

culature of *B. peripatetes* is typical of *Bufo* as opposed to *Atelopus* and *Crepidophryne*. *Bufo peripatetes* has a short m. tensor fasciae latae and a m. adductor longus is present as in other lower Central American toads with a reduced auditory apparatus (no tympanum or pseudocolumella).

The sexual dichromatism in *Bufo peripatetes* is reminiscent of that seen in the endemic Costa Rican toad *B. periglenes* (Savage, 1967). In life, male *B. periglenes* are uniform bright yellow-orange or orange-red, and in preservative they are a uniform faded yellow. In life, dorsal color varies in female *B. periglenes* from greenish yellow to black with bright scarlet spots, and the ventral surfaces frequently have black mottling. In preservative, female *B. periglenes* have dark tan to black dorsa with distinct or indistinct yellow spots; in some, the spots coalesce to form stripes. The ventral surfaces are tan with light to heavy black mottling. Savage (1967) hypothesized that sexual dichromatism in *B. periglenes* functions in sexual recognition since this diurnal species lacks an auditory apparatus and an advertisement call, although retaining Eustachian tubes and ostia pharyngea. Savage (1967) was incorrect in stating that *B. periglenes* lacks a release call, which consists of a single low chirp. *Bufo peripatetes* lacks an auditory apparatus, and the sexual differences in color also may be related to sexual recognition.

*Bufo peripatetes* apparently is most closely related to *B. holdridgei* (Cordillera Central of Costa Rica) and *B. fastidiosus* (Cordillera de Talamanca of Costa Rica and Panama), and may occur sympatrically with the latter species. As pointed out by Savage (1972), these species are similar in overall morphology and in the complete reduction of the auditory apparatus (no tympanum, pseudocolumella, Eustachian tubes, or ostia pharyngea). *Bufo holdridgei* is a smaller toad (maximum SVL 61.7 mm,  $\bar{x}$  = 41.5 mm in males, 45.7 mm in females) with reduced cranial crests and warting. *Bufo peripatetes* differs from *B. fastidiosus* in size, coloration, and in the number, size, shape, and arrangement of warts (Savage, 1972). Adult male *B. fastidiosus* have a maximum SVL of 51.5 mm, females 59.0 mm; the dorsum is black with reddish parotoids, and most warts are reddish. The dorsal warts are strongly conical and pointed.

*Acknowledgments.*—We thank W. R. Heyer and R. W. McDiarmid at the National Museum of Natural History (USNM) for calling our attention to, and allowing us to examine, the series of *Bufo peripatetes*. A. G. Kluge, Museum of Zoology, University of Michigan (UMMZ), graciously loaned us the holotype for direct comparison with the new material of this species. K. Lips commented on the manuscript.

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- Journal of Herpetology, Vol. 26, No. 1, pp. 74–76, 1992  
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### Malarial Parasitism and Home Range and Social Status of Male Western Fence Lizards, *Sceloporus occidentalis*

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Parasites have long been viewed as playing only a minor role in the behavioral ecology of their hosts. Indeed, few studies attempt to control for the confounding effects of parasitism when testing behavioral hypotheses. This prejudice probably stems from parasitologists' lore, now discredited, that argues the coevolution of parasite and host typically leads to a harmonious relationship with minimal impact on the host (Dogiel, 1966).

In recent years there has been an increased interest in the impact of parasites on the behavior of their hosts (Barnard and Behnke, 1990; Keymer and Read, in press). These studies have demonstrated that the consequences of infection for hosts can be subtle, but important. For example, a long-term study of malaria (*Plasmodium mexicanum*) in western fence lizards, *Sceloporus occidentalis*, has demonstrated that the behavioral time budgets of infected and noninfected lizards are very similar, except that infected fence lizards spend less time in social activity than noninfected animals (Schall and Sarni, 1987). In experimental manipulations using large outdoor enclosures, infected males are less able to compete with noninfected males for access to female lizards (Schall and Dearing, 1987). Furthermore, infection appears to alter the ventral color of males, an important, sexually dimorphic trait (Ressel and Schall, 1989). These results suggested to us that malarial infection may alter the social status of male fence lizards and reduce their ability in nature to maintain a territory or large home range when in competition with noninfected animals. If so, this would be a significant finding because lizards have played a substantial role as models in studies of home range and territoriality (Stamps, 1977; Ruby and Dunham, 1987), and malarial infection is common in many lizard populations (Schall, 1990a).

We examined the effect of malarial infection on the behavior of male western fence lizards, *Sceloporus occidentalis*. The study was conducted at the Hopland Field Station of the University of California, a tract of oak woodland approximately 160 km N of San Francisco. Three sites were chosen, ranging in area from 0.16 to 0.70 ha. The habitat at lower elevations at Hopland consists of rolling grassy hills with patches of open woods (a complete description is found in Schall, 1983). We chose as our sites areas of old fallen trees, branches, rocks, and boulders that were surrounded by open grassy pastures, a habitat rarely used by fence lizards. Thus, the sites were fairly discrete patches of suitable habitat for the lizards. Each site was on a hillside, or near a sharp rise; lizards could then be readily observed from the higher vantage point.

TABLE 1. Comparisons between male *Sceloporus occidentalis* infected and not infected with the malarial parasite *Plasmodium mexicanum*. Given in upper part of table are means, followed by standard deviations in parentheses and sample sizes. Results of Mann-Whitney U tests also given. In lower part of table are numbers of males rated by social status.

	Not infected	Infected	P
Minimum number of days on the site	43.4 (13.8) 24	34.5 (20.3) 10	0.198
Number of days seen on site	13.5 (8.0) 24	9.3 (8.9) 10	0.161
Number of sightings	20.5 (13.1) 24	10.5 (10.9) 10	0.031
Number of times chased another lizard	2.5 (2.6) 24	0.3 (0.7) 10	0.003
Minimum home range size (m <sup>2</sup> )	13.7 (13.5) 21	9.2 (1.9) 6	0.838
Maximum home range size (m <sup>2</sup> )	21.1 (17.6) 20	15.3 (4.2) 6	0.692
Submissive	3	6	
Neutral	4	4	
Dominant	17	0	

Adult male lizards were collected (SVL 60–78 mm, N = 41), marked with numbers painted with Liquid Paper®, and a blood smear made from a clipped toe. Lizards were returned to the point of capture within five h. Blood smears were stained with Giemsa and examined at 1000×. Infection condition of the lizards was determined only after behavioral observations were completed to avoid influencing the observers. Each site was mapped to locate logs, stumps, trees, and rocky outcrops and boulders.

Observations began five days after the lizards were marked and continued for 50 d during the normal breeding period of the lizards (17 May–5 July). Each day, the three sites were visited one to three times, from one to three hours each. The sites were scanned with binoculars to find animals and the locations of sighted lizards were marked on the site map. Each site had at least two useful locations from which to conduct visual scans; the observer would move slowly between these locations during the observation period. Whenever interaction between two individuals was seen, the animals were watched continuously to determine the outcome. We made no effort to systematically search the sites for the presence of marked animals each day because this could have altered the behavior of the lizards. Thus, only those lizards visible from our vantage points were observed. Our goal was strictly to compare the behavior of infected and noninfected lizards at the sites; therefore, values given for home range size and other measures should not be compared with those determined by more systematic methods for this or other species. In particular, our method may result in an underestimate of home range size of subordinate, or otherwise less mobile individuals.

The time between the initial capture date for each lizard and the last day the lizard was seen on the site yields the "minimum number of days on site." "Number of sightings" for each lizard gives the number of visits during which an animal was seen. Total number of visits for each site was approximately 100.

Home range size was estimated as the area of a minimum polygon connecting all the points of sighting; the area of this polygon was measured on the maps with a Zeiss digitizing planimeter. As sample size can greatly skew estimates of home range area, home range was estimated only for those lizards with

four or more sightings (Ruby and Dunham, 1987). Our observations demonstrated that male fence lizards have a core range where they spend most of their time, but they also may occasionally travel to more distant areas for brief periods. We therefore distinguish between "maximum home range" which is determined from all sightings, and "minimum home range" which is determined by casting out from analysis any one- or two-outlier sightings.

At the end of the observations, but before determining the infection status of the lizards, we ranked the dominance status of each male. "Dominants" were those males that frequently chased other males, were never seen being displaced by another male, frequently courted females, and were often seen performing push-up displays from high perches. "Neutral" males seldom or never chased other males, sometimes were displaced from a perching point by another male, and infrequently displayed from a high perch. "Submissive" males never chased other males, frequently were chased by other males, and were never seen displaying.

Of 41 adult males marked, seven were not seen again at the sites. Three of these were infected, four were not infected. Thus, a slightly higher portion of infected lizards may have left the sites immediately after being marked (23% vs. 14%), but small sample sizes precludes statistical analysis. Further analysis is presented only for the remaining 34 lizards. Table 1 demonstrates that home range size (both maximum and minimal estimates), number of days a lizard was on the site, and number of days a lizard was seen do not differ for infected and noninfected animals. However, the number of sightings for noninfected male fence lizards was significantly greater than for malarious lizards, and noninfected lizards chased other animals more often. Table 1 also presents dominance scores for infected and noninfected males. Small numbers in the table's cells required collapse of the submissive and neutral categories to allow analysis ( $\chi^2 = 14.17$ ,  $df = 1$ ,  $P = 0.0002$ ). Note that all of the male fence lizards judged dominant were noninfected.

It is conceivable that the results in Table 1 could be accounted for by differences in body size, rather than infection status, if body size distributions differ for infected and noninfected lizards, and body size

influences social status. Infection prevalence does increase with body size in this population of fence lizards, but levels off once the animals reach adult size (Schall, unpubl. data). However, there was no significant difference in body size for the infected and noninfected samples used in this study ( $\bar{x}$  = 68.0 mm [SD = 3.2, N = 10] vs.  $\bar{x}$  = 67.4 mm [SD = 4.6, N = 24] SVL; U-test,  $P$  = 0.568). We did not measure body mass in this study, but previous research demonstrated no difference between malarious and noninfected lizards in body mass corrected for SVL in this population in spring and early summer (Schall, 1983).

Our results support previous conclusions that malarial infection can play a crucial role in the behavior of male *S. occidentalis* (Schall and Dearing, 1987; Schall and Sarni, 1987). The data suggest that infection with malaria does not reduce an animal's ability to remain on a site and use a home range of normal size. However, infected males appear to spend less time actually moving about the habitat (or at least moving conspicuously so we could see them during our observation periods). Although the number of days we saw infected and noninfected lizards did not differ, the noninfected lizards were seen on more visits to the sites, indicating they tended to be active and conspicuous during a longer period each day. In the laboratory, infected *S. occidentalis* display less stamina than noninfected lizards, measured as distance run before reaching exhaustion (Schall, 1990b). We doubt, though, that infected animals are necessarily less able to move about the habitat because of limitations to locomotive performance. One of the three infected lizards never seen at the site after being marked was observed over 1 km from its original site only 1 d after being released. More likely, infected lizards are prevented from being very active in their home range by social pressure from noninfected males. This conclusion emerges from our rating of infected lizards as being less aggressive, and conforms with results from enclosure experiments showing infected lizards were forced by antagonistic interaction with the other male to spend much time hiding (Schall and Dearing, 1987). The less aggressive posture of malaria-infected males may derive from the altered hormonal state observed in infected adult males; testosterone levels are reduced and corticosterone levels increase in malarious male lizards (Dunlap and Schall, unpubl. data).

The socially submissive behavior of malarious male fence lizards suggests they would have reduced access to potential mates and would suffer reduced fitness as a consequence of infection. Discussions of the costs to fitness of parasitic infection usually center on a pathogen's effect on longevity, but more subtle effects on fitness as demonstrated here would often be important, but easily missed in field studies.

The ecological and evolutionary factors that influence use of space by animals is one of the central issues in ecology (Stamps, 1977). Ruby and Dunham (1987) note that studies on the causes of intraspecific variability of home range size are rare and of critical importance. Although parasites are known to influ-

ence territorial success of some vertebrates (Barnard and Behnke, 1990), the role of pathogens on the use of home range has not been examined before for any reptile. The lack of any apparent impact of malarial infection on home range size of *S. occidentalis* does not argue that infection with pathogens could not be important in the use of space by other lizards. The results presented here should not discourage other researchers from considering parasites as possible forces shaping the variation in home range size seen both among individuals within populations and among conspecific populations in different habitats.

*Acknowledgments.*—We thank D. Dearing for help in collecting lizards, and the staff of the Hopland Field Station for hosting this research. Funded by NSF BSR-8806235.

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Accepted: 13 November 1991.