

Growth Rates and Body Condition in *Norops polylepis* (Polychrotidae) Vary with Respect to Sex but not Mite Load¹

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ABSTRACT

Norops polylepis is a common anoline lizard that occupies both forest and pasture habitats at various elevations in southern Costa Rica. Previous studies have documented significant spatial variation in mite loads (*Eutrombicula* chiggers) on *N. polylepis*. My objective was to investigate whether mite load has a negative impact on growth rates and body condition. Growth rates were estimated in three sites using mark-recapture with three intensive sampling periods over 12 mo. Nine hundred and forty lizards were captured and 200 individuals were recaptured across sampling periods. Mite load was significantly higher in forests than in pastures, and varied significantly among study sites. Males grew faster than females, and females and juveniles had higher body condition than males. I was unable, however, to detect any influence of mite load on growth rates or body condition. I conclude that *Eutrombicula* chiggers are either largely benign for *N. polylepis* or, if they do exert a negative effect on fitness, it is mediated through a trait other than growth or body condition.

RESUMEN

Norops polylepis es un lagarto común en bosques y pastizales de alturas variables en Costa Rica meridional. Estudios previos han documentado una variación espacial significativa en cargas de ectoparasitos ("coloradillas" *Eutrombicula* spp.) en *N. polylepis*. Mi objetivo fue el de investigar si la carga de ectoparasitos tiene un impacto negativo sobre la tasas de crecimiento y la condición física de *N. polylepis*. Las tasas de crecimiento se estimaron durante 12 meses en tres sitios, utilizando tres periodos intensivos de marcaje y recaptura. Se capturaron 940 lagartos y de éstos, 200 individuos fueron recapturados durante el período del muestreo. La carga de ectoparasitos fue más alta en los bosques que en los pastizales y varió entre sitios de estudio. El crecimiento de lagartos machos fue más rápido que el de las hembras; pero las hembras y los jóvenes tuvieron una mejor condición física que los machos. Sin embargo, no hubo influencia de la carga de ectoparasitos sobre la tasas de crecimiento o la condición física. Se concluyó que las coloradillas *Eutrombicula* spp. son benignas para *N. polylepis*. En el caso de un efecto negativo de la carga de ectoparasitos, éste puede influir en otros aspectos de la salud de los lagartos.

Key words: body condition; Costa Rica; *Eutrombicula*; growth rate; *Norops polylepis*; parasitism.

LIZARDS, AND PARTICULARLY ANOLES, HAVE PROVEN MODEL ORGANISMS for assessing the ecological and evolutionary determinants of growth and body size (e.g., Andrews 1982, Shine 1990, Stamps 1993). Growth in anoles is rapid in juveniles and they approach an asymptotic size shortly after maturity (Schoener & Schoener 1978). Intrinsic growth rates are the product of numerous ecological and evolutionary factors, including resource availability (Tracy 1999), abiotic conditions (Adolph & Porter 1996, Arendt 1997), predation risks, trade-offs with developmental functions, and inter- and intrasexual selection (Andrews 1982, Anderson & Vitt 1990, Stamps *et al.* 1997).

Norops polylepis (formerly *Anolis polylepis*; Polychrotidae) is a common lizard species in southern Costa Rica, where it ranges from sea level (Andrews 1971) to 1330 m (Savage 2002). Full-grown adult males reach a longer snout-vent length (SVL) than females (ca 57 vs. 53 mm) (Savage 2002). *Norops polylepis* is commonly ectoparasitized by chiggers (*Eutrombicula* mite larvae; Order: Acari, Family: Trombiculidae; Schlaepfer & Gavin 2001), and mite loads (also known as infestation intensity) can vary from 0 to 105 per lizard (M. Schlaepfer, pers. obs). *Eutrombicula* larvae feed off the

lymph of their reptile hosts until they drop off and continue their life cycle as nonparasitic adults (Hogue 1983). *Eutrombicula* loads on anoles are higher in moist, shady habitats than in open, dry habitats, and forest edges (Zippel *et al.* 1996, Schlaepfer & Gavin 2001). Mite loads on lizards appear to mirror seasonal abundance of chiggers in the field, at least in one study conducted in Tennessee, U.S.A. (Klukowski 2004).

Perhaps because *Eutrombicula* chiggers are a nuisance to humans (Hogue 1983), it is easy to assume that chiggers will have a negative effect on lizard fitness. Studies that demonstrate a clear effect of ectoparasites on lizard fitness, however, are surprisingly rare. Sorci and Clobert (1995) found that higher mite loads correlated with increased mortality and lower body mass in the common lizard *Lacerta vivipara*. There is also anecdotal evidence that very high mite loads can lead to reduced survivorship (see Domrow 1981 and references in Klukowski 2004). I used a large mark-recapture study to test whether mite loads correlate with low body condition and growth rate in *N. polylepis*.

MATERIALS AND METHODS

STUDY SITE AND SYSTEM.—I sampled *N. polylepis* at three sites in the vicinity of the Las Cruces Biological field station, located in the

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southern end of the Province of Puntarenas, Costa Rica (see detailed site description in Schlaepfer & Gavin 2001). The three sites were within 3 km of each other along the Fila Cruces ridge. Each study site consisted of seven 15 m × 25 m plots arranged in a linear array spanning the pasture–forest boundary, from 45 m within the pastures to 145 m within the forest (Schlaepfer 2002). Two plots in the pasture were defined as “pasture” habitat; two plots within the forest, 5–45 m from the edge, were defined as “forest edge”; and the remaining three plots, 55–145 m from the edge, as “forest interior” habitat. The three sites were chosen so as to be as comparable as possible, with actively grazed pastures, mature primary forest, and similar topographical features. The following coordinates and elevations were measured using a hand-help GPS unit between the two pasture plots of each array: Lower Forest Reserve (LFR, 1100 m): 82°57.927W, 8°46.973N; Upper Forest Reserve (UFR, 1250 m): 82°58.670W, 8°47.082N; and Fragment 5 (FR5, 1320 m): 82°59.638W, 8°47.105N. The air temperature at the LFR site was, on average, 1.0°C warmer than UFR, and 2.4°C warmer than FR5 based on simultaneous, hourly temperature measurements taken over 48 h in the forest at all three sites on 28–29 November 1999 (Schlaepfer 2002).

Each study site was sampled intensively on three occasions, at 5–7 mo intervals, between November 1998 and March 2000 (Table 1). Sampling at each site spanned a full year, thereby largely controlling for any seasonal effects, although the time of the first sampling period differed between sites (Table 1). Each captured individual was measured, given a unique toe-clip, and released. Each intensive sampling period consisted of five consecutive search days, but only the first capture of each individual within a sampling period was analyzed. An estimated 90 percent of all individuals within a sampled area were captured within each sampling period (Schlaepfer 2002).

ECTOPARASITES.—I counted the number of *Eutrombicula* mites by scanning the groin, armpit, and dewlap region of each individual using eye-glasses with 10× magnification. In the growth rate analysis, an individual’s mite load was determined by averaging the number of chiggers at the initial capture and recapture. I did not attempt to distinguish between different *Eutrombicula* species (see “Results” for identified species), and I assumed that the relative impact of different chiggers species on *N. polylepis* was similar. The number of mites was heavily skewed toward zero. As a result, I applied a square root transformation to attempt to normalize the distribution of ectoparasite loads before including this variable in the statisti-

cal analyses; however, I report back-transformed means for ease of interpretation.

BODY CONDITION.—A large number of studies have regressed body mass on a body-size indicator and used the residuals as a measure of body condition (Green 2001). This approach has statistical drawbacks, however (Green 2001, Freckleton 2002). Instead, I estimated body condition using a multiple regression (General Linear Model in Minitab version 11.21), in which mass is the response variable and a body-size indicator (*e.g.*, SVL) is entered as a covariate (Green 2001, Freckleton 2002). The analysis produces a size-corrected measure of mass, *i.e.*, body condition. Only lizards without tail loss were used for this analysis. Individuals could not always be reliably sexed when initially captured, particularly preadult stages. Each individual, therefore, was scored as male, female, juvenile, probable male, or probable female. The latter two categories were ascribed to the juvenile category in the analyses. The following factors were used in the body-condition model: sex, site (LFR, UFR, or FR5), habitat (pasture, forest edge, or forest interior), SVL, and square root of number of mites. I subsequently tested interaction terms for significant factors.

GROWTH RATES.—I defined growth rate as the increase in SVL divided by the number of days between capture events. Growth rate in anoline lizards is rapid in juveniles, and then decreases asymptotically after sexual maturation (Schoener & Schoener 1978). A quadratic growth equation was used to model the nonlinear trajectory. Specifically, I used ANCOVAs to analyze growth rates with mean SVL and (mean SVL)² as a covariate in all analyses. All individuals could be reliably sexed at the time of recapture based on the presence of an enlarged dewlap (throat-fan) in males. The following factors were used in the growth model: sex (M or F), site (LFR, UFR, or FR5), habitat (pasture, forest edge, or forest interior), square root transformed mean number of mites (between capture and recapture), and tail autotomy (loss). I subsequently tested interaction terms for any significant factors.

I included tail autotomy as a variable in this study to determine if it affected growth rate, even though others found no such effect (Van Sluys 1998, Fox & McCoy 2000). Tail regrowth has a distinct appearance and, as a result, tail autotomy was easily scored. I scored tail autotomy as a categorical variable rather than attempt to estimate how recently the tail, and what percentage of the original tail tip, had broken off. Lizards that lost their tail during capture were excluded from the growth rate analysis.

TABLE 1. Dates of sampling periods, and number of recaptures from prior periods.

| Sampling period | Lower Forest Reserve | Upper Forest Reserve | Fragment 5 |
|-----------------|---------------------------------------|--|--|
| #1 | November to December 1998 | January 1999 | February to March 1999 |
| #2 | April 1999 (47 recaps from #1) | September to October 1999 (27 recaps from #1) | October 1999 (22 recaps from #1) |
| #3 | November 1999 (22 from #2; 9 from #1) | January to February 2000 (45 from #2; 2 from #1) | February to March 2000 (24 from #2; 2 from #1) |

In a few cases (25 of 175), individuals were captured in all three sampling periods (Table 1). Growth estimates between consecutive sampling periods were included in analyses and treated as independent data. I did not discard negative growth increments, which allows for small measurement error between samples (Schoener & Schoener 1978).

RESULTS

CAPTURES.—More than 1200 lizards were captured during the course of this study. Of these, 940 (431 females, 409 males, 21 probable females, 48 probable males, and 31 juveniles of unknown sex) with complete tails were used in the analysis of body condition. One hundred and fifty individuals were captured in two sampling periods and 25 individuals were captured in all three sampling periods, yielding a total of 200 recapture events (Table 1) for the growth rate analysis. The number of days between captures did not differ between sites, sexes, or habitats, and did not correlate with growth rates (ANOVAs and regression analyses; $P > 0.22$ in all cases). The sample sizes for each sex, site, and habitat are given in Table 2.

PARASITE LOADS.—*Eutrombicula goeldi*, *E. pacae*, and *E. soaldi* were identified on three museum voucher specimens collected for this study. Mean parasite load (averaged over initial capture and recapture) per recaptured individual ranged from 0 to 37 chiggers (25th percentile = 1.5, median = 4.0, 75th percentile = 10.5, $N = 200$). The number of parasites at initial captures was significantly positively correlated with the number of parasites at recapture ($r = 0.48$, $P = 0.000$). ANOVA on square root transformed mite loads revealed significant effects of site and habitat, but not of sex. Here, I report the results of univariate tests on the back-transformed parasite loads (Table 2). Mite loads (mean \pm SD) differed among habitats (ANOVA: $F_{2,197} = 11.66$, $P = 0.000$). Forest edges (8.54 ± 8.53) did not differ significantly from forest interiors (7.75 ± 7.85), but lizards in forested habitats had significantly higher loads than in pastures (0.13 ± 0.36 ; Tukey's pair-wise comparison, $P < 0.019$). Parasite loads did not differ significantly (ANOVA: $F_{1,198} = 1.84$, $P = 0.176$) between males (5.74 ± 2.96) and females (4.38 ± 1.95).

TABLE 2. Mean parasite load (SD) in recaptured *Norops polylepis* ($N = 200$) by site, habitat, and sex.

| Site (elev.) | Habitat | Female | Male |
|--------------|-----------------|-----------------------|------------------------|
| LFR (1100 m) | Pasture | 0.00 (N/A) $N = 1$ | 0.50 (0.71) $N = 2$ |
| | Forest edge | 6.24 (4.93) $N = 17$ | 5.94 (4.79) $N = 17$ |
| | Forest interior | 6.19 (6.11) $N = 24$ | 3.88 (4.57) $N = 17$ |
| UFR (1250 m) | Pasture | 0.50 (0.87) $N = 3$ | 0.00 (0.00) $N = 4$ |
| | Forest edge | 11.98 (7.75) $N = 21$ | 21.55 (11.40) $N = 11$ |
| | Forest interior | 9.13 (6.78) $N = 24$ | 17.95 (11.38) $N = 11$ |
| FR5 (1320 m) | Pasture | 0.05 (0.15) $N = 11$ | 0.00 (0.00) $N = 3$ |
| | Forest edge | 2.38 (2.51) $N = 17$ | 4.71 (3.17) $N = 7$ |
| | Forest interior | 3.63 (1.51) $N = 8$ | 3.25 (3.89) $N = 2$ |

Parasite load varied significantly across sites (ANOVA: $F_{2,197} = 33.03$, $P = 0.000$), with UFR (intermediate elevation) having significantly higher mite loads (12.25 ± 10.08) per individual than in LFR (5.42 ± 5.22) and FR5 (2.28 ± 2.61 ; Tukey's pair-wise comparison, $P < 0.019$).

Individual parasite loads based on a single capture (used in analysis of body condition) showed the same pattern as the mean parasite loads above, although they showed a greater range [0–61] because of a larger sample size. The distribution of parasite load in single captures was also more skewed toward low parasite loads (25th percentile = 0.0, median = 2.0, 75th percentile = 6.0, $N = 940$) because many more small individuals (juveniles) were included in this sample. SVL (mm) was strongly correlated with mite load (ML) in lizards ($ML^{0.5} = -1.57 + 0.0802 * SVL$, $R^2 = 0.22$, $F_{1,930} = 272.5$, $P = 0.000$).

BODY CONDITION.—Body condition differed between sexes (Table 3); females and juveniles were heavier for a given SVL than males. Body condition did not differ between habitats (pasture, forest edge, and forest interior) and sites, and did not correlate with square root transformed parasite load (Table 3).

GROWTH RATES.—Growth in SVL differed between sexes (Table 4); males grew significantly faster than females ($F_{1,189} = 31.25$, $P = 0.000$). Growth rates also differed significantly across sites ($F_{2,189} = 7.55$, $P = 0.001$) and was fastest at LFR (lowest elevation) and slowest at FR5 (highest elevation). All other factors, including square root transformed mean mite load, were nonsignificant (Table 4).

DISCUSSION

Neither body condition nor growth rate in *N. polylepis* correlated with mite loads of *Eutrombicula* in this study. However, both body condition and growth rate differed significantly between males and females. Male *Norops/Anolis* lizards generally exhibit a similar characteristic growth rate r (which describes the speed at which an individual tends toward its asymptotic size; Andrews 1976, Schoener

TABLE 3. Analysis of covariance of effects of snout-vent length (SVL), square root of mite load ($ML^{0.5}$), sex, site, and habitat on the square root of mass ($M^{0.5}$). Because SVL is included as a predictor variable, $M^{0.5}$ is an index of relative body condition rather than an absolute measure of size.

| Source | df | Seq SS | Adj SS | Adj MS | F | P |
|------------|-----|---------|--------|--------|-------------------|-------|
| SVL | 1 | 133.643 | 70.640 | 70.640 | 2.5×10^4 | 0.000 |
| $ML^{0.5}$ | 1 | 0.002 | 0.003 | 0.003 | 0.97 | 0.326 |
| Sex | 2 | 0.483 | 0.493 | 0.246 | 88.28 | 0.000 |
| Site | 2 | 0.014 | 0.016 | 0.008 | 2.81 | 0.061 |
| Habitat | 2 | 0.001 | 0.001 | 0.001 | 0.25 | 0.776 |
| Error | 931 | 2.598 | 2.598 | 0.003 | | |
| Total | 939 | 136.742 | | | | |

TABLE 4. Analysis of covariance of effects of mean snout-vent length (SVL), square root of mite load ($ML^{0.5}$), sex, site, and habitat on growth rate (Δ mm/d) in *Norops polylepsis*.

| Source | df | Seq SS | Adj SS | Adj MS | F | P |
|----------------------|-----|----------|----------|----------|-------|-------|
| meanSVL | 1 | 0.151118 | 0.002284 | 0.002284 | 12.70 | 0.000 |
| meanSVL ² | 1 | 0.001603 | 0.006452 | 0.006452 | 35.87 | 0.000 |
| ML ^{0.5} | 1 | 0.001011 | 0.000108 | 0.000108 | 0.60 | 0.439 |
| Sex | 1 | 0.013526 | 0.008986 | 0.008986 | 49.96 | 0.000 |
| Site | 2 | 0.004652 | 0.003799 | 0.001899 | 10.56 | 0.000 |
| Habitat | 2 | 0.000129 | 0.000093 | 0.000046 | 0.26 | 0.773 |
| Sex * site | 2 | 0.000147 | 0.000146 | 0.000073 | 0.41 | 0.667 |
| Tail loss | 1 | 0.000067 | 0.000067 | 0.000067 | 0.37 | 0.543 |
| Error | 188 | 0.033814 | 0.033814 | 0.000180 | | |
| Total | 199 | 0.206066 | | | | |

& Schoener 1978) to females, but grow to a larger asymptotic size than females. As a result, male anoles generally grow absolutely faster than females, as was observed in this study.

Body condition reflects the “plumpness” of an individual of a given size, and is presumed to correlate with energy stores. In this study, males were significantly lighter than females and juveniles of the same length. The relatively high body condition of adult females is likely the result of resources diverted into egg production rather than growth. The relatively low body condition of adult males relative to juveniles may be the result of adult males expending more energy on territorial defense and courtship behavior.

Information on intraspecific, small-scale variations in growth rates is generally lacking for lizards. Schoener and Schoener (1978) found that the intrinsic growth rates for *A. sagrei* varied dramatically across different habitats separated by a few hundred meters from one another, presumably due to differences in lizard density.

Although mite loads did not correlate with growth rates and body condition, they did vary between habitats and sites, and with lizard length. Consistent with previous studies (Zippel *et al.* 1996, Schlaepfer & Gavin 2001), mite loads were significantly lower in the dry, warm pastures than in cooler, moist forests. Lizards captured in pastures, even 5 m from the forest edge, generally carried zero or one mite. Mite loads were also significantly higher on lizards at UFR than at the two other sites for reasons which are not clear, but this result indicates that other ecological factors besides those included in this study can influence parasite load. Consistent with previous work (Schlaepfer & Gavin 2001), mite load also increased with lizard SVL. Based on the simple linear regression analysis, a typical 30-mm SVL juvenile had an average of 0.7 mites, whereas a 50-mm SVL (gender-neutral) adult had 6.0.

Mite load did not have a detectable effect on growth rate or body condition, even after controlling for the influence of habitat type, sex, and site. The amount of variation in body condition and growth rates explained by a lizard's mite load was at least one order of magnitude smaller than the amount of variation explained by a lizard's sex and site (see adjusted MS in ANOVA in Tables 3 and 4).

This suggests that, even if mites do have a negative effect on lizard fitness, the size effect is extremely small relative to other ecological factors.

Other studies have failed to find a relationship between ectoparasite loads and lizard fitness (Christian & Bedford 1995, Smith 1996, Abell 2000). I also failed to detect any effect of mite load despite a relatively large sample size. Collectively, these studies suggest that ectoparasites do not have a large direct impact on their host's growth rates and body condition.

It is possible, however, that mites exert a negative effect on their host only during years of unusually high mite abundance, or via mechanisms other than growth rates or body condition. For example, ectoparasites may have a synergistic effect with other diseases. Fence lizards *Sceloporus occidentalis* had a lower body condition when simultaneously infected with malaria, *Plasmodium mexicanum*, and ticks, *Ixodes pacificus*, relative to lizards infected with just one or neither parasite (Dunlap & Mathies 1993). Ectoparasites can increase the probability of mortality of a lizard, as in the case of the European fence lizards *L. vivipara* parasitized by laelapid mites (Sorci & Clobert 1995). The effects of ectoparasitism can also be behavioral. Main and Bull (2000) found that *Tiliqua rugosa* lizards with experimentally increased loads of ticks had smaller home ranges, moved shorter distances, basked more, and moved less often than lizards with reduced loads. Endoparasites such as *Plasmodium* malaria can also affect a lizard's social status (Dunlap & Schall 1995) and competitive ability (Schall 1992). Future studies should explore whether *Eutrombicula* chiggers affect *Norops* lizards in any of these ways. Based on the current study, however, I conclude that *Eutrombicula* chiggers are either largely benign or, if they do exert a negative effect on fitness, the effect is mediated through a trait other than growth or body condition.

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