event for a fence lizard to be physiologically stressed by frequent sprints. Although the effect of *Plasmodium* infection on recovery rate has not been measured, we assume that the magnitude of any decrement would be similar to that seen in maximal oxygen consumption, or about 25% (Schall et al., 1982). For malarial infection to disrupt recovery to a degree that would be ecologically important, the impact on rate of recovery would have to be much more severe than a 25% decrement. Thus, the pathology observed in the laboratory, while interesting, may not have any consequences in normal ecological situations for sprint running.

During our observations we never saw any predation on *S. occidentalis*. Frequency of broken and regenerated tails may estimate the intensity of predation (Schall and Pianka, 1980). Approximately 35% of adult females and 50% of adult males have such injuries, demonstrating that predation is common on fence lizards

(Schall et al., 1982). Do *Sceloporus* occasionally need to run long distances while fleeing a predator? When we have pursued lizards to simulate a constant attack, they sometimes made several short bursts of activity while seeking a hiding place, but the sum of these bursts never reached even 20 sec. Also, tail break frequencies do not differ between infected and noninfected fence lizards (Schall et al., 1982).

The most striking difference between animals parasitized with malaria and those unparasitized is the decreased duration and frequency of social interactions in infected males. Three known effects of malarial infection on *Sceloporus* could account for this observation (Schall, 1983a, 1983b). First, malaria negatively affects the size of testes, and thus perhaps hormonal levels. Second, infection disrupts lipid storage so infected lizards might spend a greater fraction of their time in food gathering activities such as visual patrolling of the nearby environment rather than social activities. Third, extended social interaction might require substantial aerobic metabolic activity. Some social interactions we observed lasted several minutes, so the aerobic commitment during these intense activities must be substantial. Reduction in social activity by malarious males may result in their maintaining territories of inferior size or quality, potentially a major insult to their lifetime reproductive success.

Thus, the physiological and behavioral effects of malarial infection on *S. occidentalis* that were observed in the laboratory are neatly concordant with the effects on behavior that we observed under natural conditions. Our results, though, call into question the view that parasite-induced pathology observed in the laboratory can always be used as an indication of a parasite's real virulence in a natural setting. Information gleaned from laboratory studies, such as those on effects of malarial infection on *S. occidentalis* aerobic capacities, become meaningful only in the context of ecologically relevant observations made on free-ranging animals. Coordinated laboratory and field studies must become standard before any understanding of the importance of parasites for the biology of lizards is reached.

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DEPARTMENT OF ZOOLOGY, UNIVERSITY OF VERMONT, BURLINGTON, VERMONT 05405. Accepted 18 March 1986.