

**The impact of ectoparasitism on thermoregulation in the
Yarrow's spiny lizard (*Sceloporus jarrovi*)**

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Abstract:

Many factors including disease impact thermoregulation in reptiles. The impacts of ectoparasites on reptile physiology, behaviour, and immune function suggest that they could also impact thermoregulation, although little is known about this potential. I tested the hypothesis that ectoparasites impact thermoregulation in *Sceloporus jarrovi* lizards living along an elevational gradient. I predicted a positive association between ectoparasites and body temperature (T_b), and a negative association between ectoparasites and effectiveness of thermoregulation (d_e-d_b). Because environmental temperatures impact thermal immune responses, and because the costs of thermoregulation increase with elevation, I predicted that the impacts of ectoparasites would depend on elevation and be greatest at high elevation. To test my predictions, I constructed linear mixed models of T_b and d_e-d_b as a function of ectoparasite load (chiggers and pterygosomatid mites). I found a significant association between chiggers and T_b that differed in magnitude and direction with elevation, but no association between ectoparasites and d_e-d_b . The mean infection rate was associated with a ΔT_b of + 0.18°C at low elevation (consistent with fever) and -1.07°C at high elevation (consistent with hypothermia). These findings suggest that chiggers may impact T_b , and that this effect may depend on environmental thermal quality.

Keywords: Behavioural fever, Hypothermia, Thermoregulation, Ectoparasites, Ectotherm

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Introduction:

Parasites are widespread and diverse (Poulin & Morand, 2000), representing an estimated 40% of described species (Dobson et al, 2008). This parasite diversity is reflected in the array of impacts parasites have on hosts. Parasites often cause damage and impose energetic costs (Booth et al, 1993; Sheldon & Verhulst, 1996), resulting in negative fitness consequences for hosts (Kutzer & Armitage, 2016; Møller et al, 1990). Ultimately, parasites can impact the abundance (Scott & Dobson, 1989), dynamics (Hudson et al, 1998), and reproduction of entire populations (Agnew et al, 2000).

Hosts infected with parasites often display complex phenotypic changes (Poulin, 1994). A key example is altered thermoregulation, especially in the form of fever, but also in the form of hypothermia (Goodman & Johnson, 2011; Kluger et al, 1996). Fever and hypothermia are phylogenetically conserved immune responses to pathogens and damage mediated by messenger molecules called cytokines (Evans et al, 2015). Ectotherms achieve fever and hypothermia behaviourally, and this occurs in a wide range of taxa from insects (Thomas & Blanford, 2003) to vertebrates (Kluger et al, 1998, 1996; Rakus et al, 2017). There are several possible explanations for phenotypic changes that happen during infection; the host manipulation hypothesis proposes that parasites adaptively manipulate their hosts in ways that increase transmission to a new host (Poulin, 2000; 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 (or parasite) fitness (Kluger et al, 1998). Finally, observed phenotypic changes in hosts may simply

be a side effect of infection with no clear adaptive value for the host or parasite (Weinersmith & 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 (Huey & Kingsolver, 1989; Seebacher, 2005). Reptiles rely on behavioural thermoregulation to maintain optimal T_b s, and to respond to environmental temperature changes (Glanville & Seebacher, 2006; Huey & Stevenson, 1979; Seebacher, 2005). Behavioural thermoregulation involves basking, controlling body posture, selecting micro-habitats and activity periods (Adolph, 1990; Hertz & Huey, 1981). These behavioural strategies co-occur with physiological mechanisms such as vascular and metabolic adjustments (Seebacher & Franklin, 2005).

Thermoregulation in reptiles is impacted by several factors including reproductive status (Mathies & Andrews, 1997), season (Glanville & Seebacher, 2006), sex (Patterson & Davies, 1978), age (Gilbert & 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* (Merchant et al, 2007), *Dipsosaurus* (Kluger et al, 1975), *Agama*, and *Sceloporus* (Ortega et al, 1991), display fever following bacterial injection. Reptiles may display variable thermal responses; bacterial lipopolysaccharide (LPS) can induce either fever or hypothermia in green iguanas (*Iguana iguana*) depending on individual condition (Deen & Hutchison, 2001). Blood parasites can also impact thermoregulation; malaria (*Plasmodium* sp.) induces elevated T_b in western fence lizards (*Sceloporus occidentalis*) (Scholnick et al, 2010). Conversely, common lizards (*Lacerta vivipara*) display reduced T_b when infected with

Haemogregarina sp. (Oppliger et al, 1996). Reduced T_b s are also observed in western side-blotched lizards (*Uta stansburiana*) infected with *Schellackia* and *Plasmodium* (Paranjpe et al, 2014). Hypothermic responses are likely adaptive because they can reduce blood parasite reproduction, and the costs of impaired blood oxygen transport caused by blood parasites (Oppliger et al, 1996). Similar patterns of adaptive hypothermia occur in anemic, and hypoxic lizards independently of infection (Hicks & Wood, 1985; Wood, 1991).

At least fifteen families of primarily ectoparasitic mites infect reptiles (Fajfer, 2012). These include the blood-feeding scale mites (Pterygosomatidae) (Baldwin, 1999) and ticks (Ixodidae) (Dunlap & Mathies, 1993), and the lymph-feeding chiggers (Trombiculoidea) (Arnold, 1986). Conover et al (2015) suggested that lizard ectoparasites might impact thermoregulation because of the impacts they have on their hosts. Indeed, at least one ectoparasite (a worm) induces behavioural fever in guppy fish (Mohammed et al, 2016). Reptile ectoparasites inject saliva (Shatrov, 2009) and cause tissue damage and inflammation (Goldberg & Bursey, 1991; Goldberg & Holshuh, 1993). Foreign material and tissue damage are capable of inducing thermal immune responses in vertebrates (Conti et al 2004; Desborough, 2000). Many ectoparasites also transmit vector-borne diseases (Spence et al, 2017), several of them such as *Schellackia* and *Haemogregarina* impact thermoregulation in reptiles (Amo et al, 2005; Jordan & Friend, 1971). 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 s of lizards (Crowley, 1987), ectoparasites might impact thermoregulation by causing dehydration. Additionally, blood-feeding ticks and pterygosomatid mites may alter blood composition in lizards (Baldwin, 1999; Dunlap & Mathies, 1993; Salvador

et al, 1996). Since many lizards reduce their set point temperatures in response to hypoxia caused by blood loss or changes in blood composition (Wood, 1991), ectoparasites might cause similar responses.

Ectoparasites might 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 woodii*). Australian sleepy lizards (*Tiliqua rugosa*) infected with ticks basked more and moved less than uninfected lizards (Main & Bull, 2000). These effects are expected to interfere with the ability to thermoregulate efficiently. Paranjpe et al (2014) found that the blood parasites *Schellackia* and *Plasmodium* reduced the thermoregulatory precision of side-blotched lizards (*Uta stansburiana*). They suggest that given limited energetic resources, saving energy for an immune response may outweigh the benefits of precise thermoregulation.

Despite several mechanisms through which ectoparasites could impact thermoregulation in reptiles, this potential has been overlooked. Conover et al (2015) first addressed this question by investigating the impact of chigger mites on thermoregulation in wild *Anolis* lizards. They found that mites did not elicit fever, or impact basking duration in *A. cybotes* and *A. armouri*. The authors suggest that fever may not occur in those lizards, or that the costs of infection may not have been high enough for fever to be beneficial. Investigation of other groups is necessary to determine if and how ectoparasites impact thermoregulation in wild lizards. This is important to understand given the high prevalence of ectoparasites on reptiles in nature, and the significance of thermoregulation to reptile fitness.

Hypothesis and Predictions:

The goal of this study is to test the hypothesis that ectoparasites impact thermoregulation in wild populations of the Yarrow's spiny lizard (Phrynosomatidae: *Sceloporus jarrovi* Cope). This species lives along an elevational gradient in the Chiricahua Mountains of Arizona, USA, and frequently hosts ectoparasites such as chiggers (Trombiculoidea) (Bulté et al, 2009; Halliday et al, 2014) and scale mites (Pterygosomatidae) (Goldberg & Holshuh, 1992). Febrile responses have also been confirmed within the *Sceloporus* genus (Ortega et al, 1991). I evaluate the impacts of ectoparasites on thermoregulation by modelling T_b , and the index of effectiveness of thermoregulation ($d_e - d_b$) proposed by Blouin-Demers & Weatherhead (2001) using linear mixed effects models. I test three predictions while controlling for variables that influence thermoregulation in lizards such as time, snout vent length (SVL), and reproductive status (Beal et al, 2014; Beuchat, 1986). I test the predictions that 1) lizards infected with more ectoparasites will display increased T_b s indicative of fever, and 2) that lizards infected with more ectoparasites will thermoregulate less effectively, indicating that ectoparasites interfere with behavioural thermoregulation. Habitat thermal quality declines with elevation (Figure 1), resulting in greater costs of thermoregulation (Blouin-Demers & Nadeau, 2005). This may drive elevational variation thermoregulatory responses to disease (Zamora-Camacho et al, 2016). I therefore predict that 3) the impact of ectoparasites on the effectiveness of thermoregulation ($d_e - d_b$), and body temperature (T_b) will change with elevation and be greatest at high elevations where the costs of thermoregulation are also the greatest.

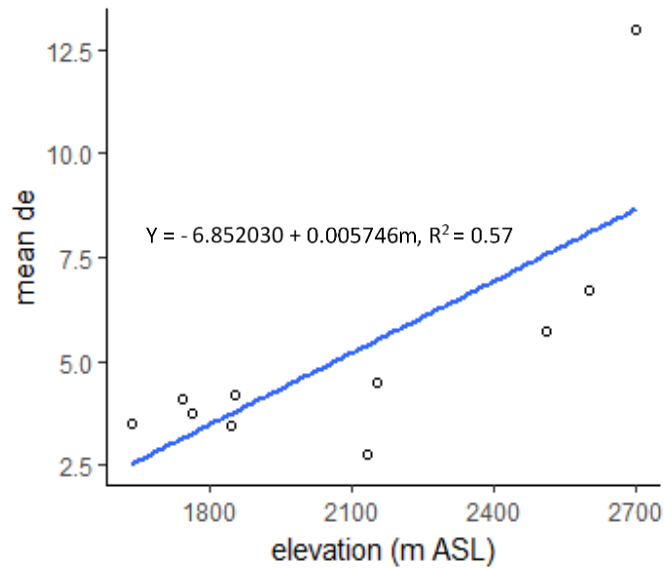


Figure 1. A regression of mean thermal quality (d_e) as a function of elevation across 10 sites in the Chiricahua Mountains, where a larger value of d_e indicates a greater deviation from the preferred temperature (T_{set}) range of *Sceloporus jarrovi* (lower thermal quality).

Materials and methods:

Study species and locations:

S. jarrovi (Figure 2) is a medium-sized viviparous alpine lizard (The lizards I captured ranged from 3.2 to 9.6 cm SVL) whose range spans from southeastern Arizona to north-central Mexico (Ballinger, 1973). *S. jarrovi* inhabits rocky areas such as talus slopes along an elevational gradient from approximately 1500 to 2800 m ASL (Burns, 1970; Smith & Ballinger, 1994), where it feeds primarily on arthropods (Simon, 1975).

Southeastern Arizona has an arid climate with minor winter and major summer bi-annual monsoons (Barton, 1994). In the Chiricahua mountains, air temperature decreases and precipitation increases with elevation resulting in dramatic changes in vegetation structure (Warshall, 1995). Low elevations are arid and vegetation is characterized by desert scrub,

grasses, and oak woodland, transitioning to mixed woodland at middle elevations, and pine forest at higher elevations (Barton, 1994; Sawyer & Kinraide, 1980). The vegetation around talus slopes is interspersed with acacia, mesquite, juniper, yucca, agave, cacti, and grasses.

From May 1st to July 23rd, 2017, I sampled 13 talus slopes ranging in elevation from 1634 to 2700 m ASL in the Chiricahua Mountains of Cochise County Arizona, near the town of Portal (31°54'49"N 109°08'29"W) (Figure 3). 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 due to their sparse vegetation (Figure 4). 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 uOttawa Animal Care Committee (BL-2812) and permission from the US National Forest Service (Douglas Ruppel).



Figure 2. A) An adult *Sceloporus jarrovi* at a slope in the Chiricahua mountains B) Juveniles basking on talus slope rocks with visible ID numbers. Note that colour differences occur at different temperatures to facilitate thermoregulation.

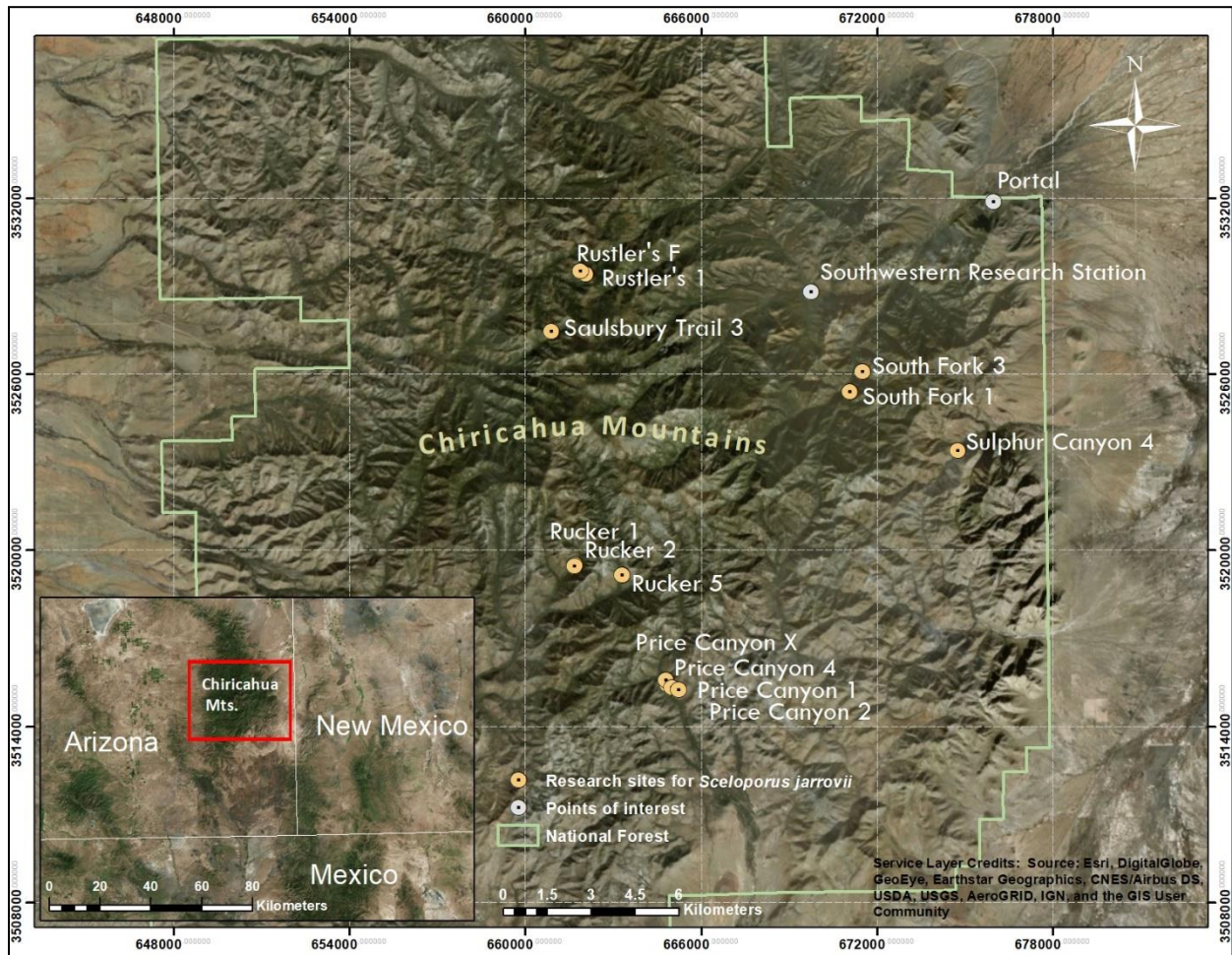


Figure 3. A map of the Chiricahua Mountains with locations of the 13 talus slopes visited during the 2017 field season to capture *Sceloporus jarrovi* lizards. Projected Coordinate system: NAD 1983 2011 UTM Zone 12N. See supplementary section for a table with exact coordinates.

Field methods:

Three observers walked the talus slopes and attempted to capture any active lizards using modified fiberglass fishing poles equipped with fishing line nooses. Lizards generally emerged shortly after illumination of the talus slope by the sun, or when temperatures under the rocks exceeded $\sim 16^{\circ}\text{C}$. They retreated when ambient temperatures exceeded $\sim 35^{\circ}\text{C}$. Immediately after capture, an infrared thermometer 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 (Andrews, 2008; Jones & Avery, 1989), and using them reduces stress and handling

time compared to traditional cloacal thermometers (Berg et al, 2015). T_b , date, time, site name, and UTM coordinates (averaged for two minutes) were then recorded on Garmin® handheld GPS units. Lizards were placed into uniquely numbered white cotton bags and stored in a shaded location until processing. Capture continued until we achieved adequate samples, or until no active lizards remained.



Figure 4. An image taken from the base of a typical talus slope in the Chiricahua Mountains of Arizona where *Sceloporus jarrovi* were captured (Saulsbury Trail 3), with satellite imagery for scale.

We processed lizards in a shaded location on each talus slope. Lizards were taped to a small white board, photographed, and individually 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 (Figure 5). Reproductive status in females was determined visually by the presence of a swollen abdomen, and by palpation. SVL was measured with digital calipers

accurate to 0.001 cm. Mass was taken by placing lizards inside a plastic bag, inserting this in a plastic cup, and placing this on a Pesola® digital scale accurate to 0.01 g.

Ectoparasites were counted visually with the aid of a magnifying glass. Mites usually remained attached and rarely crawled on lizards or inside the cotton bags. Chiggers were identified by their small size, 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 & Bursey, 1993), and dark red colouration when engorged (Walter & Shaw, 2002). Hard ticks (Ixodidae) were easily distinguished from all other mites by their body shape, scutal plate, and legs. Following counting, all lizards were placed back in cotton bags and returned to their point of capture with the aid of a GPS.

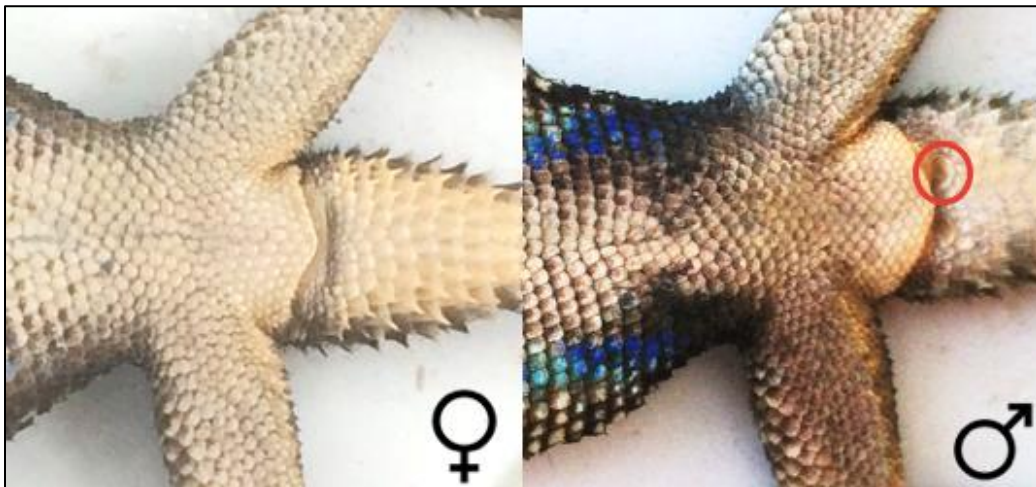


Figure 5. Images of the post-anal scales on male and female *Sceloporus jarrovi* lizards. Note the blue colouration and enlarged scales (red circle) on the male lizard. Figure reproduced with permission from A. Lymburner.

The d_e-d_b index of effectiveness of thermoregulation proposed by Blouin-Demers & Weatherhead (2001) is the difference between habitat thermal quality (d_e) and the accuracy of

body temperature (d_b). In this index, positive values indicate an actively thermoregulating lizard, values near zero indicate thermoconformity, and negative values indicate avoidance of preferred thermal conditions (Blouin-Demers & Nadeau, 2005). d_e is the difference between operative environmental temperature (T_e) and an ectotherm's preferred body temperature (T_{set}) range. d_b is the difference between T_b and the T_{set} range. I used the T_{set} range (30.4 to 33.2°C) for *S. jarrovi* obtained by Patterson (2018). For both these calculations, the upper T_{set} bound is used if T_e or T_b exceeds it, and the lower T_{set} bound is used if T_e or T_b is less than it. To measure operative environmental temperatures (T_e), we placed biophysical models on slopes (on a shaded rock, under a rock, and on a rock in sun). This was done for the entire duration of lizard capture to create a thermal profile of a non-thermoregulating lizard with which to calculate the effectiveness of thermoregulation (Dzialowski, 2005). The biophysical models were made from gray-painted copper pipes containing two iButton® temperature loggers ($\pm 1^\circ\text{C}$). Locations were recorded with handheld GPS units and rearranged randomly on each day of capture.

Statistical analyses:

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 (transformed variables hereafter referred to simply as chiggers and pterygosomatids) to make the partial residuals with T_b and d_e-d_b linear. All continuous input variables were rescaled to have a mean of zero, and an 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 variables are measured on different scales (Schielzeth, 2010).

Statistical analyses were conducted in R v. 3.4.1 (R Core Team, 2017). I 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 insufficient sample sizes (44 captures representing ca. 4.3% prevalence). To test the predictions that lizards infected with more ectoparasites display higher T_b s and thermoregulate less effectively, I added terms for chiggers and pterygosomatid mites to the global models of T_b and d_e-d_b . I then added Chigger:Elevation, and Pterygosomatid:Elevation interactions along with an Elevation main effect to both models. This was to test the predictions that the impacts of ectoparasites on T_b and on d_e-d_b depend on elevation, being greatest at high elevation.

The observational nature of this study required several statistical controls. Sex was included because female *S. jarrovi* select lower T_b s when gravid (Mathies & Andrews, 1997). SVL controls for the influence of size on T_b (Gilbert & Lattanzio, 2016), and was chosen over mass because models containing only SVL were preferable when evaluating collinearity. I included an SVL:Time interaction, because Middendorf & Simon (1988) found significant differences in thermoregulatory behaviour among *S. jarrovi* throughout the day depending on size. I added Julian Date and Time to control for the increases in temperature we observed over the field season, and during the day, respectively. Julian Date:Elevation, Julian Date:Time, and Time:Elevation interactions controlled for changes in environmental conditions over the season. I then incorporated random effects with lizard ID nested within locations to control for repeated captures and spatial autocorrelation. Model comparisons validated the inclusion of

these nested random effects. The global models of T_b and d_e-d_b were therefore 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 & Anderson, 2003). This approach recognizes that several competing models may exist to explain the data (Burnham et al, 2011). The global models of T_b and d_e-d_b were dredged in the package MuMIn (Barton, 2018) to create lists of all possible subset models. Subsets within 2 ΔAIC_c units of the best T_b and d_e-d_b models were then selected; these are considered highly supported alternative models (Burnham & Anderson, 2003). AIC_c is the recommended metric for model selection and is equivalent to AIC at large sample sizes (Burnham & 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.

Results:

We made a total of 1020 captures of 514 lizards (327 females, 187 males, 435 adults, and 79 juveniles) (SVL mean \pm SE = 6.23 ± 0.05 cm). T_b s ranged from 14.4 to 39.9 °C (mean \pm SE = 27.8 ± 0.1 °C). Values of the d_e-d_b index ranged from -12.7 to 20.5 (mean \pm SE = 3.63 ± 0.13). Ectoparasites were recorded on 1014 of 1020 total captures; most individuals had only a few ectoparasites, while a minority were severely infected (Figure 6). The prevalence of ectoparasites on all captures was 4.34% for ticks (range = 0 – 19, mean \pm SE = 0.13 ± 0.03), 89.45% for chiggers (range = 0 – 399, mean \pm SE = 23.36 ± 1.26), and 26.82% for pterygosomatid mites (range = 0 – 21, mean \pm SE = 0.80 ± 0.07). 24.35% of individuals were coinfecting with chiggers and pterygosomatid mites.

I observed at least 3 distinct species of chiggers ranging in colouration from yellow to reddish orange; likely all *Eutrombicula* sp. based on other reports from the region (Bennet, 1977; Goldberg & Bursey, 1993). They were typically found in the nuchal regions (Figure 7A), and occasionally on the sides of the body. The chigger species composition and infestation intensity appeared to change between sites and seasons, and questing chiggers were exceedingly rare in the environment. Pterygosomatid mites (Figure 7B) were likely *Geckobiella texana*, a mite frequently reported on *Sceloporus* lizards in the region (Goldberg & Bursey, 1994; Goldberg & Bursey, 1993; Goldberg & Holshuh, 1992). These mites have seven developmental stages and complete their entire lifecycles on lizards (Goodwin, 1954). I occasionally observed the sub-adult stages which ranged from pink to white along with the engorged adults. Ticks were dark brown, almost exclusively the larval stages, and likely *Amblyomma* sp.

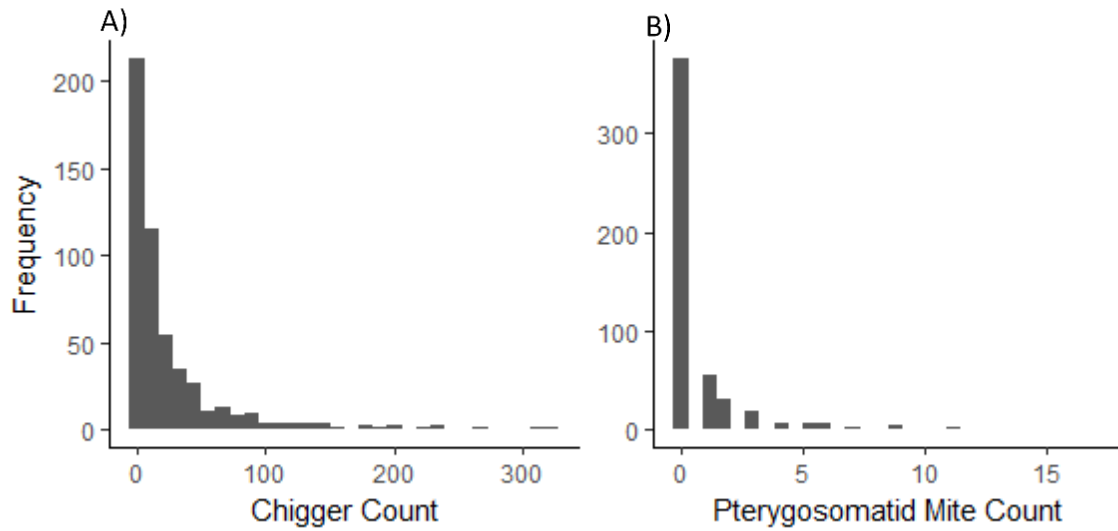


Figure 6. Frequency distributions of chiggers and pterygosomatid mites counted on first capture incidences of *Sceloporus jarrovi* captured in the Chiricahua Mountains of Arizona.



Figure 7. A gravid female *Sceloporus jarrovi* from the Chiricahua Mountains infected with A) chiggers inside the nuchal folds, and B) a large pterygosomatid mite at the base of the tail. Note the tail of this lizard has been lost and regrown, as can be seen from the different scale patterns.

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 $2 \Delta AIC_c$ of the best model. These six models were averaged to create the final model (standardized β s \pm SEs reported) (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 $\beta = -0.51 \pm 0.26$ SE, $p = 0.04756$, interaction $\beta = -1.27 \pm 0.47$ SE, $p = 0.00662$). There was no significant main effect or interaction with elevation for pterygosomatid mites and T_b (main effect $\beta = -0.09 \pm 0.20$ SE, $p = 0.65546$, interaction $\beta = -0.22 \pm 0.45$ SE, $p = 0.62232$).

If the ten sites are pooled into low and high elevation categories to examine the Chigger:Elevation interaction, chiggers are positively associated with T_b at the five lowest elevations (from 1634 to 1851 m) (average $\beta = 0.16$), and negatively associated with T_b at the five highest elevations (from 2134 to 2700 m) (average $\beta = -0.93$) (Figure 8). The significant association between chiggers and T_b supports the first prediction that lizards infected with more ectoparasites display higher T_b s, however this effect was only observed at low elevations as 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 $+0.33^\circ\text{C}$ at low elevation and -1.95°C at high elevation at maximum infection intensity (339 chiggers) using the average β s 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 then 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.

Table 1. Averaged fixed effects coefficients for the final model of T_b for *Sceloporus jarrovi* lizards captured in the Chiricahua Mountains. The final model was created from a subset of top six models within 2 ΔAIC_c of the best model (n = 1014 captures of 512 individuals nested in 10 sites).

Model Parameter	Relative Importance	Estimate ^b	Standard error	Z	p value
(Intercept)		28.47	0.69	40.93	<0.00001 ***
Julian Date	1	1.22	0.55	2.21	0.02710 *
Chiggers ^a	1	-0.51	0.26	1.98	0.04756 *
Elevation	1	-2.78	1.33	2.08	0.03722 *
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 ^a :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 ^a	0.52	-0.09	0.20	0.45	0.65546
Pterygosomatids ^a :Elevation	0.28	-0.22	0.45	0.49	0.62232

^a $\log_{10}(x+1)$ transformed. ^bEstimates standardized for continuous predictors.

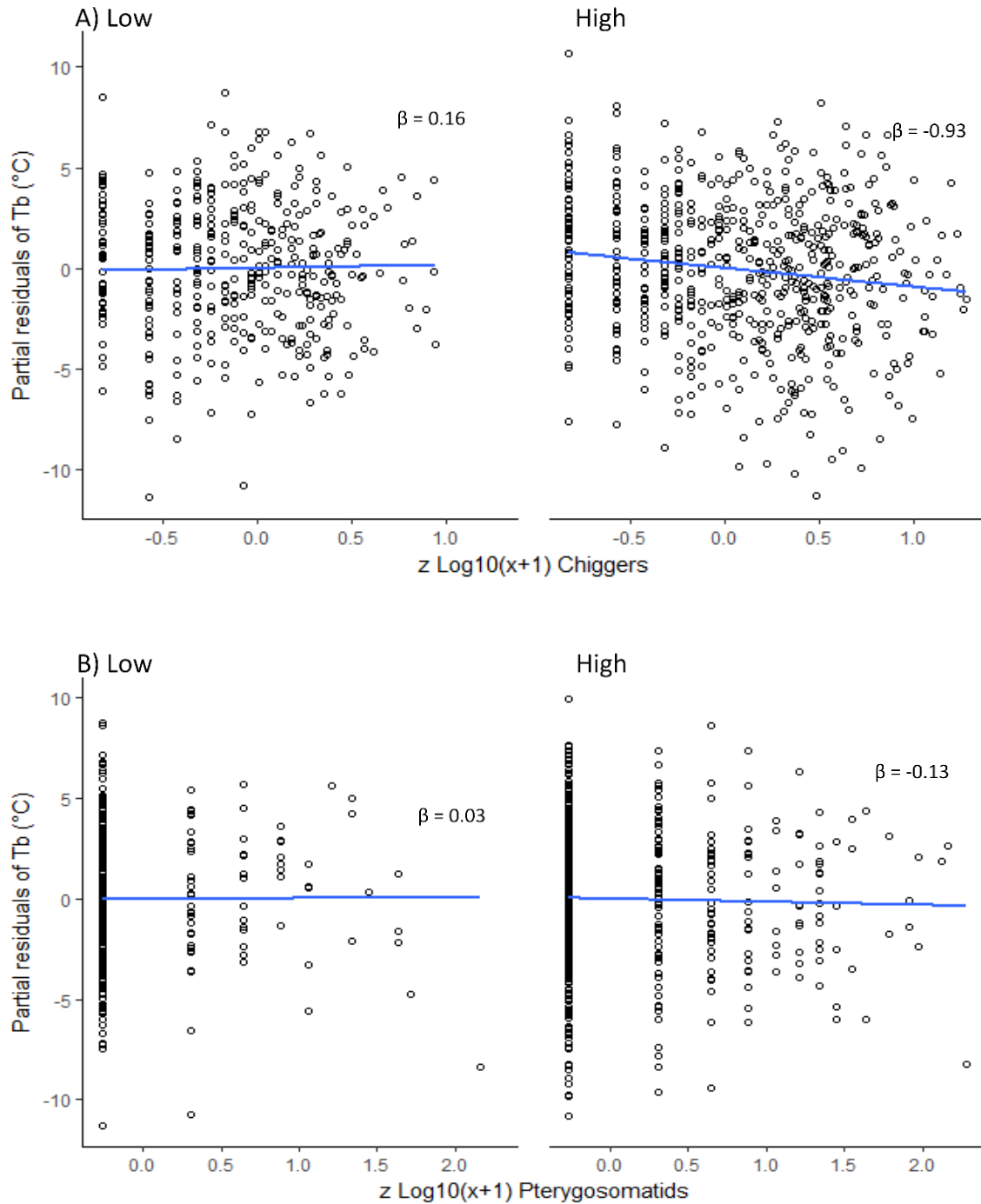


Figure 8. The partial residuals of T_b as a function of z-scaled $\log_{10}(x+1)$ ectoparasites from the final linear mixed effects model of *Sceloporus jarrovi* lizards at low and high elevations in the Chiricahua Mountains ($n = 1014$ captures of 512 individuals nested in 10 sites). Panel A) displays T_b versus chiggers (interaction $p = 0.00662$). Panel B) displays T_b versus pterygosomatid mites (interaction $p = 0.62232$). The overlaid regression lines represent the partial effects of ectoparasites on T_b extracted from the averaged model with standardized slope values (β s).

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 thirteen models within $2 \Delta AIC_c$ of the best model. This was averaged to produce the final model (standardized β s \pm SEs reported) (Table 2). The final model of d_e-d_b showed no significant main effects of ectoparasites (chiggers main effect $\beta = -0.01 \pm 0.06$ SE, $p = 0.93074$, pterygosomatids main effect $\beta = 0.22 \pm 0.24$ SE, $p = 0.36656$) (Figure 9) or interactions with elevation (chiggers interaction term not present in final model, pterygosomatids interaction $\beta = 0.88 \pm 0.62$ SE, $p = 0.15403$) (Table 2). I did not find any support for my second prediction that lizards infected with more ectoparasites thermoregulate less effectively, or for the prediction that the impact of ectoparasites on d_e-d_b would increase with elevation.

Table 2. Averaged fixed effects coefficients for the final model of d_e-d_b for *Sceloporus jarrovi* lizards captured in the Chiricahua mountains. The final model was created from a subset of 13 top models within $2 \Delta AIC_c$ of the best model ($n = 1014$ captures of 512 individuals nested in 10 sites).

Model Parameter	Relative Importance	Estimate ^b	Standard error	Z	p value
(Intercept)		3.39	0.54	0.54	<0.00001
Julian Date	1.00	2.07	0.53	0.53	0.00010 ***
Pterygosomatids ^a	0.88	0.22	0.24	0.24	0.36656
Elevation	1.00	3.49	1.00	1.00	0.00049 ***
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 ^a :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 ^a	0.05	-0.01	0.06	0.06	0.93074

^a $\log_{10}(x+1)$ transformed. ^bEstimates standardized for continuous predictors.

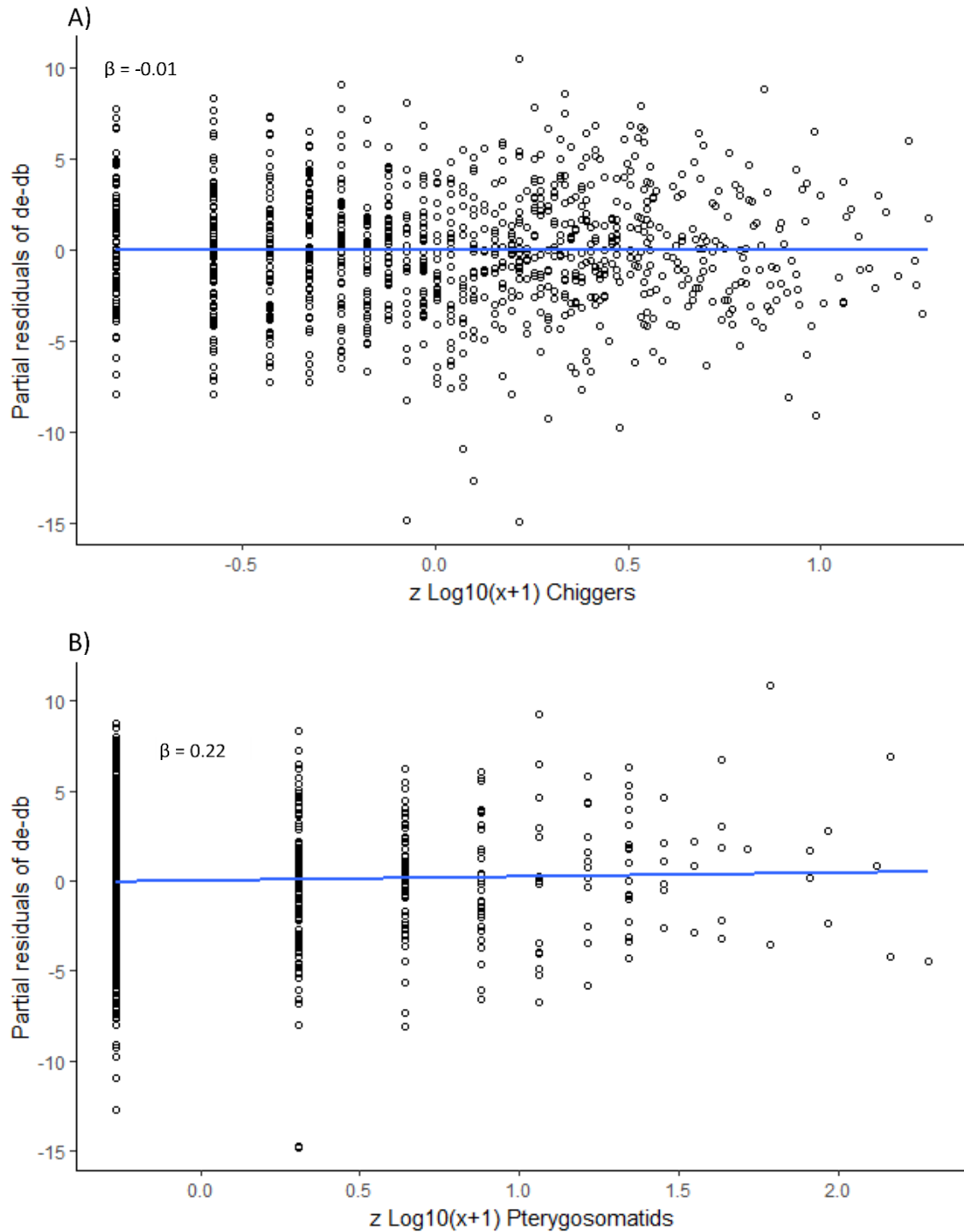


Figure 9. The partial residuals of $d_e - d_b$ as a function of z-scaled $\log_{10}(x+1)$ ectoparasites from the final linear mixed effects model of *Sceloporus jarrovi* lizards in the Chiricahua Mountains ($n = 1014$ captures of 512 individuals nested in 10 sites). Panel A) displays $d_e - d_b$ versus chiggers (main effect $p = 0.93074$). Panel B) displays $d_e - d_b$ versus pterygosomatid mites (main effect $p = 0.36656$). The overlaid regression lines represent the partial effects of ectoparasites on $d_e - d_b$ extracted from the averaged model with standardized slope values (β s).

Discussion:

I hypothesized that ectoparasites would impact thermoregulation in *Sceloporus jarrovi* lizards and I tested three major predictions: 1) that lizards infected with more ectoparasites (chiggers and pterygosomatid mites) would have higher T_b s, 2) would thermoregulate less effectively according to the d_e-d_b index, and 3) that the impacts of ectoparasites on T_b and d_e-d_b would change with elevation, being greatest at high elevation. I found a significant association between chiggers and T_b (but not pterygosomatid mites and T_b) in support of my first prediction. The association was positive at low elevations (consistent with fever), negative at high elevations (consistent with hypothermia), and greatest at high elevation in support of my third prediction. I found no support for my second prediction of a negative association between ectoparasites and the effectiveness of thermoregulation (d_e-d_b). These results suggest that chiggers may impact T_b , and that their effects may depend on environmental thermal quality.

Body temperature (T_b):

A thermal immune response induced by chigger infection is a plausible explanation for the association between chiggers and T_b . Fever and hypothermia might be induced through tissue inflammation or immune reaction to chigger saliva. Chiggers induce skin and tissue damage resulting in severe inflammation (Goldberg & Holshuh, 1992) and increased immune response (Huyghe et al, 2010; Spence et al, 2017). In response to damage and pathogens, vertebrate tissues release proteins called 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 *Dipsosaurus dorsalis* lizards (Kinney et al, 2012) and cause behavioural changes in *Sceloporus occidentalis* lizards, providing

strong evidence that cytokine-like molecules regulate response to disease and injury in reptiles (Dunlap & Church, 1996). Interestingly, compounds in the saliva of ectoparasites (ticks) manipulate the production of host cytokines in an apparent counter-adaptation to host immune and inflammatory response (Mejri et al, 2002; 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 °C can have significant impacts on host and pathogen survival (Evans et al, 2015; Kluger et al, 1975) suggesting potential biological significance of the observed effect. The statistical model predicts a ΔT_b of + 0.33°C at low elevation and - 1.95°C at high elevation at the maximum observed infection intensity (339 chiggers). However, most lizards should experience more modest T_b changes than this; the mean infection intensity (23.4 chiggers) is associated with a ΔT_b of + 0.18°C at low elevation and - 1.07°C at high elevation. These effect sizes 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 *Sceloporus orcutti*, while Wang & Adolph (1995) observed changes ranging from + 1 to - 1.1°C in *Sceloporus occidentalis* following surgery. The effect I observed is less than that of malaria infected *Sceloporus occidentalis* lizards 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 body temperatures during disease (Kluger et al, 1998; Kluger et al, 1975; Rakus et al, 2017). Although it is uncertain if small temperature changes would impact ectoparasites, temperature impacts growth rates in chiggers (Jameson, 1972) and would be expected to impact 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; Uller et al, 2006). Energetic resources may determine the outcome of a thermal immune response; green iguanas display either fever or hypothermia when injected with the fever inducer bacterial lipopolysaccharide (LPS) depending on body mass (Deen & 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. They found that *Psammodromus algirus* lizards from low and high elevation populations displayed different thermal immune responses under identical laboratory conditions, suggesting different thermal immune responses are favoured by natural selection in different thermal environments. In the lizards I studied, fever might be favoured at low elevations where thermal quality is high, and the costs of thermoregulation are lower. Hypothermia might be favoured at high elevation where thermal quality is lower if the costs of fever are too high to produce a benefit. These relative costs may explain similar responses in rats where a fever is developed under high ambient temperatures, but hypothermia results under low ambient temperatures in response to LPS injection (Almeida, 2006).

Dehydration is an unlikely explanation for the pattern I observed. Ectoparasites can cause dehydration (Baldwin, 1999), and dehydration can reduce preferred T_b s in lizards (Crowley, 1987). However, if chiggers impacted T_b by causing dehydration, they would be expected to decrease T_b and have the strongest impacts at low elevation due to the hotter and dryer conditions experienced there. Instead, I observed the opposite relationship with a

positive association at low elevation, and a negative (and stronger) 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. It is therefore possible that an effect of dehydration was masked in this study by variable activity states of lizards. Additionally, blood loss is unlikely to explain the pattern I observed. This is because chiggers feed on lymph, and not blood (Traub et al, 1975).

In the only other known study to address ectoparasites and thermoregulation in reptiles, Conover et al (2015) found no association between chiggers and T_b in *Anolis cybotes* and *Anolis armouri* lizards. The authors suggested fever may either not occur in those species, or that 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 small effect sizes I observed relative to the variability of T_b , it is possible that I detected a significant effect simply due to large sample sizes. At least one other study has documented an impact of ectoparasites on thermoregulation in an ectotherm besides reptiles; Mohammed et al (2016) found that guppies displayed behavioural fever when infected with ectoparasitic worms. This resulted in increased host, and decreased parasite survival illustrating that adaptive thermal responses to ectoparasites can occur.

I 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 %), resulting in lower power to detect a significant effect. Because a relatively large proportion of lizards (24.5 %) were coinfecting with both chiggers and pterygosomatid mites, it is also possible

that the effects of pterygosomatids could not be separated from chiggers. Additionally, the pterygosomatid mites I observed often varied in size considerably and therefore simple counts may not have accurately represented the true costs of infection.

The costs of *Geckobiella* infection may not be high enough to elicit a fever. This could be due to low physiological impacts, or because *S. jarrovi* has evolved to tolerate *Geckobiella*. Many parasites in close association with their hosts evolve reduced virulence over time, resulting in less severe host responses (Lenski & May, 1994). The same is likely true for several parasitic mite species (Walter & Proctor, 2013). *Geckobiella* mites are more specialized and complete their entire life cycles on lizards (Goodwin, 1954) while chiggers only infect hosts during their larval stage and tend to be generalists on many vertebrate species (Shatrov & Kudryashova, 2006). However, these explanations appear unlikely given that *Geckobiella* mites can have severe impacts on *Sceloporus* lizards including death (Ferner, 1976; Goldberg & 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.

Effectiveness of thermoregulation (d_e-d_b):

I did not find any impact of ectoparasites on d_e-d_b which suggests that they do not interfere significantly with the effectiveness of thermoregulation. This is surprising given that I found an association between chiggers and T_b which would be expected to also impact d_e-d_b . Ectoparasites might only begin to interfere with d_e-d_b in severely infected individuals. Since these are rare, I 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 & Bull (2000) found an impact of ticks on basking behaviour in *Tiliqua rugosa* lizards. *Uta stansburiana* lizards infected with malaria display more variable body temperatures, presumably because the energetic costs of infection reduce the energy reserves needed to behaviourally thermoregulate (Paranjpe et al, 2014). In an extreme case, Goodman & Johnson (2011) found that trematodes caused chorus frogs to thermoregulate less effectively because the parasite caused missing or non-functional extra limbs. Alternatively, Deen & Hutchison (2001) found that thermoregulatory precision actually increased in green iguanas under immune challenge.

Several potential confounds could not be completely eliminated in my observational study. Although there appear to be no reported cases of chiggers vectoring diseases to reptiles, chiggers are vectors for scrub typhus (Lerdthusnee et al, 2003) and possibly *Borrelia* sp. (Literak et al, 2008) and hantavirus (Houck et al, 2001). Pterygosomatid mites including *Geckobiella* sp. are vectors for *Schellackia* and possibly *Plasmodium* (Schall & Smith, 2006) which alter thermoregulation in lizards (Paranjpe et al, 2014). Additionally, variables such as lizard body size (SVL) may impact both ectoparasite infection (Klukowski & Nelson, 2001), and T_b (Beal et al, 2014). Although I controlled for this possibility in my statistical models, minor collinearity may still impact the reliability of statistical inferences in regressions (Cade, 2015).

The quantification of thermoregulation may not have been detailed enough to detect the small impacts ectoparasites may have. To calculate the d_e-d_b index we used point sampling for the T_b of lizards, and three iButton temperature loggers to quantify operative environmental temperatures (T_e) during active periods. Additionally, we could only measure exposed lizards and not those under rocks. Therefore, our measurements of d_e-d_b may be relatively incomplete.

Continuous sampling methods for T_b may be more accurate, and less biased than point based methods for ectotherms (Taylor et al, 2004), and could be achieved with telemetry (e.g. Blouin-Demers & Weatherhead, 2001; Cooke et al, 2004). More copper models could also be used to quantify T_e at higher resolution.

Conclusions:

I found an association between chiggers and body temperature that varied with elevation in wild populations of *Sceloporus jarrovi*. To the best of my knowledge, this is the first report of an association between ectoparasites and body temperature in reptiles. This finding provides support for the hypothesis that ectoparasites impact thermoregulation. While several biological impacts of ectoparasites could explain this pattern, it is 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. Because this was a purely observational study, 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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Supplementary information:

Table S 1. UTM coordinates and elevations for talus slopes where *Sceloporus jarrovi* lizards were captured in the Chiricahua Mountains. Projected Coordinate system: NAD 1983 2011 UTM Zone 12N.

Site	UTM X	UTM Y	Site elevation (m)
Sulphur Canyon 4	674746.99	3523402.5	1634
South Fork 1	671060.99	3525386.5	1742
South Fork 3	671484.99	3526095.5	1761
Price Canyon 1	664837.99	3515400.5	1845
Price Canyon 4	664783.99	3515556.5	1848
Price Canyon X	664976.99	3515313.5	1852
Price Canyon 2	665226.13	3515234.3	1939
Rucker 2	661683.99	3519491.5	2133
Rucker 1	661649.68	3519448.3	2137
Rucker 5	663274.99	3519156.5	2151
Saulsbury Trail 3	660861.99	3527456.5	2511
Rustler's F	661850.99	3529509.5	2600
Rustler's 1	662040.99	3529400.5	2700

Table S 2. Summary statistics for *Sceloporus jarrovi* lizards captured in the Chiricahua Mountains. Values presented are means (\pm SE) calculated based on the first capture incidences (unique captures).

Site	Captures		SVL (cm)	Mass (g)	Ectoparasites		
	Unique	Total			Ticks	Pterygosomatids	Chiggers
Sulphur Canyon 4	39	80	6.01 (0.243)	7.27 (0.81)	0.1 (0.06)	0.03 (0.03)	9.08 (1.32)
South Fork 1	33	73	6.668 (0.102)	10.45 (0.54)	0 (0)	1.03 (0.35)	4.97 (2.49)
South Fork 3	42	83	5.546 (0.231)	6.04 (0.66)	0.24 (0.16)	0.49 (0.23)	23.44 (3.25)
Price Canyon 1	53	107	5.635 (0.194)	6.53 (0.62)	0 (0)	0.46 (0.22)	20.65 (4.09)
Price Canyon 4	12	32	6.409 (0.236)	7.76 (1.34)	0 (0)	1.25 (0.75)	29.83 (9.17)
Price Canyon X	12	17	6.077 (0.156)	7.67 (0.73)	0 (0)	0.25 (0.18)	16.92 (4.65)
Price Canyon 2	1	1	7.114 (0)	14.23 (0)	0 (0)	0 (0)	0 (0)
Rucker 2	48	92	6.18 (0.2)	8.96 (0.85)	0.33 (0.18)	0.48 (0.18)	22.6 (3.27)
Rucker 1	13	13	4.925 (0.43)	6.94 (1.85)	0 (0)	0.31 (0.24)	14.92 (3.73)
Rucker 5	115	220	6.023 (0.092)	7.95 (0.36)	0 (0)	1.72 (0.26)	15.68 (3.13)
Saulsbury 3	35	62	6.078 (0.173)	7.92 (0.65)	0.06 (0.04)	1.11 (0.31)	25.17 (8.39)
Rustler's F	42	111	7.358 (0.124)	14.06 (0.71)	0.02 (0.02)	0.21 (0.08)	53.29 (8.35)
Rustler's 1	69	129	7.021 (0.134)	13.76 (0.78)	0.26 (0.17)	0.26 (0.17)	48.39 (8.87)