was present on the head, and some reddish tones were evident on the thighs. These frogs differ from *E. mendax* by having vomerine teeth, numerous supernumerary tubercles, and smooth dorsum. *Eleutherodactylus bromeliaceus* differs from *E. zimmermanae* by having vomerine teeth (absent in *E. zimmermanae*) and coarsely granular venter (almost smooth in *E. zimmermanae*). The reddish coloration pattern on the head, some spots on sacral region and reddish, orange or yellowish dorsolateral stripe are present in some specimens of *E. bromeliaceus, E. mendax,* and *E. zimmermanae.*

Acknowledgments.—William E. Duellman, Museum of Natural History, University of Kansas, (KU), Douglas Rossman, Museum of Natural History, Louisiana State University, (LSU); Jesús Córdova, Museo de Historia Natural, Universidad Nacional Mayor of the San Marcos, Perú (MUSM), S. Blair Hedges (SBH), Pennsylvania State University, and W. Ronald Heyer and Roy W. McDiarmid, National Museum of Natural History, Smithsonian Institution, (USNM) lent us specimens. John D. Lynch, William E. Duellman, and Rafael de Sá commented on the manuscript, and the Russell Program Fellowship of the World Wildlife Fund for the support to this research.

LITERATURE CITED

DE LA RIVA, I. 1993. Sinopsis del género *Eleutherodactylus* (Amphibia, Anura, Leptodactylidae) en Bolivia y adición de tres especies nuevas para el país. Rev. Española Herpetol. 7:97–105.

DUELLMAN, W. E. 1978. Three new species of *Eleutherodactylus* from Amazonian Peru (Amphibia: Anura: Leptodactylidae). Herpetologica 34:264–270.

———, AND J. D. LYNCH. 1988. Anuran amphibians from the Cordillera de Cutucú, Ecuador. Proc. Acad. Nat. Sci. Philadelphia, 140:125–142.

HEYER, W. R., AND L. M. HARDY. 1991. A new species of frog of the *Eleutherodactylus lacrimosus* assembly from Amazonia, South America (Amphibia: Anura: Leptodactylidae). Proc. Biol. Soc. Washington, 104:436–447.

LYNCH, J. D. 1979. Leptodactylid frogs of the genus *Eleutherodactylus* from the Andes of southern Ecuador. Mus. Nat. Hist. Univ. Kansas Misc. Pub., 61: 1–62.

———. 1986. Origins of the high Andean Herpetological fauna. [478–499]. *In:* F. Vuilleumier, and M. Monasterio (eds.), High Altitude Tropical Biogeography, pp. 478–499. Oxford Univ. Press, New York.

———, AND W. E. DUELLMAN. 1980. The *Eleutherodactylus* of the Amazonian slopes of the Ecuadorian Andes (Anura: Leptodactylidae). Mus. Nat. Hist. Univ. Kansas Misc. Pub., 69:1–80.

RODRÍGUEZ, L. O., AND J. E. CADLE. 1990. A preliminary overview of the herpetofauna of Cocha Cashu, Manu National Park, Peru. 410–425 pp. *In:* A. H. Gentry, (ed.)., Four Neotropical Rainforests, pp. 410–425. Yale Univ. Press, New Haven, Connecticutt.

———, AND L. H. EMMONS. 1994. Amphibians and Reptiles in the Tambopata-Candamo Reserve Zone. *In:* R. R. Foster, J. L. Carr, and A. B. Forsyth (eds.), The Tambopata-Candamo Reserve Zone of Southeastern Perú: A Biological Assessment, pp. 150–153. RAP Working Paper 6, Conservation International, Washington, D.C.

Accepted: 25 October 1999.

Journal of Herpetology, Vol. 34, No. 1, pp. 160–163, 2000

Prevalence of the Tick, *Ixodes pacificus,* on Western Fence Lizards, *Sceloporus occidentalis*: Trends by Gender, Size, Season, Site, and Mite Infestation

JOS. J. SCHALL,[1] HOLLY R. PRENDEVILLE,[1] AND KATHRYN A. HANLEY,[2] [1]*Department of Biology, University of Vermont, Burlington, Vermont 05405, USA. E-mail: jschall@zoo.uvm.edu,* [2]*Department of Biology, University of Maryland, College Park, Maryland 20742, USA.*

In California, the western fence lizard, *Sceloporus occidentalis,* is often infested with larvae and nymphs of the black-legged tick, *Ixodes pacificus* (Lane and Loye, 1989). Dunlap and Mathies (1993) found that infestation is associated with a reduction in the host's hematocrit, but body condition (mass vs. length) is harmed only when the lizard is also infected with a malaria parasite, *Plasmodium mexicanum.* This tick-lizard system is of considerable medical interest because the tick is the vector of the Lyme disease spirochete (*Borrelia burgdorferi*). The lizard's blood contains a factor that kills the spirochete, so only ticks that feed on alternative rodent hosts are likely to pass *B. burgdorferi* to humans (Lane and Quistad, 1998). Thus, the use by subadult ticks of *S. occidentalis* as their primary host may reduce Lyme disease prevalence in humans in the American west.

Because of its importance for the epidemiology of Lyme disease we studied the prevalence of *I. pacificus* ticks on fence lizards at one site in northern California and two sites in southern California. We examined variation in number of ticks among the three sites, on females vs. males, on lizards of different body size, and on lizards early vs. late in the warm season. Several mites also infest the lizards, the most common being species of *Geckobiella,* the mechanical vector of *Schellackia occidentalis,* a common protozoan parasite of the lizards' intestine and blood (Bonorris and Ball, 1955). Any ecological interaction between the ticks and mites could be expressed as a significant association, either positive or negative, in number of the ectoparasites on each lizard. Last, we sought to confirm the result of Dunlap and Mathies (1993) that the ticks do not reduce body condition in otherwise healthy lizards.

Lizards were monitored for ectoparasites in both southern and northern California, but body condition and ectoparasite attachment sites were measured and mark-recapture studies were conducted only in northern California. In southern California, lizards were collected between 1–6 April, 1997 at the Rancho Santa Ana Botanic Garden (RSABG) (34°7′N, 117°43′W) and between 8–9 April at Evey Canyon (34°10′N, 117°41'W), both of which are located in eastern Los Angeles County. RSABG is a public garden comprised of paved walkways and botanical exhibits; Evey Canyon is a nature preserve consisting primarily of riparian oak-woodland habitat. Lizards were captured by noosing and all ectoparasites counted immediately with a hand lens. The gender and snout-to-vent length (SVL) were recorded and lizards lacking ectoparasites were returned to the point of capture. Those infested with ectoparasites were brought into the laboratory, where all ectoparasites were removed and identified with the help of James Webb at the Orange County Vector Control District. Two species of ectoparasite were identified: the tick *Ixodes pacificus* and the mite *Geckobiella texana.* The captive lizards were later released at the site of capture.

In northern California, lizards were collected between May 12–18, 1997 at the Hopland Field Station of the University of California in southern Mendocino county, California (39°00'N, 123°04'W). The collection site was an oak woodland near a stream. The biology of fence lizards and their malaria parasite has been under study at Hopland for many years (review in Schall, 1996). Furthermore, a previous survey of the distribution of ticks on fence lizards was conducted by Lane et al. (1995) at this site in 1993. Lizards were captured by noosing, then brought into the laboratory where all ticks were counted and their location on the body recorded (in nuchal or neck pockets vs. elsewhere on the body). All ticks were removed from each lizard. The number of mites (combining species because a taxonomic survey of the mites at Hopland has not been conducted) and their location on the lizard was also recorded and those in the nuchal pockets removed. Mites elsewhere on the lizard were difficult to remove, so time constraints prevented complete elimination of mites from the animals, although we estimate that 90+% were removed. SVL, gender, tail condition (broken, regenerated, or intact), and body mass were also recorded. Body condition was determined only for lizards with an intact tail and was calculated as the residual for the regression between SVL and body mass. Each lizard was individually marked with a unique series of toe clips, only one toe per foot being removed, and then returned to its point of capture.

During two periods, 23–27 June and 17–25 July, the marked animals were recaptured. All data listed above were recorded again, but the ectoparasites were not disturbed. Sample sizes differ between first and subsequent captures for two reasons. First, half the lizards in the first sample were assigned to a manipulative experiment that hindered reattachment of ectoparasites at some body locations. Therefore, these lizards are not included in the analyses involving second and third captures. Second, some lizards were not observed again at the study site once they were first released.

At RSABG, none of the 49 lizards captured were infested with ticks and only three (6%) were infested with mites (range = 0–4 mites). Consequently no statistical analyses were conducted on these distributions.

At Evey Canyon, three of the 25 lizards captured (12%) were infested with ticks (range = 0–3); 48% of the lizards were infested with mites (range = 0–16).

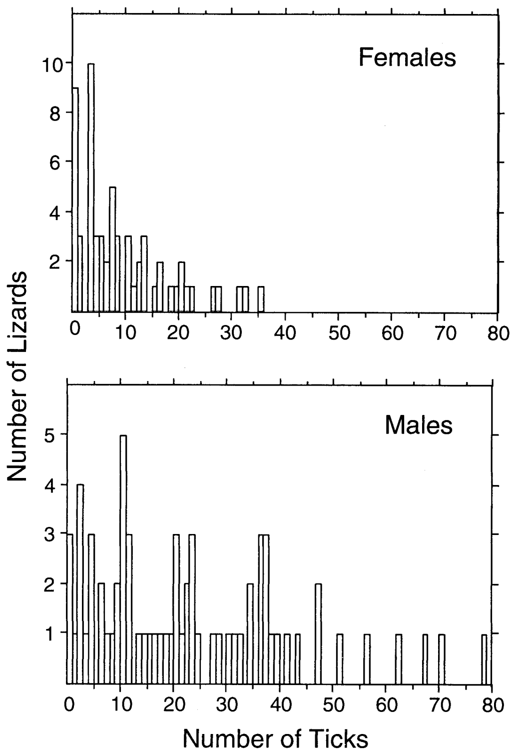

FIG. 1. Number of ticks, *Ixodes pacificus,* infesting western fence lizards, *Sceloporus occidentalis,* at the Hopland Field Station in northern California. Female lizards are compared with male lizards.

Males hosted significantly more mites (median = 3.0, range = 0–16, N = 11) than females (median = 0, range = 0–8, N = 14) (Mann-Whitney U test, P = 0.03). In addition, all three of the lizards infested with ticks were male. SVL and number of mites were not correlated for either gender (Spearman correlations, $P > 0.1$).

At Hopland at first capture, 130 lizards were infested with 0–78 ticks; only 9% lacked any ticks (Fig. 1). Males hosted more ticks (median = 20, N = 69) than females (median = 7, N = 61) (U test, $P < 0.0001$). SVL was not correlated with number of ticks present for females (Spearman correlation, $P > 0.05$; N = 61), but larger males carried more ticks ($r_s = 0.342$, $P = 0.006$, N = 69). The larger number of ticks infesting male fence lizards is not a result of differing body size by gender because the females are slightly larger (68 vs. 66 mm mean SVL). Selecting only lizards from 60–70 mm shows males still had significantly more ticks attached (U-test, $P < 0.0001$). For males, the number of ticks at first and second captures were positively correlated; males with more ticks at first capture were colonized by more ticks approximately one month later ($r_s = 0.775$, $P = 0.0007$, N = 20). No such relationship was seen for females ($r_s = 0.248$, $P = 0.4103$, N = 12). Most ticks (mean for all lizards = 90%) were attached in the nuchal pockets.

Mites were also common on the lizards at first capture (0–64), but the mites were not congregated in the

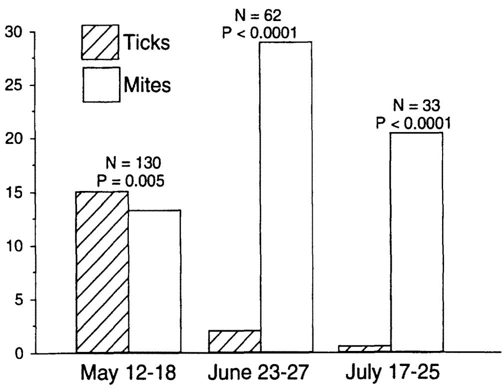

FIG. 2. Number of two kinds of ecotoparasites, ticks (*Ixodes pacificus*) and mites (primarily *Geckobiella* sp.) on western fence lizards (*Sceloporus occidentalis*) during three time periods at the Hopland Field Station. Lizards at second and third capture were subsets of the animals marked during the first capture period. Sample size of lizards and result of Mann-Whitney U test for each sample period (comparing abundance of ticks and mites) is given

nuchal pockets ($\bar{x}$ only 20%); 75% of lizards carried 1–20 mites and only 12% were free of mites. Mite number did not differ significantly between males and females (males: median = 6, range = 0–46, N = 69; females: median = 7, range 0–64, N = 61; U test, $P > 0.05$). No correlation existed between SVL and number of mites for either gender (Spearman correlations, $P > 0.05$). Comparison of the number of mites between first and second captures could not be examined because mites were not completely removed from the lizard upon first capture.

No relationship was observed for body condition vs. number of ticks at first capture for females or males (Spearman correlations, $P > 0.05$). Body condition at second capture of males and females was also not correlated with number of ticks at the first capture, thus showing no delayed effect of infestation (Spearman correlations, $P > 0.05$). However, lizards captured during the second sampling tended to be those with fewer ticks at first capture (median number of ticks on lizards captured only once = 13.0, and captured twice = 7.0; U-test, $P = 0.029$).

A weak negative correlation between mite number and tick number was seen for females ($r_s = -0.26$, $P = 0.035$) and possibly for males ($r_s = -0.22$, $P = 0.09$). Mites and ticks appear to have complementary seasonalities, with ticks common on the lizards in May, and mites more common in June and July (Kruskal-Wallis tests for each class of ectoparasite, $P < 0.0001$), followed by U-tests comparing classes for each capture; Fig. 2). As shown above, ticks congregated in the nuchal pockets, but mites did not. Perhaps ticks, when they are common on the lizards in May, exclude the mites from a preferred attachment point, the nuchal pockets. This does not appear correct because the percent of mites on each lizard that were in the nuchal pockets was similar for the first capture (mean of 18% of mites in pockets) when ticks were plentiful in the pockets, and the second capture when ticks were rare (mean of 22% of mites were in the pockets). Also, the percent of mites in pockets of lizards that had no ticks (combining first and second capture) was also similar to the above values ($\bar{x}$ = 21%).

Both tick and mite prevalence (percent of lizards infested with at least one tick/mite) differed significantly among the three sites surveyed (χ^2 contingency table analyses, N = 204 lizards, $\chi^2 = 144.8$ for ticks and 104.4 for mites, $P < 0.001$).

The results show *Ixodes pacificus* ticks and at least one species of mite infest fence lizards through California. Ectoparasite prevalence differed sharply among the three sites surveyed: infestations by ticks were undetectable and by mites were rare at RSABG; ticks were rare but mites were common at Evey Canyon, and both mites and ticks were extremely common at Hopland Field Station, where almost all of the lizards carried both kinds of ectoparasite. Survival of *I. pacificus* ticks decreases at high temperature and low humidity (Lane et al., 1995), and differences in tick prevalence among the sites may reflect differences in these factors.

Males were more often infested with ticks at both Hopland and Evey Canyon, and larger males carried larger numbers of ticks. At Evey Canyon males were also more heavily infested with mites, although this was not true at Hopland. High testosterone levels appear to reduce the immune system's competency against some classes of parasites in vertebrates (Møller et al., 1998), including lizards, and may account for the higher prevalence of ectoparasites on males (Salvador et al., 1996, 1997). However, in the case of the *I. pacificus*-*S. occidentalis* system, two kinds of evidence suggest other factors are more likely. First, mite prevalence differed by gender at only one site and did not differ by size at any site. Second, at Hopland, where ticks were counted and then removed at first capture, those lizards that had a large number of ticks at first capture acquired a larger number by the time of their second capture. The fact that this correlation was noted for both male and female lizards argues that testosterone levels were not responsible for some lizards being more prone to becoming heavily infested. We returned lizards to their original home range after each recapture. Perhaps some individuals simply spend more time in areas where ticks are questing for attachment, and males are more prone to infestation because they are more active in defending a territory and come in contact with more questing ticks. In a mark-release-recapture experiment conducted at Hopland Research Station, Lane et al. (1995) demonstrated that fence lizards usually become infested by *I. pacificus* ticks while the lizards are inactive in their burrows at night rather than while they are active during the day. If males tend to utilize a larger number of sleeping burrows, or to sleep in habitats with relatively high densities of ticks, they might thereby accumulate larger tick infections.

The presence of large numbers of ticks (up to 78 on a lizard) can have some negative consequence for the host (the reduction in density of blood cells noted by Dunlap and Mathies, 1993), but it is possible that the fairly short season for tick infestation minimizes the overall cost to body condition as observed here and by Dunlap and Mathies (1993). However, the higher number of ticks infesting lizards that were captured only once suggests that ticks may induce some mortality in the lizards. Dunlap and Mathies (1993) found that lizards infected with a malaria parasite, *Plasmodium mexicanum,* as well as infested with ticks, suffered reduction in body condition. We collected the Hopland lizards at a location where the malaria parasite is uncommon in the lizards, so unfortunately our sample size of malarious lizards was too small to determine any interaction in effect for the two kinds of parasite.

For both male and female fence lizards, ticks, but not mites, congregated in the nuchal pockets. Arnold (1986) noted that such invaginations occur in many species of lizards, on the neck (nuchal), axillae, and at the sides of the tail base, and proposed that they serve to concentrate ectoparasites to minimize the harmful effects of infestation. Salvador et al. (1999) experimentally showed with the lacertid lizard *Psammodromus algirus,* that if ticks are not permitted to enter the nuchal pocket, they will be displaced to areas that cause greater harm to the lizard.

The patterns of prevalence of ticks and mites differed substantially suggesting strongly that the two kinds of ectoparasites have different ecologies. Nonetheless, there may be some ecological interaction between ticks and mites. First, there is a negative relationship between the number of ticks and mites on individual lizards, and second there appears to be a seasonal shift, such that ticks exploit the lizard more in the early summer and mites more later in the season. Seasonal and geographical variation in attachment by *I. pacificus* ticks on fence lizards is of medical interest because of the potential role of the lizards in limiting the prevalence of Lyme disease.

Acknowledgments.—We thank S. Osgood and K. Gurski for collecting lizards, and R. Eisen and A. Salvador for technical advice. The staff of the Hopland Field Station offered logistical support. Jim Webb at Orange County Vector Control District generously identified ectoparasites, and the students in KAH's Ecology of Host-Parasite Interactions class at Pomona College aided with lizard collection and ectoparasite monitoring at the two southern California sites. The work at Hopland Field Station was funded by a grant from NSF to JJS.

LITERATURE CITED

ARNOLD, E. N. 1986. Mite pockets of lizards, a possible means of reducing damage by ectoparasites. Biol. J. Linn. Soc. 29:1–21.

BONORRIS, J. S., AND G. H. BALL. 1955. *Schellackia occidentalis* n. sp., a blood-inhabiting coccidian found in lizards in southern California. J. Parasitol. 2:31–34.

DUNLAP, K. D., AND T. MATHIES. 1993. The effects of nymphal ticks and their interaction with malaria on the physiology of male western fence lizards. Copeia 1993:1041–1045.

LANE, R. S., J. E. KLEINJAN, AND G. B. SCHOELER. 1995. Diel activity of nymphal *Dermacentor occidentalis* and *Ixodes pacificus* (Acari: Ixodidae) in relation to meteorological factors and host activity periods. J. Med. Entomol. 32:290–299.

———, AND J. E. LOYE. 1989. Lyme disease in California: interrelationship of *Ixodes pacificus* (Acari: Ixodidae), the western fence lizard (*Sceloporus occidentalis*), and *Borrelia burgdorferi.* J. Med. Entomol. 26:272–278.

———, AND G. B. QUISTAD. 1998. Borreliacidal factor in the blood of the western fence lizard (*Sceloporus occidentalis*). J. Parasitol. 84:29–34.

MØLLER, A. P., G. SORCI, AND J. ERRITZØE. 1998. Sexual dimorphism in immune defense. Amer. Natur. 152: 605–619.

SALVADOR, A., J. P. VEIGA, J. MARTIN, P. LOPEZ, M. ABELENDA, AND M. PUERTA. 1996. The cost of producing a sexual signal: testosterone increases the susceptibility of male lizards to ectoparasite infestation. Behav. Ecol. 7:145–150.

———, ———, ———, AND ———. 1997. Testosterone supplementation in subordinate small male lizards: consequences for aggressiveness, colour development, and parasite load. Behav. Ecol. 8:135–139.

———, ———, AND E. CIVANTOS. 1999. Do skin pockets of lizards reduce the deleterious effects of ectoparasites? An experimental study with *Psammodromus algirus.* Herpetologica 55:1–7.

SCHALL, J. J. 1996. Malarial parasites of lizards: diversity and ecology. Adv. Parasitol. 37:255–333.

Accepted: 26 October 1999.

Journal of Herpetology, Vol. 34, No. 1, pp. 163–168, 2000

Colonization Dynamics of Two Exotic Geckos (*Hemidactylus garnotii* and *H. mabouia*) in Everglades National Park

WALTER E. MESHAKA, JR., *Everglades Regional Collections Center, Everglades National Park, 40001 SR-9336, Homestead, Florida 33034-6733, USA. E-mail: walter_meshaka@nps.gov*

The exotic herpetofaunal community of Florida includes 37 species, most of which are found in disturbed habitats of southern Florida and have arrived in the past 25 yr (Butterfield et al., 1997; Meshaka et al., 2000). Because of continuing urbanization and influx of exotic species of amphibians and reptiles, extreme southern Florida is undergoing a profound human-mediated alteration of a major segment of its biological community that has yet to stabilize. The restructuring process of this community has resulted not only in the rapid accumulation of new exotic species but also in species succession. Among the hemidactyline geckos, *H. garnotii,* a parthenogenetic species (Kluge and Eckhardt, 1969), appears to have largely replaced *H. turcicus* in southern Florida (Meshaka, 1995), and both are outnumbered in varying degrees by *H. mabouia,* a bisexual species (Meshaka et al., 1994a, b; Meshaka and Moody, 1996). Because these species do not naturally co-occur with one another and appear to be ecologically analogous, stable coexistence has been postulated to be impossible (Meshaka et al., 1994c). To test this hypothesis, I examined populations of *H. garnotii* and *H. mabouia* in the Ev-