

- insensitivity of oxygen pulse in spontaneously-active juvenile alligators. *J. Therm. Biol.* 16:303–307.
- WAGNER, E. L., AND T. T. GLEESON. 1996. Low temperature and exercise recovery in the desert iguana. *Physiol. Zool.* 69:168–190.
- WEINSTEIN, R. B., AND R. J. FULL. 1992. Intermittent exercise alters endurance in an eight-legged ectotherm. *Am. J. Physiol.* 262:R852–859.
- WITHERS, P. C. 1977. Measurement of  $VO_2$ ,  $VCO_2$ , and evaporative water loss with a flow-through mask. *J. Appl. Physiol.* 42:120–123.
- WRIGHT, J. C. 1986. Effects of body temperature, mass, and activity on aerobic and anaerobic metabolism in juvenile *Crocodylus porosus*. *Physiol. Zool.* 59:505–513.

Accepted: 27 October 1996.

*Journal of Herpetology*, Vol. 31, No. 1, pp. 147–149, 1997  
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### Comparing Foraging Success in Submissive Malaria-infected and Territorial Noninfected Fence Lizards (*Sceloporus occidentalis*)

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Defending a territory must have significant costs, such as expenditure of energy by the territorial animal, loss of time that could be devoted to other activities, and increased danger from predation or injury during defensive activities. A fundamental assumption of studies of animal territorial behavior is that there must be some profit from the behavior that more than offsets the obvious costs; this could include protecting valuable resources, such as food or retreat site, or access to mates (reviews in Morse, 1980; Krebs and Davies, 1981). Testing this assumption is notoriously difficult because territories may have multiple functions, and the importance of these functions may differ over time for individuals (Hinde, 1956; Stamps, 1994).

Male *Sceloporus* lizards are typically territorial; suggested functions of this behavior include defending sites suitable for thermoregulation, protecting a local food supply, or defending potential mates (Marler and Moore, 1989; Martins, 1994). Territorial defense, however, is energetically expensive and defending males require more food to survive (Marler and Moore, 1991). Infection with the malarial parasite, *Plasmodium mexicanum*, has a broad spectrum of effects on its vertebrate host, the western fence lizard, *Sceloporus occidentalis* (review in Schall, 1996). With respect to territorial behavior, infected male fence lizards are socially active less often (Schall and Sarni, 1987), and in manipulative experiments infected males are displaced by noninfected males in competition for perching sites

and access to females (Schall and Dearing, 1987). Free-ranging infected males may share a home range with noninfected males, but are active in the environment less often and are quickly displaced from perches by the more dominant noninfected animals (Schall and Houle, 1992). The origin of these behavioral effects seems to be hormonal alterations of infected male lizards; infection leads to an increase in stress hormone levels and a reduction in testosterone (Dunlap and Schall, 1995). Female *S. occidentalis* seldom display aggressive behaviors and their behavior is not influenced by malarial infection (Schall and Sarni, 1987). Thus, within the same local habitat, two groups of male lizards coexist: those defending perches (perhaps prime perching locations), and those that do not defend even a small territory.

The presence of territorial and nonterritorial (infected) males in the population of *S. occidentalis* presents an opportunity to examine the proposed functions of territorial behavior in this species. Here we ask: Does territorial defense allow the fence lizards to harvest more insect prey from the environment or to harvest different kinds of prey? To examine this question we indirectly determined foraging success of infected and noninfected fence lizards by weighing the scat produced by lizards within 48 h of capture, the method devised by Rand et al. (1983). We reasoned that infection should not affect foraging success by females because females do not defend a territory, but infection should affect males.

Two sites were chosen at the University of California Hopland Field Station in southern Mendocino County, California (Schall and Marghoob, 1995). One was a SW facing slope, of approximately 7.7 ha, the other was a streambed and adjacent terrace of approximately 5.5 ha; the sites were 900 m apart and have long been areas with high prevalence of lizard malaria (Schall and Marghoob, 1995). From 22 July to 13 August 1995, lizards were collected between 1630 and 1800 h by noosing. Immediately upon capture, the lizard was placed within a 27 × 28 cm zip-top plastic bag. The bags were placed indoors where temperature was controlled to 24 C during the day, and allowed to fall to outside ambient temperature at night that ranged from 12–13 C (field station temperature records). The bags were opened after 24 h for a change of air. A preliminary trial in early July with 23 lizards found that the lizards ceased producing scat before 48 h had elapsed in the bags; therefore, 48 h was chosen as the standard duration for the observations. After 48 h, the lizard was removed, sexed, measured (snout to vent length, SVL), weighed, and a blood smear made. The scat was removed, placed into a vial, and frozen. Approximately one month later the scat was dried to constant mass at 60 C, and weighed. The blood smears were stained with Giemsa and examined for parasites. We assume here that fecal mass produced over a standard period of time (48 h) is correlated with the amount and value of foods eaten by the lizards. It is possible that assimilation efficiency could differ among prey types such that mass of the final wastes produced would not be a useful indication of foraging success. Therefore, we also examined the feces to determine types of foods eaten by the lizards. Each lizard faex was dissected prior to drying and examined for presence or absence of any hymenoptera and or-

thoptera (the two classes of prey that could be identified from the feces).

Analysis was conducted using only lizards that produced some feces during the 48 h period. Body size could influence the amount of feces produced and thus obscure any effects of infection. SVL did not differ between infected and noninfected groups (U-test,  $P = 0.066$ ). Fecal mass and body size (mass or SVL) were not correlated, partitioning the data by gender and infection status; slopes of the relationship were close to zero ( $R^2 = 0.001 - 0.044$ ;  $P > 0.05$ ). This surprising result probably derives from the small range of body sizes of the lizards used in the study (males = 61–74 mm; females = 55–79 mm). Therefore, we report results as dry fecal mass/body mass, but results using absolute fecal mass were similar.

Fecal mass did not differ between sites (data separated by gender, U-tests;  $P = 0.888$ , total  $N = 124$ ), so data for the sites were first combined. Females produced more feces, as is expected if they spend more time in catching food when males are interacting with other males (1.2% of body mass [ $N = 50$ ] vs. 1.0% [ $N = 74$ ]; U-test,  $P = 0.048$ ). Malarial infection did not affect the amount of feces produced by females, as expected (U-test,  $P = 0.154$ ,  $N = 50$ ). Also, similar proportions of infected and noninfected animals did not produce any feces (3/12 infected, and 23/64 noninfected, G-test,  $G = 0.292$ ,  $P > 0.05$ ). In conflict with expectations, infected and noninfected males also did not differ in relative fecal mass (U-test,  $P = 0.218$ ,  $N = 74$ ), nor in proportion of animals that produced no feces (3/27 vs. 7/56, G-test,  $G = 0.026$ ,  $P > 0.05$ ). The availability of prey types might have differed between sites; therefore, the sites were examined separately. G-tests revealed that there was no difference between infected and noninfected animals in the presence of either prey class in the diet (G-tests, all  $P > 0.20$ ).

Comparison of infected (submissive) and noninfected (territorial) fence lizards can be used to examine three proposed functions of territoriality in *Sceloporus* (Martins, 1994), defending sites for foraging or thermoregulation, or protecting access to potential mates. Our results suggest that aggressively holding prime perch sites and limiting the activity of conspecifics in a territory do not result in greater foraging success by the noninfected male fence lizards. Submissive males, with their more cryptic foraging behavior appear to harvest similar amounts of insect prey each day. Perhaps the extra time spent defending a territory, and the reduction in time spent foraging, are counterbalanced by the higher quality of the habitat used by the aggressive noninfected males. Our results agree with a previous observation that growth rate of infected and noninfected fence lizards does not differ (Schall, 1982; Ressel and Schall, 1989). Fat stored by infected lizards, however, is reduced (Schall, 1983). Thus, infection may not hinder the acquisition of food, but the energetic cost of infection is expressed as a reduction in lipids stored, rather than growth. Dunlap and Schall (1995) found that experimentally increasing the level of the prevalent stress hormone (cortisol) to mimic levels found in malarious fence lizards resulted in a reduction in stored fat, even when they were fed to satiation each day.

It is possible that holding a territory allows a fence lizard to thermoregulate more efficiently. This appears

unlikely because body temperature distributions for *S. occidentalis* do not differ by infection status (Schall, 1990), and air and substrate temperature of perching site also do not differ for the two groups (Schall, 1982). More likely, the benefit of territorial behavior by male fence lizards is their greater ability to court and mate with females (Stamps, 1994). Previous studies show that noninfected males spend more time associating with females, although no data are available on fitness consequences of this behavior.

Despite the growing interest in the role parasites play in shaping the behavior of their hosts (Keymer and Read, 1991), little is known about the influence of pathogens on territorial behavior (see rare examples in Jenkins, et al. [1963] for grouse and Rau [1983] for mice). As shown here, parasite-altered territorial behavior can be used as a window into the functions of territoriality in the host species.

*Acknowledgments.*—We thank Susan Perkins for assistance in collecting and processing lizards. The staff at the Hopland Field Station provided logistical support, and Sarah Osgood assisted in scanning the blood smears. The work was supported by the NSF-Vermont EPSCoR program and NSF grant DEB95-27115.

#### LITERATURE CITED

- DUNLAP, K. D., AND J. J. SCHALL. 1995. Hormonal alterations and reproductive inhibition in male fence lizards (*Sceloporus occidentalis*) infected with the malarial parasite *Plasmodium mexicanum*. *Physiol. Zool.* 68:608–621.
- JENKINS, D., A. WATSON, AND G. R. MILLER. 1963. Population studies on red grouse, *Lagopus lagopus scoticus* (Lath.) in north-east Scotland. *J. Anim. Ecol.* 32:376.
- KEYMER, A. E., AND A. F. READ. 1991. Behavioural ecology: The impact of parasitism. In C. A. Toft and A. Aeschlimann (eds.), *Parasite-Host Associations, Coexistence or Conflict?*, pp. 37–61. Oxford Univ. Press, Oxford.
- KREBS, J. R., AND N. B. DAVIES. 1981. *An Introduction to Behavioural Ecology*. Sinauer Associates, Sunderland, Massachusetts.
- HINDE, R. A. 1956. The biological significance of territories of birds. *Ibis* 98:340–369.
- MARLER, C. A., AND M. C. MOORE. 1989. Time and energy costs of aggression in testosterone-implanted free-living male mountain spiny lizards (*Sceloporus jarrovi*). *Physiol. Zool.* 62:1334–1350.
- \_\_\_\_\_, AND \_\_\_\_\_. 1991. Supplementary feeding compensates for testosterone-induced costs of aggression in male mountain spiny lizards, *Sceloporus jarrovi*. *Anim. Behav.* 42:209–219.
- MARTINS, E. P. 1994. Phylogenetic perspectives on the evolution of lizard territoriality. In L. J. Vitt and E. R. Pianka (eds.), *Lizard Ecology, Historical and Experimental Perspectives*, pp. 117–144. Princeton Univ. Press, Princeton, NJ.
- MORSE, D. H. 1980. *Behavioral Mechanisms in Ecology*. Harvard Univ. Press, Cambridge, Massachusetts.
- RAND, A. S., S. GUERRERO, AND R. M. ANDREWS. 1983. The ecological effects of malaria on populations of the lizard *Anolis limifrons* on Barro Colorado Is-

- land, Panama. In A. G. J. Rhodin and K. Miyata (eds.), *Advances in Herpetology and Evolutionary Biology*, pp. 455–471. Museum of Comparative Zoology, Cambridge, Massachusetts.
- RAU, M. E. 1983. Establishment and maintenance of behavioral dominance in male mice infected with *Trichinella spiralis*. *Parasitology* 86:319–322.
- RESSEL, S., AND J. J. SCHALL. 1989. Parasites and showy males: malarial infection and color variation in fence lizards. *Oecologia* 78:158–164.
- SCHALL, J. J. 1982. Lizard malaria: Parasite-host ecology. In R. B. Huey, T. W. Schoener, and E. R. Pianka (eds.), *Lizard Ecology: Studies on a Model Organism*, pp. 84–100. Harvard Univ. Press, Cambridge, Massachusetts.
- \_\_\_\_\_. 1983. Lizard malaria: cost to vertebrate host's reproductive success. *Parasitology* 87:1–6.
- \_\_\_\_\_. 1990. Virulence of lizard malaria: the evolutionary ecology of an ancient parasite-host association. *Parasitology* 100:S35–S52.
- \_\_\_\_\_. 1996. Malarial parasites of lizards: diversity and ecology. *Adv. Parasito.* 37:255–333.
- \_\_\_\_\_, AND M. D. DEARING. 1987. Malarial parasitism and male competition for mates in the western fence lizard, *Sceloporus occidentalis*. *Oecologia* 73:389–392.
- \_\_\_\_\_, AND G. A. SARNI. 1987. Malarial parasitism and the behavior of the lizard, *Sceloporus occidentalis*. *Copeia* 1987:84–93.
- \_\_\_\_\_, AND P. R. HOULE. 1992. Malarial parasitism and home range and social status of male western fence lizards, *Sceloporus occidentalis*. *J. Herpetol.* 26:74–76.
- \_\_\_\_\_, AND A. B. MARGHOEB. 1995. Prevalence of a malarial parasite over time and space: *Plasmodium mexicanum* in its vertebrate host, the western fence lizard, *Sceloporus occidentalis*. *J. Anim. Ecol.* 64:177–185.
- STAMPS, J. A. 1994. Territorial behavior: testing the assumptions. *Adv. Stud. Behav.* 23:173–232.

Accepted: 27 October 1996.

*Journal of Herpetology*, Vol. 31, No. 1, pp. 149–155, 1997  
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### Courtship Behavior and Vocalizations of the Frogs *Eleutherodactylus antillensis* and *E. cochranae* on the British Virgin Islands

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In addition to an advertisement call that may function both in mate attraction and intermale spacing, male frogs of many species produce a variety of other calls that are used in short-range encounters with females and other males (Wells, 1977a, b, 1988; Gerhardt, 1994). Vocalizations used during courtship are poorly

documented for most species, although they may play an important role in the courtship of particularly those species in which the male leads the female to a nest site.

Frogs of the genus *Eleutherodactylus* form a dominant component of terrestrial anuran communities in many neotropical areas (Miyamoto, 1982; Drewry and Rand, 1983; Lynch and Ruiz-Carranza, 1985). The few species examined in detail show a diversity of vocalizations, including calls associated with the defense of retreat sites (Stewart and Rand, 1991, 1992) and with courtship and mating (Townsend and Stewart, 1986; Michael, 1996). Based on observations in captivity, Michael (1996) described courtship calls that differed in structure from the advertisement calls for three species of *Eleutherodactylus* (*coqui*, *cochranae*, and *antillensis*) and noted that their courtship calls were more similar than their advertisement calls. The observations were based on courtships by only two male *E. cochranae* and one male *E. antillensis* (in interspecific courtship with female *E. cochranae*), precluding detailed analysis of the calls.

We describe the behavior and vocalizations by *E. antillensis* and *E. cochranae* during courtships under natural conditions on the British Virgin Islands. The two species are closely related based on electrophoretic analysis (subgenus *Eleutherodactylus*, *auriculatus* section; Hedges, 1989). Our observations complement those recorded in captivity (Michael, 1996) and provide a context for the vocalizations.

We observed courtships of *E. antillensis* on 10 occasions in October 1993 and 1994 on Guana Island, British Virgin Islands, and recorded calls of males on audio-tape in six of these cases. The microphone was approximately 20–80 cm from the male, and light from a headlamp directed away from the frogs provided illumination for observations. We compared calls emitted during courtship to advertisement calls of 10 male *E. antillensis* recorded on Guana Island in 1994 as a part of a study on call variation among islands. In 1993, we used a Panasonic® tape-recorder with a built-in microphone (RQ-320), whereas in 1994 we used a portable JVC® cassette recorder (CD-1636) and a Sony Professional Walkman® (WM-D6C) fitted with unidirectional Audiotechnica® shotgun microphones.

We analyzed all calls on a DSP Sona-Graph® Model 5500 (Kay Electronics). We randomly selected five long (>5 notes) and five short (≤5 notes) courtship calls emitted by each *E. antillensis* male during three stages of the courtship for detailed analysis. The stages, which corresponded to the sequential progress of the courtship, were (1) male and female in vegetation or on the ground, (2) male under leaf litter, and (3) both male and female under leaf litter. For comparisons, we also selected 10 advertisement calls from the second minute of each 5 min recording of vocalizations of males that had not been approached by females. We measured the dominant frequency of each note, time from the start of one note to start of subsequent note (note period), and total duration for each call, and calculated the average for each individual male. We applied Bonferroni's correction when using the same set of data in two analyses (Snedecor and Cochran, 1980). As a result,  $\alpha$  was set at 0.025 when comparing characteristics of the advertisement and courtship call.

In October 1995, we observed a courtship of *E. cochranae* on Tortola, British Virgin Islands, and recorded