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The impact of ectoparasitism on thermoregulation in Yarrow's Spiny Lizards (*Sceloporus jarrovii*)

N. Johnson, A.H. Lymburner, and G. Blouin-Demers

Abstract: Parasites are ubiquitous and can have large impacts on the fitness of their hosts. The effects of ectoparasites on physiology, behaviour, and immune function suggest that they could be part of the factors which impact thermoregulation. We tested the hypothesis that ectoparasites impact thermoregulation in Yarrow's Spiny Lizards (*Sceloporus jarrovii* Cope in Yarrow, 1875) living along an elevational gradient. We predicted a positive association between ectoparasite load and body temperature (T_b), and a negative association between ectoparasite load and effectiveness of thermoregulation ($d_e - d_b$ index). We also predicted that the impacts of ectoparasites would be greatest at high elevation where thermal quality of the environment is low because the costs of thermoregulation increase with elevation and these costs can impact thermal immune responses. We found a significant association between the number of chiggers (Trombiculoidea) harboured by lizards and T_b that depended on elevation, but no association between ectoparasite load and $d_e - d_b$ index. The mean chigger infection rate was associated with a ΔT_b of +0.18 °C at low elevation (consistent with fever) and of –1.07 °C at high elevation (consistent with hypothermia). These findings suggest that parasitism by chiggers impacts lizard T_b in a way that depends on environmental thermal quality.

Key words: Sceloporus jarrovii, Yarrow's Spiny Lizard, behavioural fever, immune response, ectoparasites.

Résumé : Les parasites sont omniprésents et peuvent avoir d'importants impacts sur l'aptitude de leurs hôtes. Les effets des ectoparasites sur la physiologie, le comportement et la fonction immunitaire portent à croire qu'ils pourraient faire partie des facteurs influençant la thermorégulation. Nous avons testé l'hypothèse voulant que les ectoparasites influencent la thermorégulation chez des scélopores de Yarrow (*Sceloporus jarrovii* Cope dans Yarrow, 1875) vivant le long d'un gradient d'altitude. Nous avons prédit une association positive entre la charge d'ectoparasites et la température corporelle (T_b), et une association négative entre la charge d'ectoparasites et l'efficacité de la thermorégulation (l'index de $d_e - d_b$). Nous avons aussi prédit que les impacts des ectoparasites seraient les plus grands à haute altitude où la qualité thermique du milieu est faible parce que les coûts de la thermorégulation augmentent avec l'altitude et que ces coûts peuvent influencer les réactions immunitaires thermiques. Nous avons relevé une association significative entre le nombre d'aoûtats (Trombiculoidea) sur les lézards et la température corporelle (T_b), qui dépend de l'altitude, mais aucune association entre la charge d'ectoparasites et l'index de $d_e - d_b$. Le taux moyen d'infection d'aoûtats est associé à des ΔT_b de +0,18 °C à faible altitude (ce qui indique de la fièvre) et de –1,07 °C à haute altitude (ce qui indique une hypothermie). Ces constatations portent à croire que le parasitisme d'aoûtats influence la T_b des lézards d'une manière qui dépend de la qualité thermique du milieu. [Traduit par la Rédaction]

Mots-clés : Sceloporus jarrovii, scélopore de Yarrow, fièvre comportementale, réponse immunitaire, ectoparasites.

Introduction

Parasites are widespread and diverse (Poulin and Morand 2000), representing an estimated 40% of described species (Dobson et al. 2008). Parasites often cause damage and impose energetic costs (Sheldon and Verhulst 1996), resulting in negative fitness consequences for hosts (Kutzer and Armitage 2016). Ultimately, parasites can impact the abundance (Scott and Dobson 1989), dynamics (Hudson et al. 1998), and reproduction of entire populations (Agnew et al. 2000).

Infected hosts often display complex phenotypic changes (Poulin 1994). A key example of phenotypic change is altered thermoregulation, especially in the forms of fever and hypothermia (Kluger et al. 1996; Goodman and Johnson 2011). Fever and hypothermia are phylogenetically conserved immune responses to pathogens and damage mediated by cytokines (Evans et al. 2015). Ectotherms achieve fever and hypothermia behaviourally, and this occurs in a wide range of taxa from insects (Thomas and Blanford 2003) to vertebrates (Rakus et al. 2017). There are several explanations for phenotypic changes during infection; the host manipulation hypothesis proposes that parasites adaptively manipulate their hosts in ways that increase transmission to a new host (Thomas et al. 2010). Alternatively, hosts can respond adaptively to infection; this appears to be the case with fever and hypothermia because altered temperatures stimulate immune responses and decrease pathogen fitness (Kluger et al. 1998). Finally, host phenotypic changes may simply be a side effect of infection with no clear adaptive value for host or parasite (Weinersmith and Faulkes 2014).

Temperature controls the rate of biological functions (Allen et al. 2002). In reptiles, body temperature (T_b) directly impacts physiological performances such as stamina, reaction time, escape speeds, and therefore, fitness (Seebacher 2005). Reptiles rely on behavioural thermoregulation to maintain optimal T_b and respond to environmental temperature changes (Seebacher 2005; Glanville and Seebacher 2006).

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N. Johnson, A.H. Lymburner, and G. Blouin-Demers. Department of Biology, University of Ottawa, 30 Marie-Curie Private, Ottawa, ON K1N 6N5, Canada.

Corresponding author: Noah Johnson (email: njohn028@uottawa.ca).

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Thermoregulation in reptiles is impacted by several factors including reproductive status (Mathies and Andrews 1997), season (Glanville and Seebacher 2006), sex (Patterson and Davies 1978), age (Gilbert and Lattanzio 2016), and physiological condition (Crowley 1987). Infection is another factor that can impact thermoregulation in reptiles (Kluger et al. 1998). Several genera including *Alligator* Cuvier, 1807 (Alligators; Merchant et al. 2007), *Dipsosaurus* Hallowell, 1854 (Desert Iguanas; Kluger et al. 1975), *Agama* Daudin, 1802 (Agamas), and *Sceloporus* Wiegmann, 1828 (Spiny Lizards; Ortega et al. 1991) display fever following bacterial injection. Thermal responses may be variable; bacterial lipopolysaccharide induces fever or hypothermia in Green Iguanas (*Iguana iguana* (Linnaeus, 1758)), depending on individual condition (Deen and Hutchison 2001). Different blood parasites also cause variable thermal responses; malaria (genus *Plasmodium* Marchiafava and Celli, 1885) elevates T_b in Western Fence Lizards (*Sceloporus occidentalis* Baird and Girard, 1852) (Scholnick et al. 2010), whereas the genus *Haemogregarina* Danilewsky, 1885 appear to reduce T_b in Viviparous Lizards (*Zootoca vivipara* (Lichtenstein, 1823); formerly known as *Lacerta vivipara* Jacquin, 1787) (Oppliger et al. 1996). Reduced T_b are also observed in Western Side-blotched Lizards (*Uta stansburiana* Baird and Girard, 1852) infected with the genera *Schellackia* Reichenow, 1919 and *Plasmodium* (Paranjpe et al. 2014). The hypothermic response to blood parasites may be adaptive by reducing parasite replication and the cost of impaired blood oxygen transport (Oppliger et al. 1996). Similar patterns of adaptive hypothermia occur in anemic and hypoxic lizards independently of infection (Hicks and Wood 1985; Wood 1991).

At least 15 families of primarily ectoparasitic mites infect reptiles (Fajfer 2012). These include the blood-feeding scale mites (Pterygosomatidae) (Baldwin 1999) and ticks (Ixodidae) (Dunlap and Mathies 1993), as well as the lymph-feeding chiggers (Trombiculoidea) (Arnold 1986). Conover et al. (2015) suggested that lizards may display thermal responses to the physiological impacts of ectoparasites. Indeed, at least one ectoparasite (a worm) induces behavioural fever in the guppy (*Poecilia reticulata* Peters, 1859) (Mohammed et al. 2016). Reptile ectoparasites inject saliva (Shatrov 2009) and cause tissue damage and inflammation (Goldberg and Holshuh 1993). Foreign material and tissue damage can induce thermal immune responses in vertebrates (Desborough 2000; Conti et al. 2004). Lizard ectoparasites transmit diseases (Spence et al. 2017) such as *Schellackia* and *Haemogregarina* known to impact thermoregulation in reptiles (Jordan and Friend 1971; Amo et al. 2005). Ectoparasites can also cause dehydration because they withdraw fluids and damage the integument, leading to evaporative water loss (Baldwin 1999). Since dehydration can reduce the preferred T_b of lizards (Crowley 1987), ectoparasites may impact thermoregulation by causing dehydration. Blood-feeding ticks and pterygosomatid mites can also alter lizard blood composition (Salvador et al. 1996; Baldwin 1999). Since many lizards reduce their preferred T_b in response to hypoxia caused by blood loss or changes in blood composition (Wood 1991), ectoparasites may cause similar responses.

Ectoparasites may interfere with behavioural thermoregulation by impeding mobility or increasing the costs of movement. Baldwin (1999) found that pterygosomatid mites caused joint inflammation, lowered the endurance, and reduced the sprint speeds of Florida Scrub Lizards (*Sceloporus woodi* Stejneger, 1918). Australian Sleepy Lizards (*Tiliqua rugosa* (Gray, 1825)) infected with ticks basked more and moved less than uninfected lizards (Main and Bull 2000). Paranjpe et al. (2014) suggested that the benefits of precise thermoregulation in lizards may be outweighed by conserving energy for an immune response. They found that the blood parasites *Schellackia* and *Plasmodium* reduced the thermoregulatory precision of *U. stansburiana*. The same concept may also apply to ectoparasites.

Despite several potential mechanisms through which ectoparasites could impact thermoregulation in reptiles, this potential has been largely overlooked. Conover et al. (2015) first addressed this question by investigating the impact of chigger mites on thermoregulation in wild Anole (*Anolis* Daudin, 1802) lizards. They found that mites did not elicit fever or impact basking duration in Large-headed Anoles (*Anolis cybotes* Cope, 1862) and Armoured Anoles (*Anolis armouri* (Cochran, 1934)). The authors suggested that fever may not occur at all in those lizards or that the costs of infection may not have been high enough for fever to be beneficial. Further investigations of the effects of ectoparasites on lizard thermoregulation is necessary given the high prevalence of ectoparasites on reptiles in nature and the impact of thermoregulation on fitness in reptiles.

We tested the hypothesis that ectoparasites impact thermoregulation in wild populations of Yarrow's Spiny Lizards (*Sceloporus jarrovii* Cope in Yarrow, 1875; Phrynosomatidae). *Sceloporus jarrovii* live along an elevational gradient in the Chiricahua Mountains of Arizona, USA, and frequently harbour ectoparasites such as chiggers (Bulté et al. 2009; Halliday et al. 2014) and scale mites (Goldberg and Holshuh 1992). Febrile responses have also been confirmed within the *Sceloporus* genus (Ortega et al. 1991). We tested three predictions while controlling for environmental factors and physiological variables that influence thermoregulation in lizards. First, lizards infected with more ectoparasites should display increased T_b, indicating fever. Second, lizards infected with more ectoparasites should thermoregulate less effectively, indicating that ectoparasites interfere with behavioural thermoregulation. Third, the impact of ectoparasites on the effectiveness of thermoregulation ($d_e - d_b$ index; for definitions refer to the Materials and methods below) and T_b should depend on elevation because habitat thermal quality declines with elevation resulting in greater costs of thermoregulation (Blouin-Demers and Nadeau 2005); this may drive elevational variation in thermoregulatory response to disease (Zamora-Camacho et al. 2016).

Materials and methods

Sceloporus jarrovii is a medium-sized viviparous alpine lizard (lizards in this study ranged from 3.2 to 9.6 cm snout–vent length (SVL)) whose range spans from southeastern Arizona to north-central Mexico (Ballinger 1973). *Sceloporus jarrovii* inhabits rocky areas such as talus slopes along an elevational gradient from approximately 1500 to 2800 m (Burns 1970; Smith and Ballinger 1994) and feeds mainly on arthropods (Simon 1975).

From 1 May to 23 July 2017, we sampled 13 talus slopes ranging in elevation from 1634 to 2700 m in the Chiricahua Mountains of Arizona, USA. These talus slopes are made of broken volcanic rocks (Tsuji 1984) and are optimal for studying thermoregulation because they remain structurally similar with changes in elevation. In general, we sampled each talus slope for two rounds of three consecutive days each, with no more than 17 days between rounds, to ensure our temporary markings remained on lizards. We staggered site visits to alternate between low, middle, and high elevations as evenly as possible and conducted additional sampling visits to achieve at least 50 adult captures per site. All lizards were captured under a State of Arizona Scientific Collection Permit (SP771492), with approval from the University of Ottawa Animal Care Committee (BL-2812) in accordance with the guidelines of the Canadian Council on Animal Care, and with permission from the US National Forest Service Douglas Ranger District (D. Ruppel).

Three observers walked the talus slopes and attempted to capture any active lizards with noose and pole. Immediately after capture, an infrared thermometer (emissivity = 0.95) was aimed at the cloaca to record T_b while avoiding skin contact. External infrared measurements are highly correlated with internal T_b in small lizards (Jones and Avery 1989; Andrews 2008; Bouazza et al. 2016); using external measurements reduces stress and handling time compared with traditional cloacal thermometers (Berg et al.

2015). Lizards were then placed individually into uniquely numbered white cotton bags and stored in a shaded location until processing.

Processing was done the same day and lizards were released at their capture location thereafter. Lizards were taped to a small white board and uniquely marked with permanent marker on the head and stomach. Lizards were sexed according to the presence of enlarged post-anal scales and blue colouration in males. Reproductive status in females was determined visually and by palpation for the presence of a swollen abdomen. SVL was measured with digital calipers accurate to 0.01 mm. Lizards were weighed by placing them in a plastic bag on a Pesola® digital scale accurate to 0.01 g.

Ectoparasites were counted with the aid of a magnifying glass. Chiggers were identified by their small size relative to ticks and scale mites, yellow to orange colouration, and general preference for the nuchal regions of the lizards (Arnold 1986). Pterygosomatid mites were distinguished by their large size relative to chiggers, affinity for scales on the back, tail, and joints of the hind legs (Goldberg and Bursey 1993), and deep red colouration when engorged (Walter and Shaw 2002). Hard ticks (Ixodidae) were easily distinguished from all other mites by their body shape, scutal plate, and long legs.

We measured the effectiveness of thermoregulation with the $d_e - d_b$ index proposed by Blouin-Demers and Weatherhead (2001). The $d_e - d_b$ index measures the extent to which an ectotherm achieves its preferred T_b compared with what an ectotherm behaving randomly with respect to available environmental temperatures would achieve. It is calculated by taking the difference between habitat thermal quality (d_e) and accuracy of body temperature (d_b). d_e is the absolute difference between operative environmental temperature (T_e; the temperature achieved by a non-thermoregulating lizard in the environment) and an ectotherm's preferred body temperature range (T_{set}; measured in a laboratory setting using a thermal gradient). d_b is the absolute difference between the actual T_b of a lizard in the field and the T_{set} range of a lizard (Hertz et al. 1993). Positive values of $d_e - d_b$ indicate an actively thermoregulating lizard, values near zero indicate thermoconformity, and negative values indicate avoidance of preferred thermal conditions (Blouin-Demers and Nadeau 2005).

We used the T_{set} range (30.4–33.2 °C) for *S. jarrovii* obtained by Patterson et al. (2017). To measure T_e, we placed three biophysical models on each slope (on a shaded rock, under a rock, and on a sunny rock). T_e was measured for the duration of lizard capture to create a thermal profile of a non-thermoregulating lizard with which to calculate the effectiveness of thermoregulation (Dzialowski 2005). Given the structural homogeneity of talus slopes, this thermal profile likely captured the full range of temperature conditions available to the lizards (but not the relative distributions of each temperature condition). The biophysical models were made from grey-painted copper pipes containing two iButton® temperature loggers (±1 °C).

Sex was recoded as a three-factor variable to incorporate reproductive status (male, non-gravid female, and gravid female). Date was transformed to Julian date. Chigger and pterygosomatid mite counts were $\log_{10}(x + 1)$ transformed (and hereafter referred to as simply chiggers and pterygosomatids) to meet the assumption of linear partial residuals in models of T_b and $d_e - d_b$. All continuous input variables were rescaled to have a mean of 0 and a SD of 0.5 prior to modelling. Scaling to a constant mean and SD facilitates model convergence, model selection, and comparisons of coefficients (Grueber et al. 2011). Scaling is also crucial for biological interpretation of interactions when the variables are measured on different scales (Schielzeth 2010).

All statistical analyses were conducted in R version 3.4.1 (R Core Team 2017). We constructed global (fully specified) linear mixed-effects models (LMEs) of T_b and $d_e - d_b$ with the lme4 package (Bates et al. 2014). Tick counts were not analyzed due to a small sample size (detected on 44 individuals, representing approximately 4.3% prevalence). To test the predictions that lizards infected with more ectoparasites display higher T_b and thermoregulate less effectively, we added terms for chiggers and pterygosomatid mites to the global models of T_b and $d_e - d_b$. To test the prediction that the impacts of ectoparasites on T_b and on $d_e - d_b$ depend on elevation, we added an elevation main effect with chigger × elevation and pterygosomatid × elevation interactions to the T_b and $d_e - d_b$ models.

The observational nature of our study mandated several statistical control variables. Sex was included because female *S. jarrovii* select lower T_b when gravid (Mathies and Andrews 1997). SVL controls for the influence of size on T_b (Gilbert and Lattanzio 2016). We included an SVL × time interaction because Middendorf and Simon (1988) found significant differences in thermoregulatory behaviour among *S. jarrovii* throughout the day depending on size. We added Julian date and time to control for the increases in temperature that we observed during the field season and during the day, respectively. Julian date × elevation, Julian date × time, and time × elevation interactions controlled for changes in environmental conditions during the field season. We then incorporated random effects with lizard ID nested in capture location to control for repeated captures within each site. The global models of T_b and $d_e - d_b$ were therefore both a function of time + Julian date + SVL + elevation + chiggers + pterygosomatids + sex + Julian date × elevation + Julian date × time + SVL × time + time × elevation + chiggers × elevation + pterygosomatids × elevation + (1|location/lizardID).

Global model assumptions were examined using sjPlot (Ludecke 2015). There were no major violations of linearity, homoscedasticity, normality of residuals, normality of random effects, or independence of the residuals. All variance inflation factors were less than 1.5 and the correlation between scaled predictor variables was low ($|r| < 0.35$ for all) indicating no major concerns with collinearity.

Model selection was performed using an information-theoretic approach (Burnham and Anderson 2003). This approach recognizes that several competing models may exist to explain the variation in the data (Burnham et al. 2011). The global models of T_b and $d_e - d_b$ were dredged in the package MuMIn (Bartoń 2018) to create lists of all possible subset models. Subsets within 2 ΔAIC_c units (where AIC_c is Akaike's information criterion corrected for small sample size) of the best T_b and $d_e - d_b$ models were then selected; these are considered highly supported alternative models (Burnham and Anderson 2003). AIC_c is the recommended metric for model selection and is equivalent to Akaike's information criterion (AIC) with large sample sizes (Burnham and Anderson 2004). The coefficients of the models in each 2 ΔAIC_c subset were then averaged by their likelihood weights to produce final model coefficients for the fixed effects. We also examined both the marginal (relating to only the fixed effects) and conditional (combined fixed and random effects) R^2 values.

Results

We captured 514 lizards (327 females, 187 males; 435 adults, 79 juveniles; SVL = 6.23 ± 0.05 cm (mean ± SE)) 1020 times. Lizards were captured, on average, 2 times (range of 1 (257 individuals) to 8 (1 individual)). T_b ranged from 14.4 to 39.9 °C (27.8 ± 0.1 °C (mean ± SE)). Values of the $d_e - d_b$ index ranged from –12.7 to 20.5 °C (3.63 ± 0.13 °C (mean ± SE)). Ectoparasites were recorded on 1014 of 1020 captures; most individuals had only a few ectoparasites, whereas a minority were severely infected. The prevalence of ectoparasites for all captures was 4.3% for ticks (range = 0–19, mean (±SE) abundance = 0.13 ± 0.03), 89.5% for chiggers (range = 0–399, mean (±SE) abundance = 23.36 ± 1.26), and 26.8% for pterygosomatid mites (range = 0–21, mean (±SE) abundance = 0.80 ± 0.07). Overall, 24.4%

Table 1. Averaged fixed-effects coefficients for the final model of body temperature (T_b) for Yarrow's Spiny Lizards (*Sceloporus jarrovii*) captured in the Chiricahua Mountains of Arizona, USA.

Model parameter	Relative importance	β^a	SE	Z	p
(Intercept)		28.47	0.69	40.93	<0.00001***
Julian date	1	1.22	0.55	2.21	0.02710*
Chiggers[b]	1	−0.51	0.26	1.98	0.04756*
Elevation	1	−2.78	1.33	2.08	0.03722*
Snout–vent length (SVL)	1	1.38	0.26	5.36	<0.00001***
Time	1	2.87	0.26	11.07	<0.00001***
Julian date × elevation	1	5.92	1.09	5.43	<0.00001***
Julian date × time	1	1.43	0.49	2.91	0.00359**
Chiggers[b] × elevation	1	−1.27	0.47	2.72	0.00662**
Elevation × time	1	−1.11	0.49	2.27	0.02323*
SVL × time	0.47	0.26	0.40	0.65	0.51404
Pterygosomatids[b]	0.52	−0.09	0.20	0.45	0.65546
Pterygosomatids[b] × elevation	0.28	−0.22	0.45	0.49	0.62232

Note: The final model was created from a subset of the top six models within 2 ΔAIC_c of the best model (n = 1014 captures of 512 individuals nested in 10 sites), where AIC_c is Akaike's information criterion corrected for small sample size. *, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$.

[a]Estimates (β) were standardized for continuous predictors.

[b]Chiggers (Trombiculoidea) and pterygosomatids (Pterygosomatidae) were $\log_{10}(x + 1)$ transformed.

of individuals were co-infected with chiggers and pterygosomatid mites.

There were at least three species of chiggers; likely all from the genus *Eutrombicula* Ewing, 1938 based on other reports from the region (Bennet 1977; Goldberg and Bursey 1993). Chiggers were typically found in the nuchal regions and occasionally on the sides of the body. Pterygosomatid mites were likely *Geckobiella texana* (Banks, 1904), a mite frequently reported on *Sceloporus* lizards in the region (Goldberg and Holshuh 1992; Goldberg and Bursey 1993, 1994). Ticks were dark brown, almost exclusively the larval stages, and likely a species of the genus *Amblyomma* Koch, 1844.

Body temperature (T_b)

The global model of T_b (n = 1014 records of 512 individuals in 10 sites, marginal R^2 = 0.22, conditional R^2 = 0.45) was dredged to produce a subset of six top models within 2 ΔAIC_c of the best model (the AIC_c of the best model (5418.2) was lower than that of the null model (5565.1)). The six top models were averaged to create the final model (standardized $\beta \pm$ SE values reported in Table 1). The final model showed a significant association between chiggers and T_b that differed in magnitude and direction depending on elevation (main effect: $\beta \pm$ SE = −0.51 ± 0.26, p = 0.047; interaction: $\beta \pm$ SE = −1.27 ± 0.47, p = 0.006; Fig. 1A). There was no significant main effect or interaction with elevation for pterygosomatid mites and T_b (main effect: $\beta \pm$ SE = −0.09 ± 0.20, p = 0.65; interaction: $\beta \pm$ SE = −0.22 ± 0.45, p = 0.62; Fig. 1B).

If the 10 sites are split between low and high elevations to examine the chigger × elevation interaction, chiggers are positively associated with T_b at the five lowest elevations (from 1634 to 1851 m; mean β = 0.16) and negatively associated with T_b at the five highest elevations (from 2134 to 2700 m; mean β = −0.93). The significant association between chiggers and T_b supports the first prediction that lizards infected with more ectoparasites display higher T_b at low elevation sites; however, the opposite was true at high elevations. The greater mean effect size at higher elevation supports the third prediction of a greater impact of ectoparasites with increasing elevation.

The statistical model predicts a ΔT_b of +0.33 °C at low elevation and −1.95 °C at high elevation at maximum infection intensity (339 chiggers) using the mean β of 0.16 and −0.93 for the five low and five high elevations, respectively. The mean infection rate among all captures in the population (23.4 chiggers) would be associated with a predicted ΔT_b of +0.18 °C relative to uninfected individuals at low elevation and −1.07 °C relative to uninfected individuals at high elevations.

Effectiveness of thermoregulation ($d_e - d_b$)

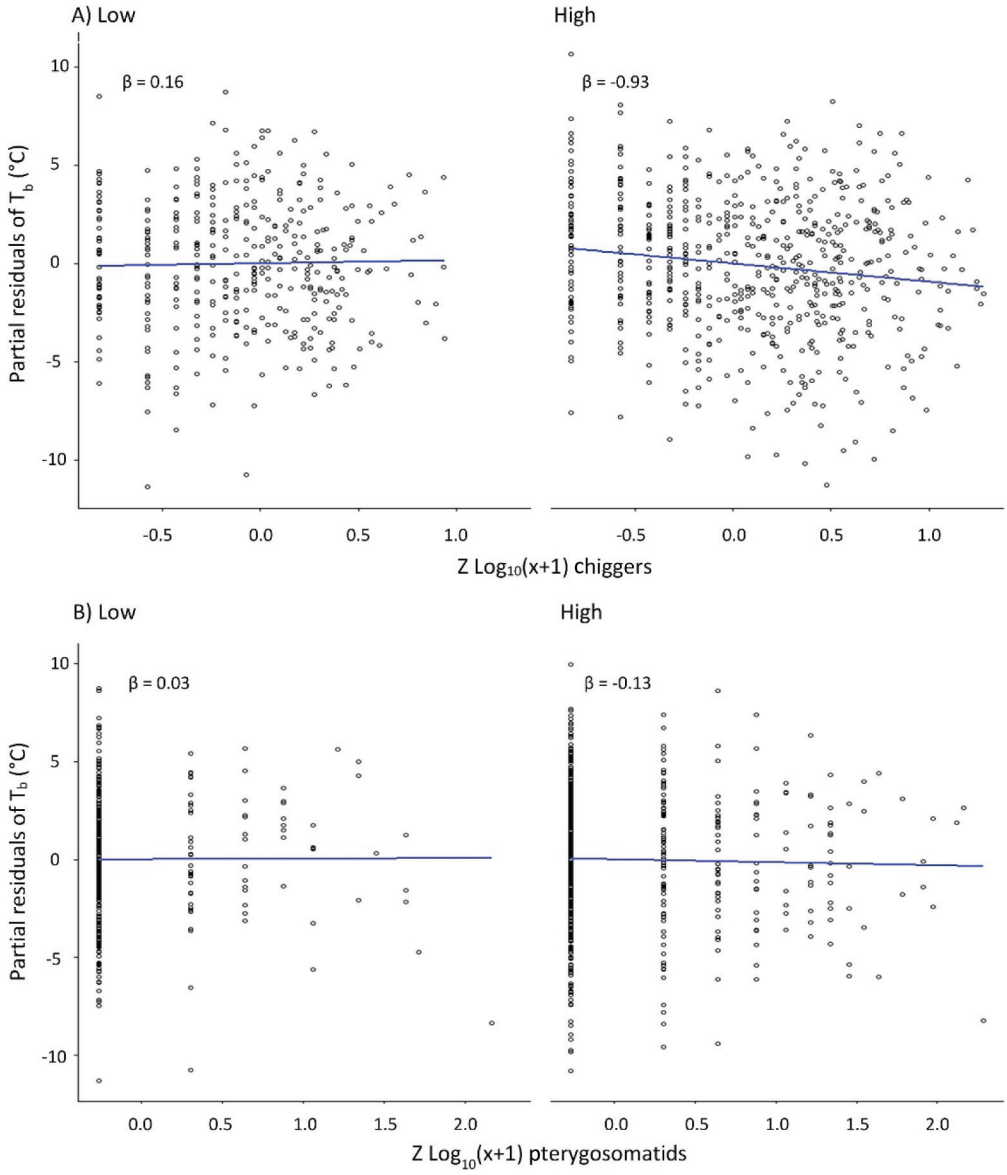
The global model of $d_e - d_b$ (n = 1014 records of 514 individuals in 10 sites, marginal R^2 = 0.25, conditional R^2 = 0.39) produced a subset of 13 models within 2 ΔAIC_c of the best model (the AIC_c of the best model (5388.3) was lower than that of the null model (5473.3)). The subset of 13 top models were averaged to produce the final model (standardized $\beta \pm$ SE reported; Table 2). The final model of $d_e - d_b$ showed no significant main effects of ectoparasites (chiggers — main effect: $\beta \pm$ SE = −0.01 ± 0.06, p = 0.93; pterygosomatids — main effect: $\beta \pm$ SE = 0.22 ± 0.24, p = 0.36; Figs. 2A and 2B) or interactions with elevation (chiggers — interaction term not present in final model; pterygosomatids — interaction: $\beta \pm$ SE = 0.88 ± 0.62, p = 0.15; Table 2). We did not find any support for our second prediction that lizards infected with more ectoparasites thermoregulate less effectively or for the component of our third prediction that the impact of ectoparasites on $d_e - d_b$ would increase with elevation.

Discussion

We hypothesized that ectoparasites would impact thermoregulation in *S. jarrovii* and tested three predictions: (1) lizards infected with more ectoparasites would have higher T_b and (2) would thermoregulate less effectively, and (3) ectoparasites would have greater impacts on thermoregulation at high elevation. We found a significant association between chiggers and T_b (but not pterygosomatid mites and T_b) in support of the first prediction. The association was positive at low elevations (consistent with fever), negative at high elevations (consistent with hypothermia), and strongest at high elevation in support of the third prediction. There was no support for the second prediction of a negative association between ectoparasites and effectiveness of thermoregulation. These results suggest that chiggers may impact T_b in a way that depends on environmental thermal quality.

A thermal immune response induced by chigger infection is a plausible explanation for the association between chiggers and T_b. Fever and hypothermia may be induced through tissue inflammation or immune reaction to chigger saliva. Chiggers induce skin and tissue damage resulting in severe inflammation (Goldberg and Holshuh 1992) and immune response (Huyghe et al. 2010). In response to damage and pathogens, vertebrate tissues release cytokines that mediate inflammatory and febrile responses (Desborough 2000; Evans et al. 2015). Similar processes likely occur in reptiles (Zimmerman et al. 2010); cytokines alter T_b when injected into Desert Iguanas (*Dipsosaurus dorsalis* (Baird and Girard,

Fig. 1. The partial residuals of body temperature (T_b) as a function of ectoparasite load on Yarrow's Spiny Lizards (*Sceloporus jarrovii*) captured in the Chiricahua Mountains of Arizona, USA (n = 1014 captures of 512 individuals nested in 10 sites). Panel A shows a significant positive T_b and chigger association at low elevation and a significant negative T_b and chigger association at high elevation (interaction: p = 0.006). Panel B shows no significant T_b and pterygosomatid mite association at low or high elevation (interaction: p = 0.62). The regression lines represent the partial effects of ectoparasites on T_b extracted from the final averaged model with standardized slope values (β). Z on the x axes refers to the transformation applied to the chigger and pterygosomatid data (see Materials and methods). Colour version online.



1852)) (Kinney et al. 2012) and cause behavioural changes in *S. occidentalis*, providing strong evidence that cytokine-like molecules regulate response to disease and injury in reptiles (Dunlap and Church 1996). Interestingly, compounds in the saliva of ticks manipulate the production of host cytokines in an apparent counter-adaptation to host immune response (Wikel et al. 1994), but it is unclear if chiggers do (Walker et al. 2013) or if this mechanism would impact thermoregulation.

Changes of only a few degrees Celsius can have significant impacts on host and pathogen survival (Kluger et al. 1975; Evans et al. 2015), suggesting potential biological significance of the observed change in T_b in *S. jarrovii* in response to infection. At the maximum observed infection intensity of 339 chiggers, the statistical model predicts a ΔT_b of +0.33 °C at low elevation and –1.95 °C at high elevation. However, most lizards should experience more modest T_b changes than this; the mean infection intensity (23.4 chiggers) corresponds to a ΔT_b of +0.18 °C at low elevation and –1.07 °C at high elevation. These changes are consistent with thermal immune responses previously observed in *Sceloporus* lizards. Ortega et al. (1991) observed an increase of 1 °C following bacterial injection in Granite Spiny Lizards (*Sceloporus orcutti* Stejneger, 1893), whereas Wang and Adolph (1995) observed changes ranging from +1 to –1.1 °C in *S. occidentalis* following surgery. The effect that we observed is less than that observed in malaria-infected *S. occidentalis* which select post-activity temperatures 4 °C above uninfected lizards (Scholnick et al. 2010). Animals can stimulate immune function and harm pathogens when they alter their T_b during disease (Kluger et al. 1975, 1998; Rakus et al. 2017). Temperature controls the growth rate of chiggers (Jameson 1972); however, it is not clear if the changes observed in this study would have positive or negative impacts on chigger growth or physiology. Increasing temperatures would be expected to harm ectoparasites by accel-

Table 2. Averaged fixed-effects coefficients for the final model of the effectiveness of thermoregulation ($d_e - d_b$ index) for Yarrow's Spiny Lizards (*Sceloporus jarrovii*) captured in the Chiricahua Mountains of Arizona, USA.

Model parameter	Relative importance	β^a	SE	Z	p
(Intercept)		3.39	0.54	0.54	<0.00001***
Julian date	1.00	2.07	0.53	0.53	0.00010***
Pterygosomatids[b]	0.88	0.22	0.24	0.24	0.36656
Elevation	1.00	3.49	1.00	1.00	0.00049***
Snout–vent length (SVL)	0.77	0.30	0.28	0.28	0.29291
Time	1.00	–1.62	0.26	0.26	<0.00001***
Julian date × elevation	0.94	–2.06	1.16	1.16	0.07646
Julian date × time	1.00	1.43	0.49	0.49	0.00325**
Pterygosomatids[b] × elevation	0.83	0.88	0.62	0.62	0.15403
Elevation × time	0.85	0.78	0.55	0.55	0.15987
SVL × time	0.60	0.43	0.48	0.48	0.37063
Sex male	0.45	0.15	0.26	0.26	0.55851
Sex non-gravid female	0.45	–0.08	0.23	0.23	0.72412
Chiggers[b]	0.05	–0.01	0.06	0.06	0.93074

Note: The final model was created from a subset of 13 top models within 2 ΔAIC_c of the best model (n = 1014 captures of 512 individuals nested in 10 sites), where AIC_c is Akaike's information criterion corrected for small sample size. **, $p < 0.01$; ***, $p < 0.001$.

[a]Estimates (β) were standardized for continuous predictors.

[b]Chiggers (Trombiculoidea) and pterygosomatids (Pterygosomatidae) were $\log_{10}(x + 1)$ transformed.

erating desiccation; something chiggers (Sasa 1961) and ticks (Benoit et al. 2007) are vulnerable to.

Immune responses are costly and dependent on energetic resources (Smith et al. 2017). Energetic resources can influence thermal immune responses; *I. iguana* display either fever or hypothermia when injected with the fever-inducing bacterial lipopolysaccharide depending on body mass (Deen and Hutchison 2001). Zamora-Camacho et al. (2016) suggest thermal immune responses in lizards may be determined by environmental thermal quality, because this factor determines the costs of thermoregulation and would therefore determine the relative energetic costs of fever or hypothermia in different environments. Zamora-Camacho et al. (2016) found that the Algerian Psammodromus (*Psammodromus algirus* (Linnaeus, 1758)) from low- and high-elevation populations displayed different thermal immune responses under identical laboratory conditions, suggesting that different thermal immune responses are favoured by natural selection in different thermal environments. In *S. jarrovii*, fever might be favoured at low elevations where thermal quality is high and the costs of thermoregulation are lower. At high elevation where thermal quality is lower, the costs of producing a fever may be excessively high and therefore the opposite strategy of hypothermia might be favoured to conserve energy. These environmentally dependent costs may explain thermal responses in rats where fever is developed under high ambient temperatures, but hypothermia results under low ambient temperatures in response to bacterial lipopolysaccharide injection (Almeida et al. 2006).

Dehydration is an unlikely explanation for the pattern that we observed. Ectoparasites can cause dehydration (Baldwin 1999) and dehydration can reduce preferred T_b in lizards (Crowley 1987). However, if chiggers impacted T_b through dehydration, then a negative chigger and T_b association would be expected at all elevations with the strongest impact at low elevation where conditions are hottest and driest. Instead, the opposite relationship was observed; a weaker positive chigger and T_b association at low elevation and a stronger negative chigger and T_b association at high elevation. It is important to note that Crowley (1987) found that the effects of dehydration on T_b were only apparent when lizards were active. Variable activity states may have masked an effect of dehydration in our study. A loss of blood–oxygen carrying capacity caused by reduced hematocrit is also unlikely to explain the association that we observed. This is because chiggers feed on lymph and not on blood (Traub et al. 1975).

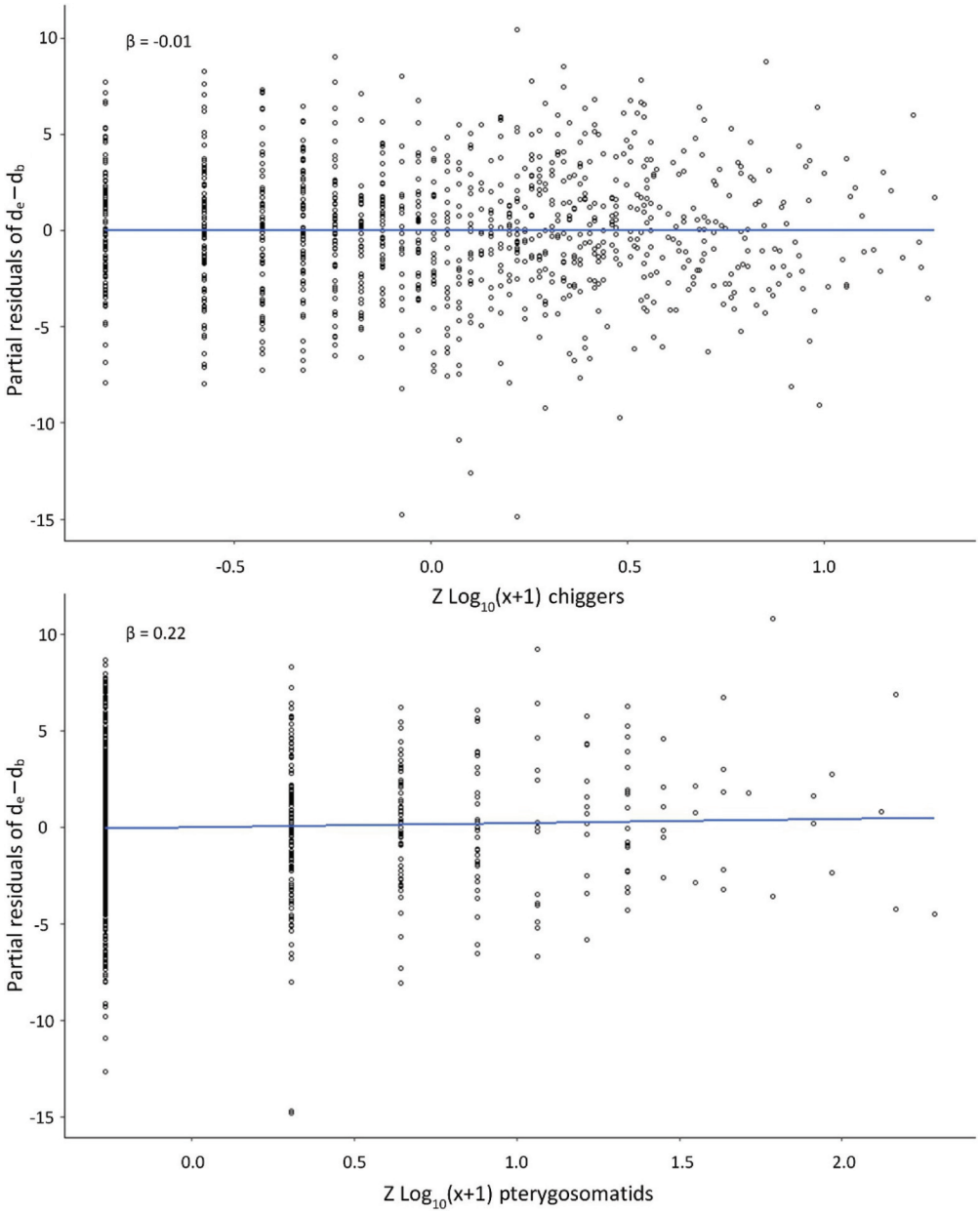
In the only other study to address ectoparasites and thermoregulation in reptiles, Conover et al. (2015) found no association between chiggers and T_b in *A. cybotes* and *A. armouri*. The authors suggested that either fever may not occur in those species or the costs of producing fever could have outweighed its benefits under their study conditions. It is also true that febrile and hypothermic responses in reptiles are highly variable and can be easily masked by other factors (Rakus et al. 2017). Considering the relatively small effect size of chiggers on T_b relative to the variability of T_b, it is possible that we detected a significant effect due to our large sample size. Mohammed et al. (2016) illustrated that adaptive thermal responses to ectoparasites can occur in ectothermic vertebrates. They found that guppies displayed behavioural fever by selecting elevated water temperatures when infected with ectoparasitic worms resulting in increased host survival and decreased parasite success.

We did not detect an impact of pterygosomatid mites on T_b. This may be because a smaller proportion of lizards were infected with pterygosomatids than chiggers (89.5% vs. 26.8%, respectively), resulting in lower statistical power. The effects of pterygosomatids may not have been statistically distinguishable from chiggers due to the relatively high incidence of co-infection (24.5%). Additionally, the pterygosomatid mites often varied considerably in size and therefore simple counts may not have accurately represented the true costs of infection.

The costs of *Geckobiella* mite infection may not be high enough to elicit a fever due to low physiological impacts or because *S. jarrovii* has evolved to tolerate *Geckobiella* mites. Many parasites that live in close association with the host evolve reduced virulence over time resulting in less severe host responses (Lenski and May 1994). This effect likely applies to several parasitic mite species (Walter and Proctor 2013). Indeed, *Geckobiella* mites complete their entire life cycles on lizards (Goodwin 1954), whereas chiggers only infect hosts during their larval stage and tend to be generalists on many vertebrate species (Shatrov and Kudryashova 2006). However, these explanations appear unlikely given that *Geckobiella* mites can have severe impacts on *Sceloporus* lizards, including death (Goldberg and Holshuh 1992). Alternatively, it is plausible that pterygosomatids possess an ability to suppress host immune responses the way ticks do (Mejri et al. 2002) and therefore do not elicit a fever.

We did not find any impact of ectoparasites on $d_e - d_b$, which suggests that they do not interfere significantly with the effective-

Fig. 2. The partial residuals of effectiveness of thermoregulation as a function of ectoparasite load on Yarrow's Spiny Lizards (*Sceloporus jarrovii*) captured in the Chiricahua Mountains of Arizona, USA (n = 1014 captures of 512 individuals nested in 10 sites). Panel A shows no significant relationship between $d_e - d_b$ and chiggers (main effect: p = 0.93). Panel B shows no significant relationship between $d_e - d_b$ and pterygosomatid mites (main effect: p = 0.36). The regression lines represent the partial effects of ectoparasites on $d_e - d_b$ extracted from the averaged model with standardized slope values (β). Z on the x axes refers the transformation applied to the chigger and pterygosomatid data (see Materials and methods). Colour version online.



ness of thermoregulation. This is surprising given that we found an association between chiggers and T_b, which would be expected to also impact $d_e - d_b$. Ectoparasites might only interfere with $d_e - d_b$ in severely infected individuals, and since these were rare, we may not have been able to detect a significant effect.

The impact of infection on the ability of ectotherms to thermoregulate effectively is highly variable. Conover et al. (2015) also found no impact of chiggers on basking behaviour in *Anolis* lizards. Main and Bull (2000) found an impact of ticks on basking behaviour in *T. rugosa*. *Uta stansburiana* infected with malaria display more variable T_b, presumably because the energetic costs of infection reduce the energy reserves needed to behaviourally thermoregulate (Paranjpe et al. 2014). In an extreme case, Goodman and Johnson (2011) found that trematodes caused Chorus Frogs (genus *Pseudacris* Fitzinger, 1843) to thermoregulate less effectively because the parasite caused missing or nonfunctional extra limbs. Alternatively, Deen and Hutchison (2001) found that thermoregulatory precision actually increased in *I. iguana* under immune challenge.

We found an association between chigger mites and T_b that varied with elevation in wild populations of *S. jarrovii*. To the best of our knowledge, this is the first report of an association between ectoparasites and T_b in reptiles. This finding provides support for the hypothesis that ectoparasites impact thermoregulation. Although several physiological impacts of ectoparasites could explain this pattern, it is most consistent with a thermal immune

response involving fever at low elevation and hypothermia at high elevation. The elevational variation in the association may be explained by energetic trade-offs that favour different thermal responses under different environmental conditions, a phenomenon supported by previous experiments in other vertebrates. Future research should confirm if and how ectoparasites impact thermoregulation in wild lizards by conducting a semi-natural field experiment. Ectoparasites could be experimentally added or removed, and thermal responses could be measured with high-resolution telemetry.

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