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Body Condition of a Puerto Rican Anole, *Anolis gundlachi*: Effect of a Malaria Parasite and Weather Variation

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Over 70 species of malaria parasites, *Plasmodium* spp., exploit lizards as their vertebrate hosts throughout the warmer regions of the world (Schall, 1996). Detailed information on the impact of infection is known for only a few *Plasmodium*-lizard associations: *P. mexicanum* and *Sceloporus occidentalis* in California, *P. agamae* and *P. giganteum* in *Agama agama* in west Africa, and *P. azurophilum* and *Anolis gingivinus* on St. Martin. Those data indicated that infection can reduce reproductive success for both male and female lizards (Schall, 1983, 1990), change the host's behavior (Schall and Sarni, 1987), disrupt its physiology (Schall, 1990; Dunlap and Schall, 1995), reduce body condition (mass vs. length) (Dunlap and Mathies, 1993), and perhaps alter the competitive ability of entire populations of lizards (Schall, 1992). These results are striking, but should not imply that malaria parasites are always important for the biology of lizard hosts. More likely, additional studies will reveal variation in the pathologies induced by these parasites.

Plasmodium parasites commonly infect anoles throughout the Caribbean islands (Staats and Schall, 1996), but the impact of infection is poorly known (but see Schall, 1992). We studied malaria in a common anole, *Anolis gundlachi*, at the El Verde Field Station, a site in the Luquillo Experimental Forest in eastern Puerto Rico (18°19'N, 65°45'W). Although five species of *Anolis* are abundant at El Verde, only individuals of *P. gundlachi* are frequently parasitized. Approximately 30% are infected with two species of malaria parasites, *P. floridense* and *P. azurophilum* (Schall and Vogt, 1993). We examined the mass of the lizards relative to snout-to-vent length (SVL) in order to determine the effect of malaria on this indicator of overall health of the animals.

Attempts to measure the virulence of a parasite are often confounded by the frequently cryptic nature of any infection-induced costs to the host. That is, such costs may be patent only when the host is stressed, such as during its reproductive season or when the environment deteriorates. Long-term studies on the virulence of parasites may be required to reveal the often cryptic impact of parasites on host populations (Hudson et al., 1998). We therefore collected multiple samples of anoles at El Verde over a three-year period. During that time, the site was disturbed by hurricanes and severe droughts. We sought to determine if body condition was affected by weather, and if the consequences of infection were more severe after the site suffered reduced rain or physical disruption by a tropical storm. Malaria may only cause harm to the lizards occasionally, but still could have a substantial influence on the population biology of *A. gundlachi*.

Study System and Methods.—A description of the study site and details of its natural history are in Reagan and Wade (1996). *Anolis gundlachi* lizards are common at the site, perching on trees and large logs within reach of human observers. Anoles were captured along trails within a 36 ha plot with a slip noose attached to a pole or by hand during five periods: July 1996, July 1997, January 1998, May 1998, and March 1999. Only males with an intact tail were used for this study because the mass of females would vary with reproductive condition, and animals with broken or regenerated tails would have a body mass atypical for their SVL.

Each lizard was maintained in a mesh sack until evening when a blood smear was made from a drop of blood extracted from a clipped toe, SVL measured, and body mass taken with a Pesola spring scale calibrated against an electronic balance. The next morning, all lizards were released at their points of capture. In the lab, the smears were fixed in absolute methanol and stained with Giemsa at pH 7.0 for 50 min. These stained smears were scanned at 1000× for 6 min, allowing examination of approximately 10,000 erythrocytes. Both species of parasite were combined to score animals as infected or noninfected. This was acceptable because the relative prevalence (% lizards infected) of the two species remained constant over the study period (Schall et al., 2000a).

We extracted rainfall and temperature data from records maintained by the field station staff. Body condition was determined from the relationship between SVL and body mass. A curve was fit to the data using the JMP package (SAS Institute) which uses a series of third-degree polynomials over 50 segments of the data set. In essence, this results in a curve that runs through the smoothed mean mass for each SVL. Residuals were then calculated for each lizard; positive residuals indicated an animal heavier than average, and negative residuals indicated an animal with reduce mass. Heavier animals could have a greater mass because they contained more fat, larger muscle tissue, or perhaps were simply more hydrated. No matter what the reason, we assumed heavier animals were healthier. This method has been widely used as a measure of lizard health (Dunlap and Mathies, 1993; Van Slys, 1998; Schall et al., 2000b).

Body Condition by Infection and Weather Conditions.—A total of 940 male *A. gundlachi* anoles were sampled. Although mean body condition seemed to follow the predicted trend, with positive residuals for noninfected lizards and generally negative residuals for infected animals (Table 1), ANOVA revealed no effect of infection (residuals for each sample were normally distributed). There was no interaction between sample and infection ($F = 0.03$; df = 4, 929; $P = 0.998$), nor a significant effect of infection ($F = 2.69$; df = 1, 929; $P = 0.101$). However, body condition differed significantly among samples ($F = 6.36$; df = 4, 929; $P < 0.0001$). Because the interaction term was not significant, we excluded that term from another analysis to search for a possible effect of infection; again none was detected ($F = 3.24$; df = 1, 929; $P = 0.07$). A final analysis scored lizards as healthy (residual > 0) or unhealthy (residual < 0), and cast the data into a 2 × 2 contingency table; no effect of infection was detected ($\chi^2 = 1.94$; $P = 0.16$).

Variation in body condition could not be accounted

TABLE 1. Mean residual from curve fitted for body mass versus SVL for infected and noninfected *Anolis gundlachi* collected during five sampling periods. Dates of samples, standard error of mean, and sample sizes are given.

Sample	Noninfected	Infected
July 1996	0.042 (0.103, 63)	−0.023 (0.147, 35)
July 1997	0.021 (0.050, 221)	−0.045 (0.072, 152)
January 1998	0.039 (0.051, 166)	−0.105 (0.102, 61)
May 1998	0.045 (0.086, 79)	−0.053 (0.113, 67)
March 1999	0.049 (0.079, 69)	0.065 (0.119, 27)
Overall	0.045 (0.031, 598)	−0.077 (0.048, 342)

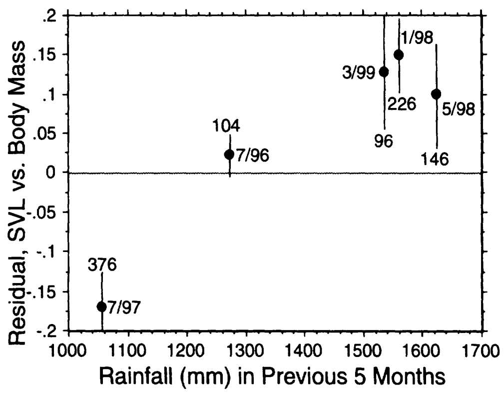

FIG. 1. Relation between body condition (residual of mass vs. SVL) and cumulative rainfall during the previous five months for anoles (*Anolis gundlachi*) in eastern Puerto Rico (sample sizes are given along with mean residual indicated by dots and one standard error by bars; r = 0.943).

for by total cumulative rainfall 1–3 mo before the date of the sample (r = −0.256 to 0.711, $P > 0.05$), nor mean low temperature for those periods of time (r = −0.644 to −0.021; $P > 0.05$). However, total rainfall summed over the previous 4–6 mo and mean low temperature for that period were significantly correlated with body condition (Fig. 1, all r = 0.837–0.943 for rainfall, and all r ≅ 0.90 for temperature, $P < 0.05$). Thus, body condition was highest after several months of warm, wet weather.

Discussion.—Researchers long assumed that parasites have only a minor influence on the biology of host individuals and populations. Parasites were thought to be generally rather benign, with little negative impact on behavior, feeding, reproduction, growth, or other important aspects of the host's daily activities. Such views have undergone substantial revision in the past two decades, and parasites are now viewed as major players in the ecology and evolution of their hosts (Dobson and Hudson, 1995; Gulland, 1995). This revised outlook has unfortunately not been accompanied by a substantial increase in knowledge of the affects of parasites on their hosts under natural conditions and long-term data are particularly lacking.

Studies on Caribbean anoles have played a central role in modern ecology (Roughgarden, 1995), and the El Verde *Anolis* populations have been the subject of major long-term studies of population dynamics in a changing environment (Reagan, 1996). We suspected that malaria parasites, so important for other lizard populations, might have a previously undetected impact on a common anole at El Verde. Data on body condition do not support this hypothesis because no effect of infection on body condition was observed, even during periods when weather conditions appeared to have been stressing the lizards.

Perhaps our measure of body condition does not actually reflect the health of the lizards, but two kinds of information argue against this possibility. First, Dunlap and Mathies (1993) implicated malaria with reduction in body condition for *Sceloporus occidentalis* fence lizards in California. Second, our results revealed that body condition of *A. gundlachi* male lizards was influenced by weather conditions over several months. Periods of warm, wet weather resulted in an increase in body condition, perhaps because of an increase in insect prey density. The changes in body condition were not a result simply of lizards being more hydrated from drinking from water drops. The driest period occurred during the two months just prior to the March 1999 sample, but body condition was second highest among the five samples. Hurricane Georges struck the site in December 1998, stripping most of the canopy vegetation away, but also depositing torrential rains that may have had a positive effect on the food supply by March. This result complements previous findings that availability of water for drinking can increase growth rate of lizards (Andrews, 1982). The correlation between rainfall and temperature with body condition suggests that the mass vs. SVL measure provides a biologically meaningful insight into the anoles' health, at least those aspects of the lizards' activities that would increase relative body mass. However, infection could still reduce reproductive output or affect ability of males to maintain territories.

The same species of malaria parasites infect the St. Martin island anole, *A. gingivinus*, and cause substantial changes in blood cell composition and chemistry and may alter the competitive ability of populations harboring the parasites (Schall, 1992). If the malaria parasites, *P. floridense* and *P. azurophilum*, are benign in *A. gundlachi* anoles, in contrast to their detrimental effects on the St. Martin anole, this would provide an excellent window into the evolution of *Plasmodium* virulence in lizards, the most common vertebrate host for malaria parasites (Schall, 1996).

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Sexual Dimorphism in Malodorousness of Musk Secretions of Snakes

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Sexual dimorphism is a widespread phenomenon among animals (Darwin, 1871; Andersson, 1994). Differences between the sexes come in many forms, including both morphology (e.g., size, shape, coloration) and behavior (e.g., risk-taking or defensive behavior). Sexual differences in physiology also occur, with the best known examples being hormonal differences associated with reproduction. Sexual dimorphism also may take other forms, and here we report on sexual differences in the odor of musk secretions produced by two species of snakes.

Snakes produce musk in cloacal glands at the base of their tails. Snake musk is assumed to have a defensive function because it is malodorous and is commonly secreted when a snake is captured or disturbed both within and outside the breeding season (Whiting, 1969; Greene, 1997). We had several reasons to think that the odor of musk might differ between males and females. First, Kissner et al. (1998a) found female-biased sexual dimorphism in cloacal gland size in plains garter snakes (*Thamnophis radix*) that did not appear to be a result of male gland size being constrained due to the hemipenes sharing space in the tail with the glands. They suggested that this difference may be a consequence of females relying more than males on musk secretions for defense from predators. Second, other studies of reptiles have shown that gravid female reptiles typically use defensive behaviors other than flight more than nongravid females or males, presumably because carrying eggs or embryos impairs movement (e.g., Bauwens and Thoen, 1981; Seigel et al., 1987; Schwarzkopf and Shine, 1992; Kissner et al., 1998b). Hence, females may rely on musk secretion in defense more than males, leading to differences in the quantity or the quality of the musk they produce. Third, Oldak (1976) found a difference in the composition of musk of male and female garter snakes (*Thamnophis elegans*), although he

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