

Factors influencing parasite load in male ornate tree
lizards (*Urosaurus ornatus*): throat colour, population
density, and habitat type

Agneta Szabo
5993954

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Dr. Gabriel Blouin-Demers

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Department of Earth Sciences
University of Ottawa

Abstract

Parasite load can lead to numerous fitness consequences within a host, and often varies widely between individuals of a population under the influence of numerous physiological and environmental factors. Male ornate tree lizards present a complex form of colour polymorphism on their extensible throat fan, which is indicative of their dominance and territoriality. If males exhibiting territorial behaviour suffer testosterone-derived immunosuppression or stress associated with territorial behaviour, this could increase their parasite loads. Population density may also increase parasite loads as a result of increased probability of transmission between individuals, or reduced immune function resulting from density-dependent territorial interactions. Levels of parasitism within a particular habitat can affect the quality of the habitat for the host. Habitat type may influence parasite load as a result of the suitability of the habitat for the completion of the parasite's life-cycle. I examined these three competing, although not mutually exclusive, hypotheses in six wild populations of male ornate tree lizards (*Urosaurus ornatus*) in the Chiricahua Mountains of Arizona. I compared the chigger (ectoparasite) and *Plasmodium* (haemoparasite) loads in individual males 1) with different throat colours, 2) from six populations varying in density, and 3) from one of either two habitat types (a treed riparian habitat and a creek bed). Parasite loads did not differ significantly between males of different throat colours or between males from different habitat types. Chigger loads decreased significantly with population density, although the effect size was very small, and *Plasmodium* levels did not vary significantly with density. I did not find support for any of the three hypotheses, but more data need to be collected on non-territorial males and overall host density (including other lizard species in the area) before reaching more definitive conclusions about the effects of throat colour and population density on parasite load.

Introduction

Parasitism is a well-documented biological relationship in which the parasitic species exploits a host species for its own reproductive benefits. This relationship is known to affect a wide array of taxa and has remarkable impacts on the evolution of hosts through its effects on sexual selection and population dynamics (Anderson & May 1982). The degree of parasitism varies widely between individuals of a host species as a result of numerous factors concerning the state of the individual and that of its environment. There exists a complex relationship between these factors and parasite loads, as different types of parasites are affected dissimilarly as a result of the pathway (*e.g.* ectoparasitism versus endoparasitism) through which they infect the host (*e.g.* Halliday *et al.* 2014; Fuxjager *et al.* 2011; Roberts *et al.* 2004).

Lizards are hosts to a variety of internal and external parasites, and may experience a diversity of fitness-related consequences as a result of these associations. For instance, skin infection by chiggers (ectoparasitic larvae of Trombiculidae mites) has been found to cause lesions and inflammation in wild lizard populations (Goldberg and Bursey 1991; Goldberg and Holshuh 1992), although fitness consequences resulting from chigger infection have not been demonstrated (Schlaepfer 2006; Sorci *et al.* 1997). Infection of red blood cells by *Plasmodium* (haemoparasitic protozoa that cause malaria) was found to reduce haemoglobin content of cells in parasitized lizards, thus affecting the oxygen-carrying capacity of the blood and reducing running stamina (Schall 1990; 1982). Additionally, malarial infection decreased fat stores of infected lizards, and reduced clutch size (in females) and testes size (in males) (Schall 1990; 1983). The objective of this study was to test three competing (but not mutually exclusive) hypotheses to explain the high level of variance in chigger and *Plasmodium* parasite loads in

male ornate tree lizards, *Urosaurus ornatus*. The three causal factors that I consider are throat colour, population density, and habitat type.

Male ornate tree lizards present a complex form of colour polymorphism on their throat. Populations of these lizards vary in the degree of male throat colour polymorphism, ranging from monomorphic to populations where several colour morphs co-exist (Carpenter 1995a; Thompson & Moore 1991a). Morphs include males with throat colours consisting of solid blue, green, orange, or bicoloured combinations of these aforementioned colours. Although throat colour may change through juvenile stages (Carpenter 1995b), it is fixed during adult life (Jennings *et al.* 2004; Moore *et al.* 1998; Hews & Moore 1996; Carpenter 1995b; Thompson & Moore 1991a). Studies show an early (< 60 days post-hatching) influence of gonadal androgens (*e.g.* testosterone) on the differentiation of throat colour as a secondary sex characteristic in *U. ornatus* (Jennings *et al.* 2004; Hews & Moore 1996; 1995; Hews *et al.* 1994), with more recent studies citing an additional influence of adrenal progesterone in the early developmental stages (Jennings *et al.* 2004; Weiss & Moore 2004).

The various colour morphs are commonly classified into two behavioural morphs, consisting of alternative male reproductive strategies. Studies have shown that blue or green throated males and bicoloured males belong to a territorial behavioural morph, whereas males with orange throats constitute a non-territorial behavioural morph (Knapp *et al.* 2003; Carpenter 1995a; 1995b; Thompson & Moore 1991a; 1991b; Hover 1985). In the wild, non-territorial orange males have been observed to behave as nomadic wanderers in some years and sedentary satellites in others. This is a form of behavioural plasticity, which is believed to be a result of hormonal responses to environmental stressors, such as drought (Knapp *et al.* 2003; Moore *et al.* 1998).

Studies have found that throat colour patches are reliable signals of fighting ability and dominance (Carpenter 1995a; Thompson & Moore 1991a; 1991b; Hover 1985). Although a few studies did not observe an effect of throat colour on dominance (McElroy et al., 2007; Zucker & Murray, 1996), territorial behavioural morphs are generally found to be dominant in laboratory encounters, more aggressive toward intruder males in the field, court females more often, patrol their territories and display more frequently (Thompson & Moore 1991a). These forms of behaviour are typically associated with elevated levels of testosterone, and as a result, testosterone-derived immunosuppressive effects could be taking place in these lizards in addition to, or in conjunction with, increased stress from territorial behaviour (as seen in monomorphic lizard species Halliday *et al.* 2014; Fuxjager *et al.* 2011; reviewed in Roberts *et al.* 2004; Olsson *et al.* 2000). This could increase the susceptibility of territorial individuals to parasitic infection, as a result I expected that morphs with blue or green on their throat would have higher chigger and *Plasmodium* parasite loads.

Parasite load is generally regarded to increase with crowding within a habitat (Oppliger *et al.* 1998; Côté & Poulin 1995), because proximity may facilitate parasite transmission between individuals. Additionally, density-dependent territorial interactions have been found to lead to decreased immune function in lizards (Svensson *et al.* 2001), which could affect an individual's ability to fight off a parasitic infection. As a result, I predicted a positive relationship between lizard density and mean parasite load at the various sites.

Parasite load has also been found to vary according to habitat type, as a result of the environmental suitability for the parasite (Bulté *et al.* 2009; Rubio & Simonetti 2009). I examined two habitat types in this study: a creek bed and a treed riparian habitat. Non-parasitic adult chiggers live in leaf litter, thus the treed habitat would be more suitable for chiggers to

complete their life cycles (Bulté *et al.* 2009; Rubio & Simonetti 2009). As a result, I expected that the intensity of chigger infection would be higher in the treed habitat. The vectors of the form of malaria-causing protozoans studied (*Plasmodium chiricahuae*) belong to the sandfly genus *Lutzomyia* which is known to seek moist habitats to breed (Yuval 2006; Mahrt 1987). As a result, I expected a greater abundance of sandflies near the creek, which would increase the prevalence of malaria in the area. Accordingly, I predicted higher *Plasmodium* parasite loads in the male ornate tree lizards found in the creek bed.

Methods

Field collection

Data were collected from 1 May to 25 July 2014 in the Chiricahua Mountains of southeastern Arizona in Coronado National Forest. Lizards were captured at six sites that varied in population density from 20-150 lizards/ha. Each site had two adjacent habitat types: creek bed and a treed riparian habitat. Sites were approximately 300 m long and extended 50 m perpendicular to the creek bed on one side. Between two to five observers walked transects through habitats and captured lizards using a rod and noose. After capture, male lizards (N = 233) were photographed, measured with digital callipers (snout-vent length; SVL [cm]), and the chiggers on the lizards were counted using a hand lens. Lizard throat colour was identified in the field by consensus of three observers. A single toe was clipped on the right rear limb of a subset of lizards (N = 81) to create blood smears and quantify intensity of *Plasmodium* infections. Slides were fixed in the field in 95% methanol and stored for staining in the lab. Animals were

collected with an Arizona State Scientific Collecting Permit (#SP674241) and animal care protocols were approved by the University of Ottawa's Animal Care Committee (#BL-286).

Lab work

The blood smears were stained using Wright-Giemsa solution (Fisher Scientific Company, Middleton, Virginia, USA). I used a compound microscope at a magnification of 400x for counting the number of infected red blood cells. Using 10 smears, there was a strong correlation ($r = 0.995$) between the infected red blood cell counts per 5,000 and per 10,000 cells. Therefore, the remainder of samples were done counting 5,000 cells for determining relative infection rates for each lizard. The throat colours of lizards were qualitatively rescored using photographs to confirm the field throat colour identification. The throat colour categories assigned using photographs were the same as field-assigned categories in 95% of the samples. The remaining 5% represents a potential error, comparable to the 5-10% error in the identification of throat colour reported in another study (Thompson & Moore 1991b). Based on the photographs, the throat colour categories found in males of the studied populations are blue, green, green-blue, orange-blue, and orange-green.

Analyses

For the evaluation of the effects of throat colour, population density, and habitat type on parasite load, I used R (R Core Team 2013) to create generalized linear models (GLMs) to test competing hypotheses. For the chigger analysis, I used data from the first capture of each lizard to avoid pseudo-replication. For the malaria analysis, I used data from the capture corresponding to the date when the toe clips were taken. Separate models were fitted for ectoparasites and haemoparasites.

Previous studies have found strong positive relationships between lizard body size and parasite load (Halliday *et al.* 2014; Garrido & Pérez-Mellado 2013; Schall 1996) so I included snout-vent length (SVL) as an independent variable in the GLM to control for its effect. Studies have also found that parasite loads fluctuate over the course of the year, with *Plasmodium* parasite levels increasing later in the warm season, when sand-fly vectors are active (Eisen 2000; Schall & Marghoob 1995; Bromwich & Schall 1986). A similar pattern was found with chigger parasite loads which, in one study, increased eightfold throughout the summer (June-August) as compared to spring (April-May) (Klukowski 2004). Accordingly, I included capture date (as Julian date) in the GLM to control for its effect.

The chigger data were positively skewed and could not be transformed to a normal distribution. Because these are count data, I used a Poisson regression to model the data. Due to overdispersion, a quasi-likelihood estimation was needed (in R, family = quasipoisson). The malaria data were also positively skewed, but this was corrected by transforming the data using the natural logarithm ($\ln[\textit{Plasmodium}+1]$). The transformed malaria data followed a normal distribution, so I used a linear regression model to analyse these data.

I began my analyses with the complete model for both parasite types, including all terms and two-way interactions. For the quasi-Poisson model (chiggers), I used an F-test for the analysis of deviance of the GLM to determine the model with the best fit. For the linear regression model (*Plasmodium*), I used the Akaike information criterion (AIC) to measure the relative fit of various models and determine the model with the best fit (Burnham & Anderson 2002). AIC could not be used for evaluation of model fit for chiggers due to the non-parametric nature of the quasi-Poisson analysis.

Results

Chiggers

In the 233 lizards included in the analyses, chigger parasite loads varied from zero to 57 chiggers per individual. Analysis of deviance of the complete model determined that the model that best explained the variability in chigger load in the lizards sampled included population density (coefficient = -8.1×10^{-3} ; $F = 16.2$, $p < 0.001$; Figure 1), SVL ($p = 0.082$) and date of capture ($p < 0.001$). SVL was only nearly significant, however I took a conservative approach and included it in the final model in order to control for the effects of lizard size on chigger load. Throat colour (Figure 2) and habitat type (Figure 3) did not have a significant effect on chigger parasite load in any of the models considered. None of the two-way interactions were significant. The reported coefficient, F-value, and p-values are from the final model (Chiggers ~ Density + SVL + Date).

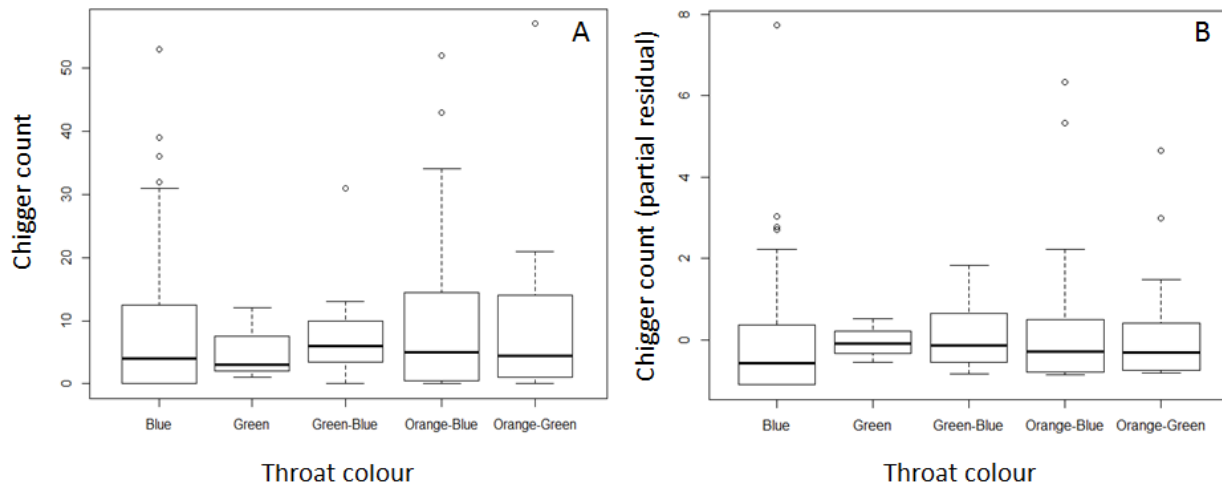


Figure 1: Relationship between chigger parasite load and throat colour for *U. ornatus* in the Chiricahua Mountains, AZ. The raw data (A) and the partial residual plot of the full model (Chiggers ~ Throat Colour + Density + Habitat + SVL + Date; B) are presented.

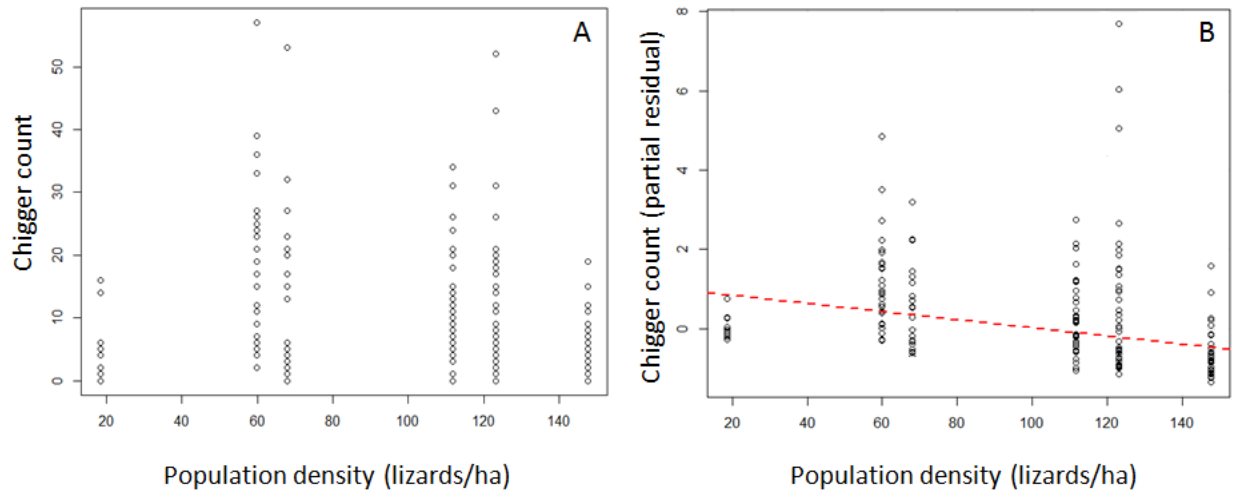


Figure 2: Relationship between chigger parasite load and population density for *U. ornatus* in the Chiricahua Mountains, AZ. The raw data (A) and the partial residual plot of the full model (Chiggers ~ Throat Colour + Density + Habitat + SVL + Date; B) are presented.

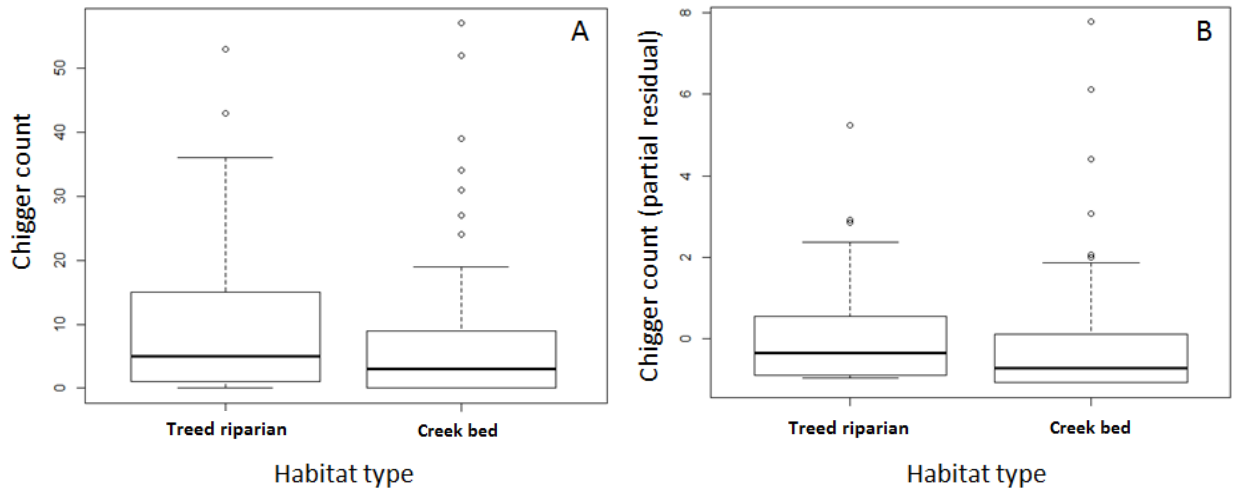


Figure 3: Relationship between chigger parasite load and habitat type for *U. ornatus* in the Chiricahua Mountains, AZ. The raw data (A) and the partial residual plot of the full model (Chiggers ~ Throat Colour + Density + Habitat + SVL + Date; B) are presented.

Malaria

In the 83 lizards included in the analyses, *Plasmodium* parasite loads varied from zero to 402 infected red blood cells per 5,000. Using AIC (see Table 1), the model that best explained the variability in *Plasmodium* levels in the lizards sampled included only date of capture ($\ln[Plasmodium+1] \sim \text{Date}$; $R^2 = 0.054$; $p = 0.036$). Throat colour (Figure 4), population density (Figure 5), habitat type (Figure 6), and SVL did not have a significant effect on *Plasmodium* parasite load in any of the models considered.

Table 1: Models considered and the associated Akaike information criterion (AIC) values used to determine the best fit. The best fit model is presented in bold font.

Model Considered	AIC
$\ln(Plasmodium+1) \sim \text{Date}$	243.98
$\ln(Plasmodium+1) \sim \text{Density} + \text{Date}$	245.16
$\ln(Plasmodium+1) \sim \text{ThroatC} + \text{Density} + \text{Habitat} + \text{SVL} + \text{Date} + \text{Date:ThroatC}$	246.01
$\ln(Plasmodium+1) \sim \text{Density} + \text{Habitat} + \text{Date}$	246.23
$\ln(Plasmodium+1) \sim \text{SVL} + \text{ThroatC} + \text{Date} + \text{Habitat} + \text{Density} + \text{SVL:ThroatC} + \text{SVL:Date} + \text{ThroatC:Date} + \text{SVL:Habitat} + \text{ThroatC:Habitat} + \text{Date:Habitat} + \text{SVL:Density} + \text{ThroatC:Density} + \text{Date:Density} + \text{Habitat:Density}$	247.08
$\ln(Plasmodium+1) \sim \text{Density} + \text{Habitat} + \text{SVL} + \text{Date}$	247.62
$\ln(Plasmodium+1) \sim \text{ThroatC} + \text{Density} + \text{Habitat} + \text{SVL} + \text{Date}$	249.70

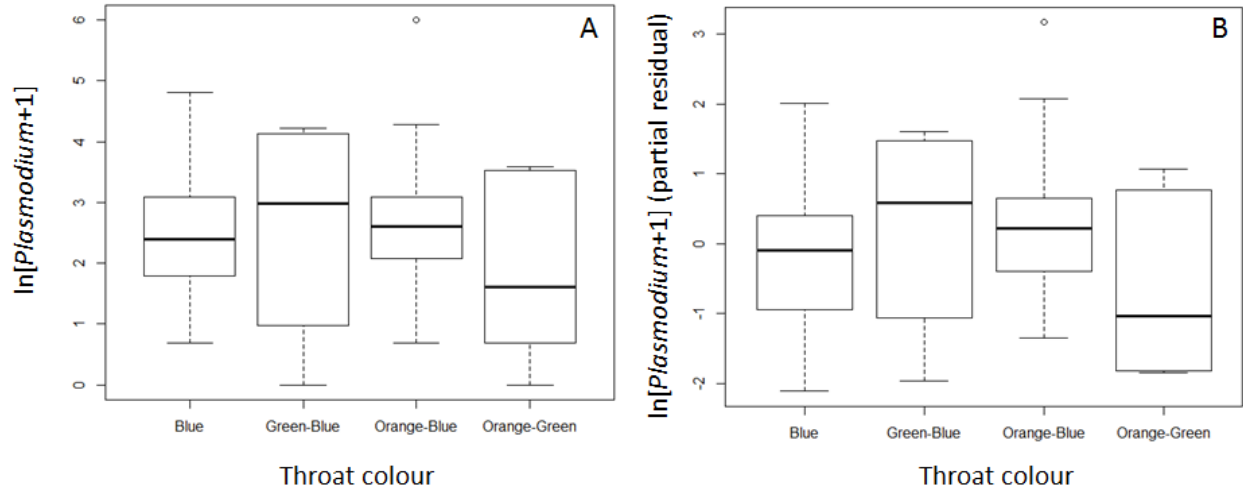


Figure 4: Relationship between *Plasmodium* parasite load and throat colour for *U. ornatus* in the Chiricahua Mountains, AZ. The raw data (A) and the partial residual plot of the full model ($\ln[Plasmodium+1] \sim \text{Throat Colour} + \text{Density} + \text{Habitat} + \text{SVL} + \text{Date}$) are presented.

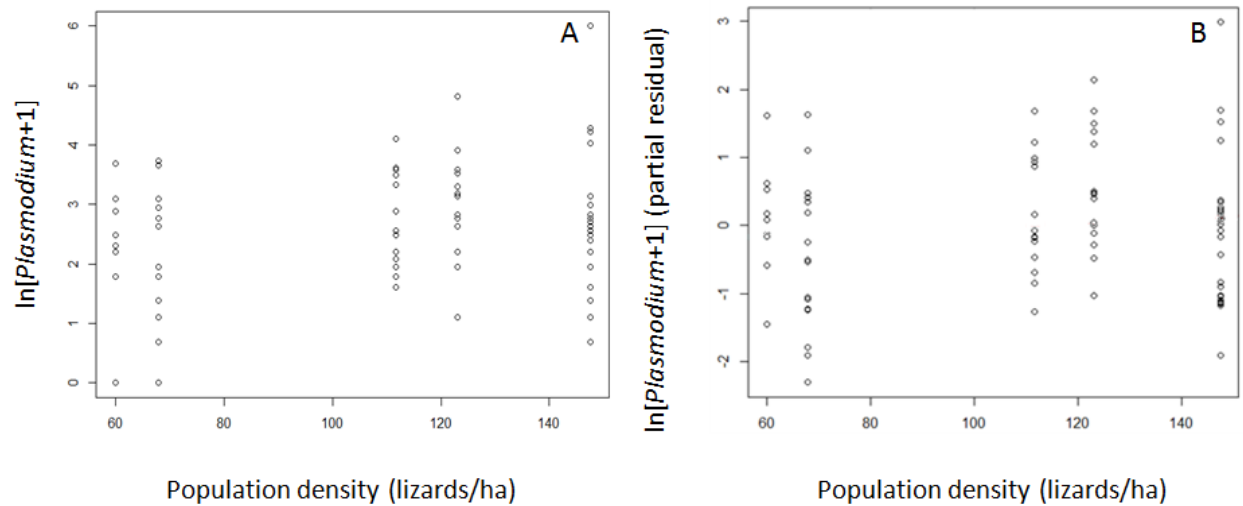


Figure 5: Relationship between *Plasmodium* parasite load and population density for *U. ornatus* in the Chiricahua Mountains, AZ. The raw data (A) and the partial residual plot of the full model ($\ln[Plasmodium+1] \sim \text{Throat Colour} + \text{Density} + \text{Habitat} + \text{SVL} + \text{Date}$) are presented.

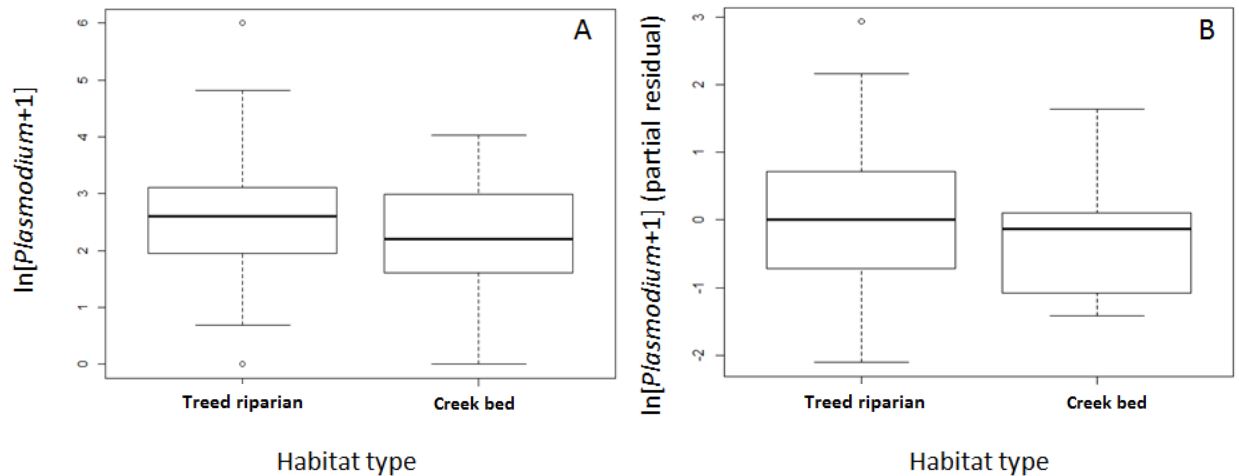


Figure 6: Relationship between *Plasmodium* parasite load and habitat type for *U. ornatus* in the Chiricahua Mountains, AZ. The raw data (A) and the partial residual plot of the full model ($\ln[Plasmodium+1] \sim \text{Throat Colour} + \text{Density} + \text{Habitat} + \text{SVL} + \text{Date}$) are presented.

Discussion

In this study, I tested three competing (but not mutually exclusive) hypotheses to explain the variability of individual parasite load in male ornate tree lizards. I looked at infection by chiggers (ectoparasites) and *Plasmodium* (haemoparasites), and evaluated how the relative individual infection levels vary as a function of throat colour, population density, and habitat type. I did not find support for any of my hypotheses. Despite the large sample sizes (chiggers $N = 233$; *Plasmodium* $N = 81$) none of the factors of interest were significant except population density which, contrary to my prediction, appears to have a negative influence on chigger parasite load. However, data for the evaluation of the effects of throat colour and population density were insufficient to adequately test these hypotheses (I elaborate on the reasons below).

As a result more data should be collected to better understand the effects of these factors on parasite load in *U. ornatus*.

If testosterone-derived immunosuppressive effects or stress from territorial behaviour are taking place in territorial morphs of male ornate tree lizards (Fuxjager *et al.* 2011; Roberts *et al.* 2004), it would be expected that morphs with blue or green on their throat would have higher counts of chiggers. Due to a lack of data for orange males (which are described as non-territorial in the scientific literature) (Knapp *et al.* 2003; Carpenter 1995a; 1995b; Thompson & Moore 1991a; 1991b; Hover 1985), I was not able to evaluate this hypothesis. Despite this set-back I proceeded to analyse parasite loads of the other throat colour categories (which are described as territorial in the scientific literature) (Knapp *et al.* 2003; Carpenter 1995a; 1995b; Thompson & Moore 1991a; 1991b; Hover 1985) to evaluate the possibility of a difference between the various throat colour morphs. According to my analyses, throat colour did not have a significant effect on parasite loads. However, the possibility remains that males with orange throats have a different parasite load than other male lizards in the population. In the six populations studied, the frequency of orange-throated males was very low (2/235 males caught in about 30 days of sampling). It would be interesting to sample different populations of *U. ornatus* where the frequency of orange males is higher (*e.g.*, Tonto National Forest in central Arizona studied by Knapp *et al.* [2003]) to evaluate the possibility that these non-territorial males experience lower levels of parasitism.

Another notable shortcoming in this study is that testosterone levels were not measured, so it is uncertain whether there was actually variation between the individuals in this population. It would be beneficial to include these measures in future studies. Based on current literature on the subject, testosterone levels do not differ significantly between territorial and non-territorial

males under normal, stress-free conditions (Knapp *et al.* 2003; Knapp & Moore 1997; 1996). However, unlike territorial males, non-territorial males experience a significant drop in testosterone levels when their corticosterone levels increase as a result of stress induced by factors such as aggressive encounters (Knapp & Moore 1997; 1996; 1995) and periods of drought (Moore *et al.* 1998; Knapp *et al.* 2003;). It is believed that this is the underlying mechanism for the behavioural plasticity expressed by non-territorial orange males who are observed to be site-faithful satellites during wetter years and nomadic rovers during drier years (Moore *et al.* 1998; Knapp *et al.* 2003). Territorial males, on the other hand, have consistently elevated levels of testosterone and continue to defend their territories under all circumstances. As a result, it is possible that territorial males experience a heightened susceptibility to parasitic infection due to immunosuppressive effects of testosterone or the stress associated with territorial behaviour (as seen in monomorphic lizard species Halliday *et al.* 2014; Fuxjager *et al.* 2011; reviewed in Roberts *et al.* 2004; Olsson *et al.* 2000).

Although some studies have found that testosterone increases parasite load, others did not find a relationship (*e.g.*, Oppliger *et al.* 2004; reviewed in Roberts *et al.* 2004). This could be a result of the different types of parasites examined, which infect their hosts through distinct pathways. Notably, studies have found that in lizards ectoparasite loads commonly increase under the influence of testosterone while blood-borne parasite species were found to be primarily affected by environmental (in contrast to physiological) factors (Halliday *et al.* 2014; Fuxjager *et al.* 2011; Roberts *et al.* 2004). Thus, there is also the possibility that throat colour does not have an influence on parasite load, or that it influences only one of the two parasite types examined. Until more data are collected on the non-territorial orange males for further analyses, it remains

to be determined whether chigger and *Plasmodium* parasite loads differ between territorial and non-territorial morphs of male ornate tree lizards.

If population density increases the probability of parasite transmission between individuals (Oppliger *et al.* 1998; Côté & Poulin 1995), or has an effect of decreasing immune function as a result of density-dependent territorial interactions (Svensson *et al.* 2001), it would be expected that mean chigger and *Plasmodium* levels would increase with population density at the various sites. Contrary to my predictions, my analyses found a negative effect of density on chigger load and no effect of density on *Plasmodium* levels.

Despite the significance of the negative relationship between population density and chigger counts, the effect was weak. A study by Sorci *et al.* (1997) also found a negative relationship between host density and ectoparasite load in a population of the common lizard (*Lacerta vivipara*). Possible explanations for this relationship included parasite dilution, where each host is just one of several potential targets, thereby decreasing the mean individual parasite load at higher densities. Additionally, it was suggested that lizards in areas with fewer parasites may be in better condition, allowing for greater population growth. Collecting data on the prevalence of chiggers in the soil and leaf litter at the various sites could lend a degree of clarification in terms of this possibility.

Another important fact to consider is that the parasites studied are not specific to ornate tree lizards, but parasitize other lizards species also found in the study area. While it is known that the distribution of male and female ornate tree lizards at the six sites was comparable (approximately 1:1), it is possible that the abundance of other lizard populations at the sites were quite different. Because these other lizards are also hosts to chiggers and *P. chiricahuae*, there is

a strong likelihood that the results of my analyses are not accurately depicting the effects of host density on parasite loads. Evaluating the overall host density at the various sites would likely provide a much more accurate picture. Additionally, the evaluation of other sites (beyond the six included in this study) would increase the sample size and could improve our understanding of the effects of host population density on parasite load.

There was no significant difference between chigger and *Plasmodium* parasite levels between the two habitat types. My predictions for the variation in parasite load in function of habitat type rested on the assumption that the suitability of the habitats differed for the completion of the parasites' life-cycles, and as a result there would be more chiggers in the treed riparian habitat and more sandfly vectors of *P. chiricahuae* in the creek bed. Such differences in the distribution of the parasites and parasite vectors were not measured or observed over the course of this study. Male lizards in this study are highly territorial; 76% of recaptures were in the same habitat type. For the other 24%, the recaptures were only 2.5 m away from the habitat edge. Overall this suggests the habitat assignment is accurate and lizards maintain small, consistent home ranges. As a result, it is unlikely that the homogeneous distribution of parasite loads between the two habitat types is a result of the lizards wandering freely between the two habitat types.

Previous studies have found significantly higher chigger loads in treed habitats (Bulté *et al.* 2009) and in the interiors of forested patches as compared to the edges (Rubio & Simonetti 2009), attributing the differences to the known fact that non-parasitic adult chiggers live in leaf litter which would render treed habitats more suitable for chiggers to complete their life cycles. It is possible, however, that the proximity of the creek bed to the treed habitats (which border it on either side) renders it easy for chiggers to distribute themselves evenly throughout the two

habitats. Collecting data on the abundance of chiggers in the soil and leaf litter at the two habitats would provide insight into this possibility. Sandflies are highly mobile as well, so it is very possible that they are evenly distributed between the habitats. The data collection period overlapped both dry and wet season. The rainy period started early July so there was a month of data where there could have been water in the creek, however the first two months of the data collection period the creek bed was dry. Although it is expected that sandflies would aggregate near the creek during the wet season (Yuval 2006; Mahrt 1987), this may not be the case when the creek bed is dry.

Of the two factors included in the GLMs for control, date had a significant positive effect on both chigger and *Plasmodium* parasite loads. This increasing trend in parasite levels over the summer season was in accordance with previous findings (Klukowski 2004; Eisen 2000; Schall & Marghoob 1995; Bromwich & Schall 1986). Although it was close to the threshold, SVL did not have a significant effect on the levels of either parasite. Studies show that ectoparasite levels tend to increase with SVL (Halliday *et al.* 2014; Garrido & Pérez-Mellado 2013; Schall 1996) either because larger lizards are more detectable, have room to support more parasites, or because they have had more time to accumulate parasites (Blanckenhorn, 2000). The lack of significant effect of SVL on parasite loads in this study is likely due to the limited size variability between individuals (the percent increase between the largest and smallest lizards was about 38%) and the short lifespan of these lizards (most only live for one reproductive season).

This study set out to evaluate the effect of throat colour, population density and habitat type on chigger and *Plasmodium* parasite loads in male ornate tree lizards. Due to a lack of data for males of the non-territorial orange throated morph, and insufficient data on true host density in the populations studied, I was not able to adequately test my hypotheses relating to throat

colour and population density. As a result, I cannot draw reasonable conclusions concerning the effects of these two factors on parasite loads at this time. Habitat type was not found to have a significant effect on the parasite loads of either species studied, which implies that the parasites are evenly distributed throughout the treed riparian habitat and the creek bed habitat. As a result, within the studied populations, neither habitat appears to be more beneficial to male ornate tree lizards in terms of parasitism by chiggers and *Plasmodium*.

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