

High tolerance of two parasites in ornate tree lizards reduces the fitness costs of parasitism

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Keywords

ectoparasite; haemoparasite; mark-recapture; *Plasmodium*; ornate tree lizard; parasite resistance; *Urosaurus ornatus*; fitness cost.

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Editor: Mark-Oliver Rödel
Associate Editor: Anthony Herrel

Received 23 January 2020; revised 20 April 2020; accepted 29 April 2020

doi:10.1111/jzo.12795

Abstract

Parasites are ubiquitous and are presumed to have strong negative effects on host fitness. Despite this expectation, many parasites have negligible effects on their hosts in nature. Two hypotheses can explain why this might occur. Hosts can evolve resistance to parasites where their immune system attacks parasites (resistance hypothesis). The resistance hypothesis predicts that parasite load will decrease through time because of immune activity and that parasites have fitness costs to hosts. Alternatively, hosts can evolve tolerance to parasites and invest little energy in repelling attacks (tolerance hypothesis). The tolerance hypothesis predicts that parasites have no fitness costs to hosts. We tested these hypotheses with mark-recapture data from six populations of a lizard host (*Urosaurus ornatus*) and two common parasites (ectoparasitic Trombiculid mites and haemoparasitic *Plasmodium*). We found that parasite load was unrelated to lizard growth rates or survival. In addition, mite parasite load did not decrease through time. Thus, our data support the tolerance hypothesis. Ectoparasitic mites and haemoparasitic *Plasmodium* are therefore unlikely to be strong drivers of variation in *Urosaurus ornatus* population density at our study sites because of their negligible effects on host fitness. We encourage ecologists to measure carefully the effects of parasites on hosts, rather than assuming fitness costs of parasitism are present.

Introduction

Parasites are ubiquitous and are presumed to have strong negative effects on host fitness (Sheldon & Verhulst, 1996). Parasites decrease host fitness by decreasing reproduction or survival, and the conflict between hosts and parasites often imposes antagonistic arms-race selection pressures on both (Decaestecker *et al.*, 2007). Parasite virulence, measured as the fitness cost on hosts, varies based on the life history strategies of the parasite and of the host (Gandon, Agnew & Michalakis, 2002; Barrett *et al.*, 2008), and on how long host-parasites have been co-evolving (May & Anderson, 1990; Toft & Karter, 1990). For example, the reproductive strategy of the parasite and its host specificity (Lajeunesse & Forbes, 2002) as well as the relative investment in survival versus reproduction of the host (Miller, White & Boots, 2007) affect virulence.

Parasites often have strong negative effects on host body condition, survival and reproduction (Lehmann, 1993). The pathological pathways through which parasites affect their hosts are incredibly varied, but the pathways are often related to energetic investment. For example, lizards infected with haemogregarine blood parasites shift energy allocation towards reproduction, which may decrease survival (Sorci, Clobert & Michalakis, 1996). Sometimes, there is a direct survival cost to increased parasite load; ectoparasite load decreases survival in

gerbils because ectoparasites cause anaemia (Lehmann, 1992). In other cases, parasite infection decreases reproduction: birds with mild chronic malaria from *Plasmodium* infection lay fewer eggs and are less successful at raising offspring than uninfected birds (Asghar *et al.*, 2015).

Despite well-documented fitness costs of parasites (Lehmann, 1993), there are many examples of high parasite loads having negligible effects on host fitness. Indeed, many parasites have almost undetectable effects on fitness in natural populations (Bull & Burzacott, 1993; Brown, Shilton & Shine, 2006; Mayer *et al.*, 2015; Jones *et al.*, 2016). Why would some parasites have strong fitness costs whereas others apparently have none? Answering this question is necessary to explain temporal and spatial patterns in host survival, reproduction and abundance. Several hypotheses have been proposed to explain why parasites have undetectable fitness costs on their hosts. First, the ability of hosts to attack parasites after infection (resistance hypothesis) can reduce the cost of parasitism because parasites are attacked by the immune system before parasites exert their fitness costs (Råberg, Graham & Read, 2009; Svensson & Råberg, 2010). The resistance hypothesis predicts that (1) individual infection load decreases through time because of host immune activity attacking parasites and that (2) host fitness is negatively related to infection load. Alternatively, the fitness costs of parasites may be low

when hosts have high tolerance (Råberg *et al.*, 2009; Svensson & Råberg, 2010) that allow them to buffer the fitness costs associated with a parasite attack (tolerance hypothesis). Tolerance of parasites can evolve independently of resistance (Mazé-Guilmo *et al.*, 2014), and thus hosts may still have high infection loads. The tolerance hypothesis predicts that (1) individual infection load does not decrease through time and that (2) host fitness is unrelated to infection load. These two hypotheses for explaining why parasites may have negligible fitness costs on hosts are not mutually exclusive, and there may be variation between individuals in resistance and tolerance. Further, the host–parasite relationship is dynamic and the red queen hypothesis predicts that both hosts and parasites will continue to evolve defences against and attacks towards each other (Decaestecker *et al.*, 2007).

We tested the resistance and tolerance hypotheses about the fitness costs of parasitism in a study system consisting of one lizard host (*Urosaurus ornatus*) and two abundant parasites: ectoparasitic Trombiculid mites and haemoparasitic *Plasmodium*. There is evidence from studies in captivity that *Plasmodium* infection affects traits correlated with fitness in lizards (Schall, 1982), but limited evidence from field studies (Eisen, 2001). Trombiculid mites feed on blood and there is some evidence they have effects on lizard fitness (Cox & John-Alder, 2007; Johnson, Lymburner & Blouin-Demers, 2019). We used mark-recapture data collected at six sites over three years to measure how parasite load affects growth and survival, and to determine whether infection load changes through time. More specifically, we started by exploring what drives variation among hosts in parasite load. Then, we tested whether individual parasite load decreases (consistent with the resistance hypothesis) or is stable or increases (consistent with the tolerance hypothesis) through time. Finally, we tested whether parasite load decreases (consistent with the resistance hypothesis) or is unrelated to (consistent with the tolerance hypothesis) fitness. We used growth and survival as proxies for fitness. Growth is a good fitness correlate in our study system because body size is correlated with clutch size in females (Martin, 1977) and with social dominance in males (Carpenter, 1995). Survival is also a good fitness correlate for our study system because most ornate tree lizards only live for one breeding season and young lizards have low survival rates (Paterson & Blouin-Demers, 2018a).

Materials and methods

Study species, study sites & parasite loads

The ornate tree lizard (*Urosaurus ornatus*) is a small, short-lived, and widespread lizard that lives in the southwestern United States of America and northern Mexico. We studied ornate tree lizards in the Chiricahua Mountains of southeastern Arizona at six sites from 2014 to 2016. At our study sites, ornate tree lizards hatch in late summer or early fall and reach maturity the following spring. Thus, our study spanned three cohorts of lizards. Adults have a snout-vent-length (SVL) of 48.6 ± 0.1 mm (range 37.0–57.8 mm; Paterson & Blouin-Demers, 2018b). Although most lizards survive one breeding

season only, some individuals can live more than 4 years (Paterson & Blouin-Demers, 2018b). Each site (all separated by >300 m) was 300 m long and followed a creek bed. Each site extended 50 m perpendicular from the creek bed into the adjacent upland habitat. The density of ornate tree lizards varied from 11–251 lizards/ha (Paterson & Blouin-Demers, 2018a); other lizard species present at the study sites included striped plateau lizards (*Sceloporus virgatus*), Yarrow's spiny lizards (*Sceloporus jarrovi*), and Clark's spiny lizards (*Sceloporus clarkii*). We captured ornate tree lizards during 12 capture sessions (four per year) at each site. Because we sampled from May to August, all ornate tree lizards we captured were sexually mature.

We conducted one capture session per day. During a capture session, we walked continuously through the site and captured lizards with a pole and lasso (García-muñoz & Sillero, 2010). At least two people searched the site at least three times. We recorded the total search effort (person*hours) for each capture session. We marked each individual lizard by heat-branding scales with a medical cauterizer (Winne *et al.*, 2006; Ekner *et al.*, 2011). We assumed that marks were permanent because lizards from the first capture sessions had identifiable marks more than two years later and because previous studies have demonstrated marks are readable after three years (Winne *et al.*, 2006). We measured the SVL of each lizard with digital calipers (± 0.1 mm) and the mite infection load by counting the number of Trombiculid mites on the body with a hand lens. Tree lizards have small, stable home ranges during the active season (M'Closkey, Baia & Russell, 1987; Paterson & Blouin-Demers, 2018a) allowing repeated captures of individuals and thus making them particularly suitable for measuring growth and survival.

In a subsample of lizards, we also examined blood smears to quantify *Plasmodium* infection. We removed a single toe on the hind right foot as part of a skeletochronology study (Paterson & Blouin-Demers, 2018b) and smeared blood on a glass slide. We fixed slides in methanol for one minute and then stained them with Wright–Giemsa stain. To assess *Plasmodium* infection load, we examined 5000 red blood cells under a light microscope at 400x magnification and counted the number of infected red blood cells (Halliday *et al.*, 2014; Watkins & Blouin-Demers, 2019). We used the number of infected red blood cells (per 5000 cells) as an index of *Plasmodium* parasite load.

Variation in parasite load

To examine how mite infection load varied between captures and lizards, we used a generalized linear mixed-effects model. We used mite infection load as the response variable and body size (SVL), sex and day of the year (quadratic) as fixed effects. We included body size because larger individuals harbour more parasites in related lizard species in our study area (Halliday *et al.*, 2014; Watkins & Blouin-Demers, 2019) and we included sex because male lizards often harbour more parasites than females (Klukowski & Nelson, 2001; Halliday *et al.*, 2014). We used a quadratic effect for day of the year because environmental temperatures increase in the spring and decline

once the summer monsoons start in mid-summer; a quadratic effect fit the data significantly better than a linear effect (log-likelihood ratio test, $\chi^2 = 76.30$, $P < 0.0001$). We included random effects for lizard identity nested within site, year, and observation. We fit the model with a Poisson error distribution. We included a random effect for observation because the data were overdispersed. We analysed all data in R (R Core Team, 2017) and fit generalized linear mixed-effects models with the *lme4* package (Bates *et al.*, 2015). We checked for multicollinearity between predictor variables in each model using (generalized) variance inflation factors (VIFs); the VIFs in all mixed-effects models were less than five and there was no evidence of multicollinearity.

To test which variables were associated with *Plasmodium* infection load, we used a generalized linear mixed-effects model with infection load as the response variable, and SVL, sex and day of the year (quadratic) as fixed effects. As above, a quadratic effect fit the data better than a linear effect (log-likelihood ratio test, $\chi^2 = 3.57$, $P = 0.06$). We included site, year and observation as random effects. We could not test for changes in infection load between captures for *Plasmodium* because we only sampled blood from lizards once. Finally, to investigate the effects of co-infection on lizard hosts, we tested whether mite infection load was related to *Plasmodium* infection load with a linear regression for instances where we counted both parasites on the same individual at the same time.

Variation in mite infection load through time

We tested how mite infection load varied over time with a linear mixed-effects model. For every lizard that we recaptured, we measured the slope of the linear relationship between days since first capture and mite infection load. We used the slope estimate for change in mite infection load per day as the response variable, and included fixed effects for the mean SVL for each lizard and sex. We included site as a random effect. We only included individuals caught more than once in this analysis.

Fitness consequences of parasitism

We used two fitness proxies to test if parasitism reduced lizard fitness. First, we used growth rates estimated from recaptures of lizards. We divided the difference in SVL ($SVL_2 - SVL_1$) by the number of days between captures to quantify daily growth rate. We removed inactive days between 1 November and 1 April (Dunham, 1982) when lizards are not growing. For lizards captured multiple times, we estimated daily growth rate between the first and last capture. We tested how growth rate was related to mite infection load using a linear mixed-effects model with growth rate as the response variable, the mean number of mites on a lizard, sex and the starting body size (SVL) as fixed effect predictors. We included site as a random effect. We tested how growth rate was related to *Plasmodium* infection using a linear mixed-effects model with growth rate as the response variable, *Plasmodium* infection load, initial SVL and sex as fixed effect predictors. We included site as a random effect.

Second, we estimated the effect of mite infection on monthly survival using mark-recapture models and estimated the effect of *Plasmodium* infection on annual survival with generalized linear mixed-effects models. We estimated the effect of mite infection load on survival using Cormack-Jolly-Seber (CJS) models (Jolly, 1965; Seber, 1965; Cormack, 1989) with the package *RMark* (Laake, 2013) to access the program MARK (White & Burnham, 1999). We fit CJS models using maximum likelihood to estimate apparent survival (ϕ), the probability of an individual surviving to the next month and not permanently emigrating, and detection probability (p), the probability of a lizard being captured during a capture event. To test the effect of mite infection on ϕ , we used an individual covariate for the mean number of mites counted on a lizard. We also included an individual covariate for body size (mean SVL) because larger lizards harboured more mites. We started with a general model where ϕ varied with mean SVL, mean number of mites, sex, season (active season 2 April to 31 October; inactive season 1 November to 1 April), and year. In the general model, p was a function of sex, search effort (person*hours per capture session) and weather. To include a covariate of weather on p , we used a principal component analysis on daily summaries of precipitation, maximum temperature, minimum temperature and mean observed temperature from a nearby weather station at the Southwestern Research Station operated by the National Oceanic and Atmospheric Administration (Menne *et al.*, 2012). We conducted model selection in two steps. First, we constructed all subsets of the general model for p with the full variable set for ϕ and ranked them using (Q)AIC_c for each site (Burnham & Anderson, 2002) to determine the most-supported model explaining variation in detection probability. Next, we tested all subsets of the general model for ϕ using the most-supported variables explaining variation in p . If there was more than one model with strong support when we performed selection for variation in p (< 2 (Q) AIC_c from the most-supported model), then we included those variables in the model selection for ϕ . We tested for goodness-of-fit on the general model by estimating the variance inflation factor (\hat{c}) using the median, bootstrap and Fletcher methods (Lebreton *et al.*, 1992; Fletcher, 2012). For models with a \hat{c} greater than 1, we adjusted model results for this extra-binomial noise using the largest estimate of \hat{c} . The individual covariate effects of body size and mite load were not included in our estimates of \hat{c} because there are no goodness-of-fit tests for CJS models with individual covariates (White & Burnham, 1999).

To assess whether infection with *Plasmodium* affected survival rates, we compared the number of lizards that survived to the next year to *Plasmodium* infection load. We did not use mark-recapture models because only a subsample of lizards at each site were assessed for *Plasmodium* infection and we sampled lizards for *Plasmodium* infection only once. We used a generalized linear mixed-effects model with survival to the next year as the response (binary), and *Plasmodium* infection load, sex, and SVL as fixed effect predictors. We included a random effect for site and fit the model with a binomial error structure.

Results

Variation in parasite load

In 1539 captures of 1000 lizards (1.5 ± 0.03 captures per lizard, range 1–8 captures per lizard), lizards harboured at least one mite on their body on 1136 (74%) occasions. Mite load varied from 0 to 120 mites per lizard (mean = 9, median = 4). Larger lizards harboured more mites (Wald $\chi^2 = 4.80$, $P = 0.03$), males (11 ± 0.55) harboured more mites than females (7 ± 0.42 , Wald $\chi^2 = 72.59$, $P < 0.001$), and infection was most intense in the middle of the active season (Wald $\chi^2 = 76.39$, $P < 0.001$; Fig. 1; Table S1). There were considerable differences between observations (variance = 0.78), lizard identity (variance = 0.73), and site (variance = 0.68). There were only minor differences in mite infection load between years (variance = 0.05).

In a subsample of 416 lizards, 110 (26%) were infected with *Plasmodium*. The infection load varied from 0 to 300 infected cells per 5000 (mean = 12, median = 0). Again, larger lizards had higher infection loads (Wald $\chi^2 = 35.28$, $P < 0.001$) and males (14 ± 2 infected per 5000 red blood cells) were more infected than females (10 ± 2 infected per 5000 red blood cells; Wald $\chi^2 = 9.60$, $P = 0.002$; Table S2). The *Plasmodium* infection load was highest in the middle of the active season (Wald $\chi^2 = 3.44$, $P = 0.06$). There were considerable differences between observations (variance = 6.65), site (variance = 1.26), and year (variance = 0.52) in *Plasmodium* infection load.

Mite infection load and *Plasmodium* infection loads were unrelated ($F = 0.93$, d.f. = 1, 414, $P = 0.33$).

Variation in mite infection load through time

There was no evidence that individual mite load changed over time (slope: -0.22 ± 0.35 mites per day, $F = 0.35$, d.f. = 1, 193, $P = 0.56$; Fig. 2; Table S3) for lizards caught multiple

times ($n = 352$). Changes in mite infection load did not differ between sites (site variance estimate < 0.001).

Fitness consequences of parasitism

Lizard growth rate was unaffected by mite load ($n = 345$ lizards, $F = 1.86$, d.f. = 1, 48, $P = 0.18$; Fig. 3a; Table S4). Although unrelated to our predictions, it is interesting to note that females and males grew at similar rates ($F = 1.52$, d.f. = 1, 322, $P = 0.22$) and that growth rate decreased linearly with body size ($F = 144.91$, d.f. = 1, 278, $P < 0.001$). Site did not affect lizard growth rates (variance of random site effect < 0.001).

Survival was not strongly affected by the number of mites harboured by a lizard at any of the six study sites (Fig. 3b). The general mark-recapture models all fit the data well ($\hat{c} < 4$ at all sites; Table S5). The model tables for each site are presented in Tables S6–S11. The coefficient for the effect of mite infection load on survival rate was not significantly different from zero in the most-supported model at any study site (Fig. 3b).

Growth rates were unrelated to *Plasmodium* infection load ($n = 122$, $F = 0.01$, d.f. = 1, 108, $P = 0.91$; Fig. 4a; Table S12). Growth rates did not vary between sites (variance < 0.001). Of 276 lizards sampled in 2014 and 2015, 21 infected lizards and 37 uninfected lizards were caught the following year. Lizards more heavily infected with *Plasmodium* were slightly more likely to survive to the next year ($\beta = 0.0087 \pm 0.0038$; Wald $\chi^2 = 5.38$, $P = 0.02$; Fig. 4b; Table S13). Survival to the next year was unaffected by sex (Wald $\chi^2 = 0.04$, $P = 0.84$) or body size (Wald $\chi^2 = 1.47$, $P = 0.22$). Survival to the next year did not vary between sites (variance < 0.001).

Discussion

Based on three years of mark-recapture data on one thousand lizards, we show that their two common parasites do not have

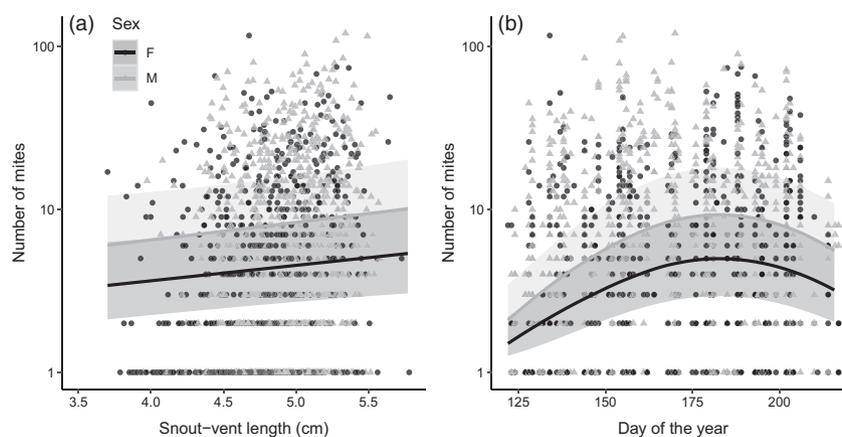


Figure 1 The effect of (a) Snout-vent length and (b) Day of the year on mite infection load (log-transformed axis) in ornate tree lizards (*Urosaurus ornatus*) in the Chiricahua Mountains of southeastern Arizona, USA. The solid lines and shading represent predictions and 95% confidence intervals from generalized linear mixed-effects models with mean day of the year in (a) and mean body size in (b) and while ignoring random effects.

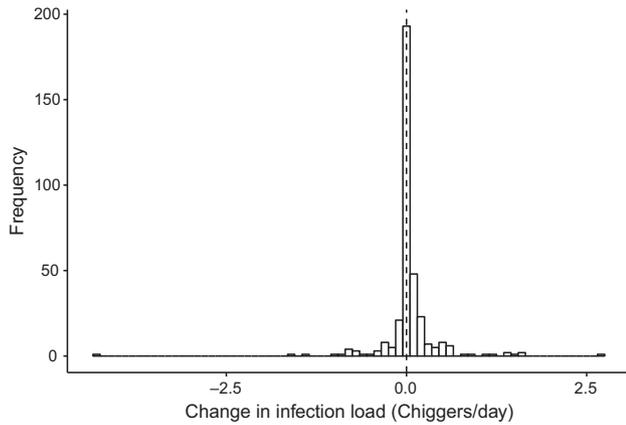


Figure 2 The slope estimates for the effect of time (days since first capture) on mite infection load for ornate tree lizards (*Urosaurus ornatus*) that were recaptured at least once ($n = 352$) in the Chiricahua Mountains of southeastern Arizona, USA. The vertical dashed line represents no change in mite infection load (0 mites/per day).

detectable effects on fitness as estimated from growth rates and survival. The lack of fitness costs of parasitism in lizard hosts is likely because of tolerance, rather than because of resistance through immune activity. The lizard hosts' parasite loads did not decrease through time and we did not detect any fitness costs, even with very high parasite loads.

Larger lizards harboured more parasites. This association between parasite load and body size is consistent with previous observations in lizards (Schall, 1996; Garrido & Pérez-Melgado, 2013; Halliday *et al.*, 2014) and fish (Lo, Morand & Galzin, 1998). Larger hosts may harbour more parasites because they have more surface area for attachment or entry, are easier to detect by parasites and their vectors, or because larger hosts

are older and have had a longer time to accumulate parasites (Ruby & Dunham, 1984; Lo *et al.*, 1998; Blackenhorn, 2000; Watkins & Blouin-Demers, 2019). Considering that blood-feeding mite larvae and haemoparasitic *Plasmodium* infection did not decrease survival rates or growth rates of ornate tree lizard hosts, we posit that likely mechanisms are that older and larger hosts have more time to accumulate a higher parasite load, are easier to detect by parasites, or provide more space for attachment.

The number of mites a lizard harboured did not decrease through time, which is consistent with the tolerance hypothesis. Stability in mite parasite load occurred either because lizard hosts did not invest significantly in immune activity to attack parasites once infected, or because the immune activity was insufficient to decrease a host's infection load. Mite infection is associated with increased immune activity in other lizard species (Huyghe *et al.*, 2010), but the relationship was weak and peaked at intermediate mite infection loads (quadratic relationship). Thus, the relationship between ectoparasitic mite load and immune activity in lizard hosts may be complex and non-linear. If ectoparasitic mites have coevolved with ornate tree lizards to have low virulence, then hosts should only invest a small amount of energy in attacking parasites because there is little to no fitness cost of parasitism. We did not measure immune activity of lizards directly; measuring the relationship between host-parasite load and immune activity by manipulating the number of ectoparasitic mites would provide a stronger test of the predictions of the resistance hypothesis.

Neither mite nor *Plasmodium* parasite load decreased fitness proxies in ornate tree lizards. Variance in lizard growth rates was explained by the starting body size of the lizard, as expected from asymptotic growth in ornate tree lizards (Paterson & Blouin-Demers, 2018b). Lizard survival was unrelated to mite parasite load at any of the six study sites. Lizard survival increased with *Plasmodium* infection loads (opposite of our prediction), but the effect was small with wide confidence

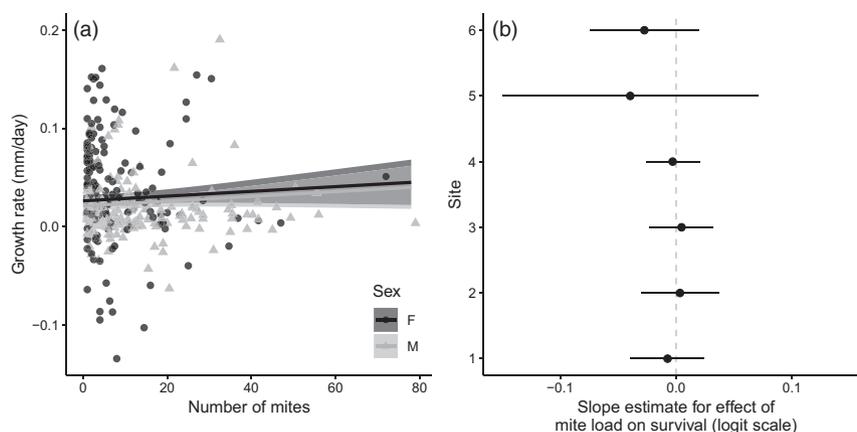


Figure 3 The effect of mite load on (a) growth rate and (b) survival rate in ornate tree lizards (*Urosaurus ornatus*) in the Chiricahua Mountains of southeastern Arizona, USA. For (a), solid lines and shading represent predictions and 95% confidence intervals from generalized linear mixed-effects models with mean body size and mean day of the year while ignoring random effects. For (b), points and lines represent estimates and 95% confidence intervals of the coefficient for the effect of mite load on survival using the top-ranked Cormack-Jolly-Seber mark-recapture model from the six study sites.

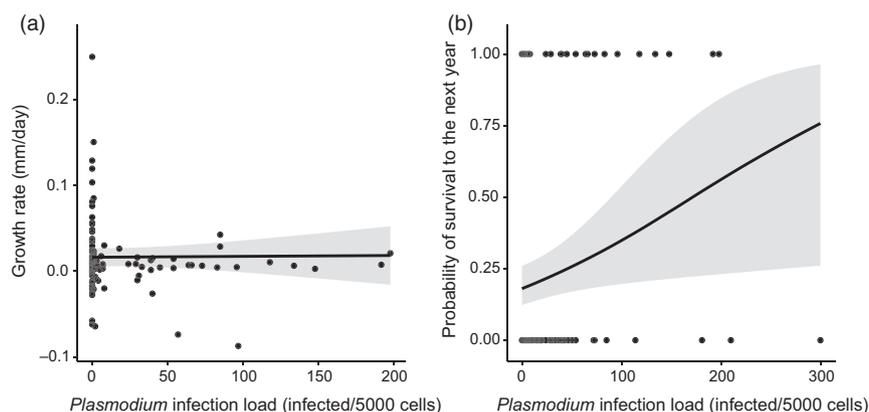


Figure 4 The effect of *Plasmodium* infection load on (a) growth rate ($n = 122$) and (b) probability of surviving to the next year ($n = 273$) for ornate tree lizards (*Urosaurus ornatus*) in the Chiricahua Mountains of southeastern Arizona, USA. Solid lines and shading represent predictions and 95% confidence intervals from generalized linear mixed-effects models with mean body size and mean day of the year while ignoring random effects.

intervals and few lizards had very high *Plasmodium* infection loads. We studied lizards and their parasites in six populations that varied widely in density (Paterson & Blouin-Demers, 2018a), so it is unlikely our results are unrepresentative of this host–parasite system. Our data are consistent with several studies where parasites had negligible fitness consequences on hosts and where host–parasite pairs have a long coevolutionary history (Bull & Burzacott, 1993; Brown *et al.*, 2006; Mayer *et al.*, 2015). It is possible fitness costs of parasitism in this system may manifest themselves in other responses, such as effects on reproductive output (Schwanz, 2008) or may only occur during extreme conditions (Jones *et al.*, 2016). Future work should investigate the effects of mite and *Plasmodium* infection on reproductive output and whether the host–parasite relationship changes during extreme environmental conditions.

Our study was observational, and our inferences are thus limited to the variation in parasite load and the hosts we sampled in our study populations. One limitation to our approach is that there may be unobservable patterns arising from the sampling process. If high parasite loads cause hosts to die quickly, our sampling may have missed these individuals and thus our observations are only of more tolerant individuals. For example, fitness costs of chytridiomycosis in anurans develop beyond a threshold of parasite load (Stockwell, Clulow & Mahony, 2010). Future tests of the fitness costs of parasites should include experimental manipulation of parasite load in natural conditions to rule out the possibility of a threshold effect of parasite load on lizard fitness.

Overall, our data on the effects of parasite infection on lizard hosts are consistent with the tolerance hypothesis, but not with the resistance hypothesis. Given the high tolerance to parasites and the negligible effects of parasite load on fitness, ectoparasitic mites and haemoparasitic *Plasmodium* are unlikely to be important factors driving variation in ornate tree lizard population density at our study sites. Parasites might still impact their lizard hosts, but we could not detect the cost of parasitism in survival or growth rates. We encourage ecologists

to measure carefully the effects of parasites on hosts, rather than assuming fitness costs of parasitism are present.

Acknowledgements

We thank Valérie Bertrand, Martine Doucet, Liam Eaton, Lucy Patterson, Peter Soroye, Agneta Szabo, Dariya Quenneville, Hannah Watkins, and Troy Webster for assistance with data collection. We are grateful for logistical support provided by Barbara Roth and the Southwestern Research Station. Lizards were collected under Arizona Fish and Game Department Scientific Collector's Permits: SP674341, SP713940, and SP740592. Animal use was approved by the University of Ottawa Animal Care Committee (protocols BL286 and BL-2300-R1) and by Coronado National Forest (Douglas Ruppel). This research was funded by a Natural Sciences and Engineering Research Council of Canada (NSERC) grant to G.B.D. and an NSERC scholarship and Ontario Graduate Scholarship to J.E.P.

References

- Asghar, M., Hasselquist, D., Hansson, B., Zehtindjiev, P., Westerdaal, H. & Bensch, S. (2015). Hidden costs of infection: chronic malaria accelerates telomere degradation and senescence in wild birds. *Science* **347**, 436–438.
- Barrett, L.G., Thrall, P.H., Burdon, J.J. & Linde, C.C. (2008). Life history determines genetic structure and evolutionary potential of host–parasite interactions. *Trends Ecol. Evol.* **23**, 678–685.
- Bates, D.M., Maechler, M., Bolker, B. & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *J. Stat. Softw.* **67**, 1–48.
- Blackenhorn, W.U. (2000). The evolution of body size: what keeps organisms small? *Q. Rev. Biol.* **75**, 385–407.
- Brown, G.P., Shilton, C.M. & Shine, R. (2006). Do parasites matter? Assessing the fitness consequences of haemogregarine infection in snakes. *Can. J. Zool.* **84**, 668–676.

- Bull, C.M. & Burzacott, D. (1993). The impact of tick load on the fitness of their lizard hosts. *Oecologia* **96**, 415–419.
- Burnham, K.P. & Anderson, D.R. (2002). *Model selection and multi-model inference: a practical information-theoretic approach*. New York: Springer.
- Carpenter, G.C. (1995). Modeling dominance: the influence of size, coloration, and experience on dominance relations in tree lizards (*Urosaurus ornatus*). *Herpetol. Monogr.* **9**, 88–101.
- Cormack, R.M. (1989). Log-linear models for capture-recapture. *Biometrics* **45**, 395–413.
- Cox, R.M. & John-Alder, H.B. (2007). Increased mite parasitism as a cost of testosterone in male striped plateau lizards *Sceloporus virgatus*. *Funct. Ecol.* **21**, 327–334.
- Decaestecker, E., Gaba, S., Raeymaekers, J.A.M., Stoks, R., Van Kerckhoven, L., Ebert, D. & De Meester, L. (2007). Host-parasite “Red Queen” dynamics archived in pond sediment. *Nature* **450**, 870–873.
- Dunham, A.E. (1982). Demographic and life-history variation among populations of the iguanid lizard *Urosaurus ornatus*: implications for the study of life-history phenomena in lizards. *Herpetologica* **38**, 208–221.
- Eisen, R.J. (2001). Absence of measurable malaria-induced mortality in western fence lizards (*Sceloporus occidentalis*) in nature: a 4-year study of annual and over-winter mortality. *Oecologia* **127**, 586–589.
- Ekner, A., Sajkowska, Z., Dudek, K. & Tryjanowski, P. (2011). Medical cautery units as a permanent and non-invasive method of marking lizards. *Acta Herpetol.* **6**, 229–236.
- Fletcher, D.J. (2012). Estimating overdispersion when fitting a generalized linear model to sparse data. *Biometrika* **99**, 230–237.
- Gandon, S., Agnew, P. & Michalakis, Y. (2002). Coevolution between parasite virulence and host life-history traits. *Am. Nat.* **160**, 374–388.
- García-muñoz, E. & Sillero, N. (2010). Two new types of noose for capturing herps. *Acta Herpetol.* **5**, 259–263.
- Garrido, M. & Pérez-Mellado, V. (2013). Patterns of parasitism in insular lizards: effects of body size, condition and resource availability. *Zoology (Jena)*. **116**, 106–12.
- Halliday, W.D., Paterson, J.E., Patterson, L.D., Cooke, S.J. & Blouin-Demers, G. (2014). Testosterone, body size, and sexual signals predict parasite load in Yarrow’s Spiny Lizards (*Sceloporus jarrovii*). *Can. J. Zool.* **92**, 1075–1082.
- Huyghe, K., Van Oystaeyen, A., Pasmans, F., Tadić, Z., Vanhooydonck, B. & Van Damme, R. (2010). Seasonal changes in parasite load and a cellular immune response in a colour polymorphic lizard. *Oecologia* **163**, 867–874.
- Johnson, N., Lymburner, A.H. & Blouin-Demers, G. (2019). The impact of ectoparasitism on thermoregulation in Yarrow’s Spiny Lizards (*Sceloporus jarrovii*). *Can. J. Zool.* **97**, 1004–1012.
- Jolly, G.M. (1965). Explicit estimates from capture-recapture data with both death and immigration-stochastic model. *Biometrika* **52**, 225–247.
- Jones, A.R., Bull, C.M., Brook, B.W., Wells, K., Pollock, K.H. & Fordham, D.A. (2016). Tick exposure and extreme climate events impact survival and threaten the persistence of a long-lived lizard. *J. Anim. Ecol.* **85**, 598–610.
- Klukowski, M. & Nelson, C.E. (2001). Ectoparasite loads in free-ranging northern fence lizards, *Sceloporus undulatus hyacinthinus*: Effects of testosterone and sex. *Behav. Ecol. Sociobiol.* **49**, 289–295.
- Laake, J. (2013). RMark: an R interface for analysis of capture-recapture data with MARK. *Version* **2(2)**, 2.
- Lajeunesse, M.J. & Forbes, M.R. (2002). Host range and local parasite adaptation. *Proc. R. Soc. B Biol. Sci.* **269**, 703–710.
- Lebreton, J.-D., Burnham, K.P., Clobert, J. & Anderson, D.R. (1992). Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. *Ecol. Monogr.* **62**, 67–118.
- Lehmann, T. (1992). Ectoparasite impacts on *Gerrhonotus allenbyi* under natural conditions. *Parasitology* **104**, 479–488.
- Lehmann, T. (1993). Ectoparasites: direct impact on host fitness. *Parasitol. Today* **9**, 8–13.
- Lo, C.M., Morand, S. & Galzin, R. (1998). Parasite diversity: host age and size relationship in three coral-reef fishes from French Polynesia. *Int. J. Parasitology* **28**, 1695–1708.
- Martin, R.F. (1977). Variation in reproductive productivity of range margin tree lizards (*Urosaurus ornatus*). *Copeia* **1977**, 83–92.
- May, R.M. & Anderson, R.M. (1990). Parasite–host coevolution. *Parasitology* **100**, S89–S101.
- Mayer, M., Brown, G.P., Zimmermann, B. & Shine, R. (2015). High infection intensities, but negligible fitness costs, suggest tolerance of gastrointestinal nematodes in a tropical snake. *Austral Ecol.* **40**, 683–692.
- Mazé-Guilmo, E., Loot, G., Páez, D.J., Lefèvre, T. & Blanchet, S. (2014). Heritable variation in host tolerance and resistance inferred from a wild host–parasite system. *Proc. R. Soc. B Biol. Sci.* **281**, 20132567.
- M’Closkey, R.T.M., Baia, K.A. & Russell, R.W. (1987). Tree lizard (*Urosaurus ornatus*) territories: experimental perturbation of the sex ratio. *Ecology* **68**, 2059–2062.
- Menne, M.J., Durre, I., Vose, R.S., Gleason, B.E. & Houston, T.G. (2012). An overview of the global historical climatology network-daily database. *J. Atmos. Ocean. Technol.* **29**, 897–910.
- Miller, M.R., White, A. & Boots, M. (2007). Host life span and the evolution of resistance characteristics. *Evolution* **61**, 2–14.
- Paterson, J.E. & Blouin-Demers, G. (2018a). Density-dependent habitat selection predicts fitness and abundance in a small lizard. *Oikos* **127**, 448–459.
- Paterson, J.E. & Blouin-Demers, G. (2018b). Tree lizard (*Urosaurus ornatus*) growth decreases with population density, but increases with habitat quality. *J. Exp. Zool. Part A Ecol. Integr. Physiol.* **329**, 527–535.

- R Core Team. (2017). *R: a language and environment for statistical computing*. Version 3.4.3. Vienna, Austria: <https://www.R-project.org/>.
- Råberg, L., Graham, A.L. & Read, A.F. (2009). Decomposing health: tolerance and resistance to parasites in animals. *Philos. Trans. R. Soc. B Biol. Sci.* **364**, 37–49.
- Ruby, D.E. & Dunham, A.E. (1984). A population analysis of the ovoviviparous lizard *Sceloporus jarrovi* in the Pinaleno Mountains of southeastern Arizona. *Herpetologica* **40**, 425–436.
- Schall, J.J. (1982). Lizards infected with malaria: physiological and behavioral consequences. *Science* **217**, 1057–1059.
- Schall, J.J. (1996). Malarial parasites of lizards: diversity and ecology. *Adv. Parasitol.* **37**, 255–333.
- Schwanz, L.E. (2008). Chronic parasitic infection alters reproductive output in deer mice. *Behav. Ecol. Sociobiol.* **62**, 1351–1358.
- Seber, G.A.F. (1965). A note on the multiple-recapture census. *Biometrika* **52**, 249–259.
- Sheldon, B.C. & Verhulst, S. (1996). Ecological immunology: costly parasite defences and trade-offs in evolutionary ecology. *Trends Ecol. Evol.* **11**, 317–321.
- Sorci, G., Clobert, J. & Michalakis, Y. (1996). Cost of reproduction and cost of parasitism in the common lizard, *Lacerta vivipara*. *Oikos* **76**, 121.
- Stockwell, M.P., Clulow, J. & Mahony, M.J. (2010). Host species determines whether infection load increases beyond disease-causing thresholds following exposure to the amphibian chytrid fungus. *Anim. Conserv.* **13**, 62–71.
- Svensson, E.I. & Råberg, L. (2010). Resistance and tolerance in animal enemy-victim coevolution. *Trends Ecol. Evol.* **25**, 267–274.
- Toft, C.A. & Karter, A.J. (1990). Parasite-host coevolution. *Trends Ecol. Evol.* **5**, 326–329.
- Watkins, H.V. & Blouin-Demers, G. (2019). Body size, not age, predicts parasite load in Clark's Spiny Lizards (*Sceloporus clarkii*). *Can. J. Zool.* **97**, 220–224.
- White, G.C. & Burnham, K.P. (1999). Program MARK: survival estimation from populations of marked animals. *Bird Study* **46**, S120–S139.
- Winne, C.T., Willson, J.D., Andrews, K.M. & Reed, R.N. (2006). Efficacy of marking snakes with disposable medical cautery units. *Herpetol. Rev.* **37**, 2004–2006.

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. Generalized linear mixed-effects model results for the effects of sex, body size, and day of year on mite infection load in ornate tree lizards (*Urosaurus ornatus*) at six study sites in the Chiricahua Mountains of southeastern Arizona, USA.

Table S2. Generalized linear mixed-effects model results for the effects of sex, body size, and day of year on *Plasmodium* infection load in ornate tree lizards (*Urosaurus ornatus*) at six study sites in the Chiricahua Mountains of southeastern Arizona, USA.

Table S3. Linear mixed-effects model results for the effects of sex and body size on the change in mite infection load (mites/day) in ornate tree lizards (*Urosaurus ornatus*) at six study sites in the Chiricahua Mountains of southeastern Arizona, USA.

Table S4. Linear mixed-effects model results for the effects of mite infection load, sex, and initial body size on the growth rates of ornate tree lizards (*Urosaurus ornatus*) at six study sites in the Chiricahua Mountains of southeastern Arizona, USA.

Table S5. Variance inflation factors (\hat{c}) for general Cormack-Jolly-Seber mark-recapture models for ornate tree lizards (*Urosaurus ornatus*) at six study sites in the Chiricahua Mountains of southeastern Arizona, USA using bootstrapping (1000 iterations), the median \hat{c} method, and Fletcher's \hat{c} .

Table S6. Most supported ($<4 \Delta AIC_c$ of most supported model) Cormack-Jolly-Seber models at site 1 for ornate tree lizards (*Urosaurus ornatus*) in the Chiricahua Mountains of southeastern Arizona, USA. The full model was: ϕ (~size + mites + sex + season + year) P (~sex + effort * weather). k , number of parameters in a model; AIC_c , bias-corrected Akaike's information criterion for a model; ΔAIC_c , difference in AIC_c between a model and the top-ranked model; ω , Akaike weight for a model.

Table S7. Most supported ($<4 \Delta AIC_c$ of most supported model) Cormack-Jolly-Seber models at site 2 for ornate tree lizards (*Urosaurus ornatus*) in the Chiricahua Mountains of southeastern Arizona, USA. The full model was: ϕ (~size + mites + sex + season + year) P (~sex + effort * weather). k , number of parameters in a model; AIC_c , bias-corrected Akaike's information criterion for a model; ΔAIC_c , difference in AIC_c between a model and the top-ranked model; ω , Akaike weight for a model.

Table S8. Most supported ($<4 \Delta AIC_c$ of most supported model) Cormack-Jolly-Seber models at site 3 for ornate tree lizards (*Urosaurus ornatus*) in the Chiricahua Mountains of southeastern Arizona, USA. The full model was: ϕ (~size + mites + sex + season + year) P (~sex + effort * weather). k , number of parameters in a model; AIC_c , bias-corrected Akaike's information criterion for a model; ΔAIC_c , difference in AIC_c between a model and the top-ranked model; ω , Akaike weight for a model.

Table S9. Most supported ($<4 \Delta AIC_c$ of most supported model) Cormack-Jolly-Seber models at site 4 for ornate tree lizards (*Urosaurus ornatus*) in the Chiricahua Mountains of southeastern Arizona, USA. The full model was: ϕ (~size + mites + sex + season + year) P (~sex + effort * weather). k , number of parameters in a model; $QAIC_c$, bias-corrected quasi-Akaike's information criterion for a model; $\Delta QAIC_c$, difference in $QAIC_c$ between a model and the top-ranked model; ω , Akaike weight for a model.

Table S10. Most supported ($<4 \Delta AIC_c$ of most supported model) Cormack-Jolly-Seber models at site 5 for ornate tree lizards (*Urosaurus ornatus*) in the Chiricahua Mountains of southeastern Arizona, USA. The full model was: ϕ (~size + mites + sex + season + year) P (~sex + effort * weather). k , number of parameters in a model; $QAIC_c$, bias-corrected quasi-Akaike's information criterion for a model; $\Delta QAIC_c$, difference in $QAIC_c$ between a model and the top-ranked model; ω , Akaike weight for a model.

Table S11. Most supported ($<4 \Delta AIC_c$ of most supported model) Cormack-Jolly-Seber models at site 6 for ornate tree lizards (*Urosaurus ornatus*) in the Chiricahua Mountains of southeastern Arizona, USA. The full model was: Φ (~size + mites + sex + season + year) p (~sex + effort * weather). k ,

number of parameters in a model; $QAIC_c$, bias-corrected quasi-Akaike's information criterion for a model; $\Delta QAIC_c$, difference in $QAIC_c$ between a model and the top-ranked model; ω , Akaike weight for a model.

Table S12. Linear mixed-effects model results for the effects of *Plasmodium* infection load, sex, and initial body size on the growth rates of ornate tree lizards (*Urosaurus ornatus*) at six study sites in the Chiricahua Mountains of southeastern Arizona, USA.

Table S13. Generalized linear mixed-effects model results for the effects of *Plasmodium* infection load, sex, and initial body size on survival of ornate tree lizards (*Urosaurus ornatus*) at six study sites in the Chiricahua Mountains of southeastern Arizona, USA.