Body condition, sex, and elevation in relation to mite parasitism in a high-mountain gecko

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Running title: Mite parasitism in an alpine gecko

Abstract

Parasitism is one of the main selective forces in nature, strongly affecting host fitness. Still, knowledge is incomplete concerning how variation in probability and intensity of infestation depends on body condition, sex or geographic variables. Here, I study the variation in probability and intensity of infestation of blood-sucking mites parasitizing the Atlas day gecko (*Quedenfeldtia trachyblepharus*) depending on host body condition, sex, and elevation, in the High Atlas (Morocco). Parasite prevalence was 58.75% and probability of infection decreased with host body condition. However, parasitism intensity tended to increase with body condition. The parasite load ranged from 0 to 16 mites per individual, with a mean intensity of 3.0 ± 0.37 (SE) in infested geckos. Prevalence was higher in males (2/3 parasitized) than in females (1/2 parasitized), but intensity did not significantly differ with sex. Neither prevalence nor intensity varied with elevation. In conclusion, geckos in better body condition harboured heavier parasite loads, but animals with the highest body condition were not infested. These findings suggest that animals with good body condition may tolerate heavier mite infestations, but only animals with the highest body condition may resist infestation.

Keywords
Atlas day gecko, prevalence, *Quedenfeldtia trachyblepharus,* tolerance, resistance.

Introduction

Parasites, by taking resources from hosts, reduce host fitness (Schmid-Hempel, 2011). The deleterious effects of parasitism on host fitness include a decreased reproductive success as well as increased mortality (Rätti, Dufva & Alatalo, 1993; Hakkarainen et al., 2007). Moreover, parasites consume energy and hence often reduce host energy stores, harming body condition (Hakkarainen et al., 2007; Mougeot et al., 2009; Sánchez et al., 2018). Therefore, parasitism has consequences in most aspects of host's life history (e.g. Combes, 2001; Marzal et al., 2005). Altogether, parasites constitute a strong selective pressure, affecting host population structure and ultimately ecosystem functioning (Hudson et al., 2002). Consequently, the immune system of hosts has evolved different defence mechanisms against parasites, such as resistance and tolerance (Dawkins, 1990; Schmid-Hempel, 2011; Owen & Hawley, 2014). Resistance is the host's ability to reduce parasite establishment. Meanwhile, tolerance is the host's ability to withstand a given parasite load and maintain fitness in the presence of infestation (Råberg, Sim & Read, 2007; Råberg, Graham & Read, 2009; Ayres & Schneider, 2008; Medzhitov, Schneider & Soares, 2012). Then, to combat the parasite, a host may bolster its resistance to infection by reducing pathogen fitness or, alternatively, may increase its tolerance by reducing the damage caused by the pathogen (Ayres & Schneider, 2008). Nevertheless, the development of mechanisms against parasites, either resistance or tolerance, is costly in terms of energy, structural resources such as amino-acids, or the generation of free radicals (Toft & Karter, 1990; Schmid-Hempel, 2011; Demas & Nelson, 2012). Thus, there is often a trade-off between the immune response and other physiological demands such as self-maintenance, growth, and reproduction (Demas & Nelson, 2012).

Body condition typically reflects an animal's overall health, energetic state, and survival capabilities (Schulte-Hostedde et al., 2005; Beldomenico et al., 2008; Budischak et al., 2018). Examining the relationship between body condition and infestation may be a good proxy to measure parasite impact on the host (Sánchez et al., 2018). However, the relationship between host body condition and parasitism is complex (e.g. Amo, López & Martín, 2004; Knapp et al., 2019). Immune function is condition-dependent (Møller et al., 1998), and hosts in good condition may use more resources to resist infestation or to tolerate high intensities of parasitism (Budischak et al., 2018; Sánchez et al., 2018; Carbayo, Martín & Civantos, 2019).

If hosts use resources to fight parasites, hosts in poor condition could suffer impaired immune defence that would lead to greater probability of infection and heavier parasite loads, and ultimately higher mortality (Merino et al., 2000; Botzler & Brown, 2014). However, if the hosts with better body condition use more resources to tolerate heavier parasitic loads, then a positive relationship may be expected between host body condition and parasite intensity (Budischak et al., 2018). Moreover, other aspects may affect the relationship between body condition and parasite intensity. Parasites are expected to diminish the host body condition (Hatchwell et al., 2001; Garvin, Szell & Moore, 2006) and, in fact, several studies report negative associations between host body condition and infestation (Dawson & Bortolotti, 2000; Mougeot et al., 2009; Cook et al 2013). Nevertheless, if heavily parasitized individuals in bad body condition suffer an increase in mortality, parasitized individuals may show a higher body condition compared to non-infested ones (Amo, López & Martín, 2005).

Parasitism often proves decisive in sexual-selection processes, females usually choosing less parasitized males (Hamilton & Zuk, 1982; Andersson, 1994; Able, 1996, Kelly et al., 2018). Overall, across species, females usually have stronger immune responses to parasite infestation than males (Klein, 2000; Klein, 2004; Roberts, Buchanan & Evans, 2004; Foo et al., 2017). Especially in reptiles, prevalence and intensity of ectoparasite infestations tend to be lower in females (e.g. Václav, Prokop & Fekiač, 2007; Dudek et al., 2016; Llanos-Garrido et al., 2017). Males have higher testosterone levels than females do, and testosterone (or certain behavioural and physiological processes associated with testosterone) may have an immunosuppressive effect (Roberts et al., 2004; Foo et al., 2017). Furthermore, males with higher testosterone levels typically show greater mobility, which may increase the exposure to parasites from infested conspecifics during encounters with females as well as during fights with other males (Olsson et al., 2000; Amo et al., 2005).

Environmental conditions such as community composition, temperature, and humidity affect parasite prevalence and load, and consequently host-parasite dynamics typically vary geographically (Poisot et al., 2017). In this sense, elevational gradients, which imply a huge variation in several biotic and abiotic factors, constitute a good model to examine geographic variation in host-parasite interactions. It is generally thought that parasite intensity declines with elevation (Badyaev, 1997). As one ascends in elevation, ectoparasites are typically exposed to lower temperatures, reduced daily and annual time available to complete their life cycles, and long periods of host hibernation. Altogether, these factors likely increase ectoparasite mortality (Postawa & Nagy, 2016). For lizard-mites systems, although increased mite prevalence with elevation has been reported (Spoecker, 1967; Llanos-Garrido et al., 2017), several studies indeed report reduced mite prevalence and load at higher elevations (e.g. Carothers & Jaksic, 2001; Álvarez-Ruiz et al., 2018; Carbayo et al., 2019).

In this study, I examine the interaction between a reptile endemic to the Moroccan High Atlas, the Atlas day gecko *Quedenfeldtia trachyblepharus* (Boettger, 1874), and blood-sucking mites along an elevational gradient. Specifically, I test: 1) The relationship between probability of infection and intensity of mites with gecko body condition. If geckos in better body condition are more resistant to parasites, then I predict a negative relationship between body condition and mite probability of infection and intensity; but if enhanced body condition improves tolerance to parasitism, then a positive relationship between body condition and parasite intensity is expected. 2) Differences in probability of infection and intensity of mites depending on sex. I expect males to harbour more parasites than females, given their higher testosterone levels. 3) Differences in prevalence and intensity depending on elevation. Specifically, I expect reduced mite parasitism at higher elevations, given that harsh conditions at high elevations are expected to negatively affect parasite survival and life cycle.

Material and Methods

Study system

The study was performed along an elevational gradient at six localities in Oukaïmedene, in the High Atlas of Morocco (31.21ºN, 7.83ºW; Fig. 1). The study area has a Mediterranean climate, with average annual precipitation of approximately 400–500 mm. Average temperatures range from 23.5ºC in the warmest month (July) to −2.7ºC in the coldest month (January), with 82 to 139 days of frost per year (Alaoui Haroni, Alifriqui & Simonneaux, 2009). Snowfall occurs mainly between November and March (corresponding to the hibernation period of geckos). However, sometimes snow cover remains until the end of May (Bouazza et al. 2016). The vegetation consists of grasslands, with richer vegetal communities at lower elevations (Mediterranean shrubs of *Retama spp.* and Atlas Cedars *Cedrus atlantica* plantations).

The Atlas day gecko (*Quedenfeldtia trachyblepharus*) is a member of the Sphaerodactylidae family endemic to the Moroccan High Atlas that inhabits from 1200 to 4000 m above the sea level, but is particularly abundant from 2500 m on (Arnold, 1990; Bons & Geniez, 1996; Schleich, Kästle & Kabisch, 1996; Bouazza et al. 2016). This gecko is strictly diurnal (Blouin-Demers et al. 2013) and the dominant species in lizard communities at alpine levels becoming scarcer at lower elevations. Above 2500 m, the Atlas day gecko shares its habitat with the lizard *Atlantolacerta andreanszkyi* (Bons & Geniez, 1996). Nevertheless, populations below 2500 m must share the habitat with an increasing diversity of other lizard species such as *Podarcis vaucheri*, *Scelarcis perspicillata*, *Tarentola mauritanica*, *Psammodromus algirus*, *Timon tangitanus*, and *Agama impalearis* (Bons & Geniez, 1996; Schleich et al., 1996). The reproductive period for the geckos is from March to June (Bouazza et al. 2016).

Sampling

Sampling was conducted in September 2010. The specimens of Atlas day gecko were captured by hand and later released at the capture site. No specimen suffered permanent damage as a consequence of this study and sampling were done following animal care protocols. A total of 42 adult males and 38 adult females were captured from different elevations (ranging from 2096 to 2755 m). The captured individuals were assigned to two elevation categories, i.e. under 2500 m (n = 21) or above 2500 m (n = 59), based on the preferred habitat of the gecko, more abundant above 2500 m asl. Thus, elevation was considered to depend on two intervals, low elevation (L) from 2096 to 2385 m and high elevation (H) from 2725 to 2755 m. Sex was distinguished visually, male geckos having dark spots on their bellies and undersides of their legs (Blouin-Demers et al. 2013). The snout-vent length (SVL) was measured from the tip of the snout to the posterior border of the vent with digital callipers (Gyros Digi-science Accumatic Pro, Gyros Precisions Tools, Inc, Monsey, NY, USA; accuracy 0.01 mm), and weight was recorded using a precision balance (Denver Instrument Company Model 100A; Denver Instrument, Bohemia, NY, USA; accuracy 0.1 g). Body condition was estimated as residuals from logarithm of body weight regressed against the logarithm of SVL (Schulte-Hostedde et al., 2005). Captured geckos were carefully inspected searching to count mites on their body surface, especially those under scales. Probability of infection was estimated as the presence or absence of mites, and intensity as the quantity of mites in infested individuals (Margolis et al. 1982; Bush et al. 1997; Rózsa, Reicsigel & Majoros, 2000).

Statistical analysis

To test for the variation in probability of infection I used Generalized Linear Models (GLM) with binomial distribution, linked to a logit function, with body condition (continuous), elevation (two levels), and sex (two levels), as independent variables. Also, to test for variation in intensity, I performed several linear models (LM) with intensity (log-transformed) as a dependent variable, and body condition, elevation, and sex as predictors. No interaction between independent variables proved significant (results not shown), and hence interactions were not included in the final models. To select the best models I used Akaike Information Criterion (AIC) and I chose those with the smaller value of AIC (Quinn & Keough, 2002). Normality and homoscedasticity of variables and model residuals were checked following Zuur, Ieno & Elphick (2010). Some variables (such as intensity) were transformed with the Naperian logarithm in order to satisfy model assumptions. Basic statistics are given as mean ± SE (standard error). All analyses were performed with R 3.5.1 (R Development Core Team, 2017).

Results

Mite prevalence was 58.75% (47/80; Fig. 2). The best model depending on AIC was which included the three predictor variables, being this model indistinguishable of that which only included sex and BCI (Table 1). The GLM showed a negative relationship between probability of mite infection and body condition (Estimate = -8.34, z = 2.66, P = 0.008; Fig. 3), as well as a significant variation with sex: higher probability of mite infection in males than in females (Males = 67%, n = 42; Females = 50%, n = 38; z = -2.03, P = 0.042), but no variation in probability of mite infection with elevation was found (z = -1.46, P = 0.145). When the analyses were repeated without the two more extreme values, the effects of body condition and sex on probability of mite infection remained significant (data not shown for simplicity).

The number of mites per host ranged from 0 to 16 mites, and in infested geckos, mean intensity was 3.0 ± 0.37 mites per host (n = 47). The best model depending on AIC was which included only BCI (Table 1). The LM analysing the relationship between parasite intensity and body condition was significant (t = 2.51, P = 0.016, Fig. 4), but no significant differences in intensity were found depending on sex (Males = 3.14 ± 0.57, n = 28; Females = 2.79 ± 0.42, n = 19; t = −0.45, P = 0.65) or elevation (Low elevation = 2.00 ± 0.30, n = 11; High elevation = 3.31 ± 0.47; n = 36; t = −1.80, P = 0.079).

Discussion

The results in this study show complex relationships between gecko body condition and mite parasitism, probability of infection being lower in geckos having better body condition, but infestation tending to intensify with body condition. These apparently contradictory results suggest that the better the body condition of an individual, the lower the likelihood of being parasitized, but a good body condition also implied more tolerance to parasites, allowing the individual to deal with a greater parasitic load after the initial infestation (Amo et al., 2005). Anti-parasitic defences are costly (Hakkarainen et al., 2007), requiring allocation of resources to the immune system. Therefore, individuals with a better body condition may invest more resources to their immune system to fight parasites, but also may invest more resources to deal with parasites and to be more tolerant. Additionally, it is possible that different mite species specialize in geckos depending of its tolerance or resistance. Nevertheless, if the infestation reduces survival, only individuals in good body condition could survive and, consequently, individuals with the poorest body condition might have died before the sampling (Amo et al., 2005). This might explain the greater infestation in individuals with greater body condition.

As expected, prevalence proved greater in males than females, with two-thirds of the males but only half of the females parasitized. However, the intensity of infestation did not change according to sex, in agreement with another study conducted in the same area with the same species (Blouin-Demers et al. 2013). High testosterone levels may imply immunosuppressive effects that, particularly in reptiles, boosts ectoparasite intensity (Salvador et al., 1996; Olsson et al., 2000; Klukowski & Nelson, 2001). These factors may explain greater prevalence in males. However, males registered higher values of body condition than females (Comas, Escoriza & Moreno-Rueda, 2014). Better body condition implies more resources to fight parasites, allowing more resistance to parasites (Arriero et al. 2018), perhaps explaining why males do not show a higher intensity of infestation than females do, although the absence of significant interaction sex*body condition does not support this contention. Still, males suffered more prevalence of mites. Higher mobility and more frequent social interactions of males may facilitate parasite transmission during contacts with females and in fights with other males (Olsson et al., 2000; Amo et al., 2005). If higher male mobility applies to Atlas day geckos, increased mobility could explain their higher prevalence.

Selective pressures may vary with elevation as a consequence of the changing biotic and abiotic conditions (Körner, 2007). For example, at higher elevations, hibernation lasts longer, resulting in a narrow temporal window for both host and parasites to reproduce and grow. Moreover, at higher elevations ectoparasites are exposed longer to lower temperatures which may increase ectoparasite mortality during hibernation (Postawa & Nagy, 2016). In fact, other studies show differences in parasitism with elevation, lizards typically harbouring more parasites at low elevations (e.g. Álvarez-Ruiz et al., 2018). However, this contention was not supported by the results, given that both prevalence and intensity did not differ with altitude. This result could be explained in several ways. The reptile community composition and gecko's population density change with elevation. The Atlas day gecko is alpine, being the most common reptile above 2500 m, with lower densities below this elevation (Schleich et al., 1996). The high density of individuals intensifies the risk of parasite transmission (Altizer et al., 2004; Hakkarainen et al., 2007). However, as elevation decreases, gecko densities also decrease but many other lizard species occur, with the reptile community being richer in the lowlands, which could act as a mite reservoir. Moreover, other factors could intervene, such as the fact that body condition is better in highland populations (Comas et al., 2014) and geckos in better body condition may divert more resources to fight parasites. Consequently, different conflicting effects could be acting: environmental conditions change with elevation, as well as gecko's body condition, population densities, and reptile communities. The contradictory results with respect to those reported in the literature suggest that elevational patterns in the lizard-mite interaction may be complex and specific for each system.

In conclusion, the findings suggest that the patterns of probability and intensity of infestation of mites parasitizing the Atlas day gecko did not vary with elevation, but are complex: factors encouraging a higher probability of infection not necessarily promoting higher intensity. Geckos in better body condition were less likely to be parasitized, probably as a consequence of higher investment in resistance against mites. However, on being parasitized, geckos in better body condition trended to harbour more mites, either as a consequence of a higher mortality of geckos in worse body condition, or because of a greater capacity in geckos in better condition to invest in tolerance to mites. Males were more likely to be parasitized than females. However, once infested, males and females did not differ in the intensity of the infestation.

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Variable	AIC	ΔAIC
	Probability of infection	
BCI, **sex**, altitude	105.65	0.00
BCI, **sex**	105.82	0.17
BCI, altitude	108.01	2.36
BCI	108.16	2.51
Sex, altitude	110.15	4.50
Sex, altitude	111.78	6.13
Altitude	111.97	6.32
	Intensity	
BCI	89.36	0.00
BCI, altitude	90.53	1.17
BCI, sex	91.33	1.97
Altitude	92.22	2.86
BCI, sex, altitude	92.46	3.10
Altitude, sex	93.88	4.52
Sex	95.28	5.92

Table 1: AIC values and AIC increment of the models done for probability of infection and intensity with the variables included in the models indicated, in bold those that were significant at $P < 0.05$.

FIGURES:

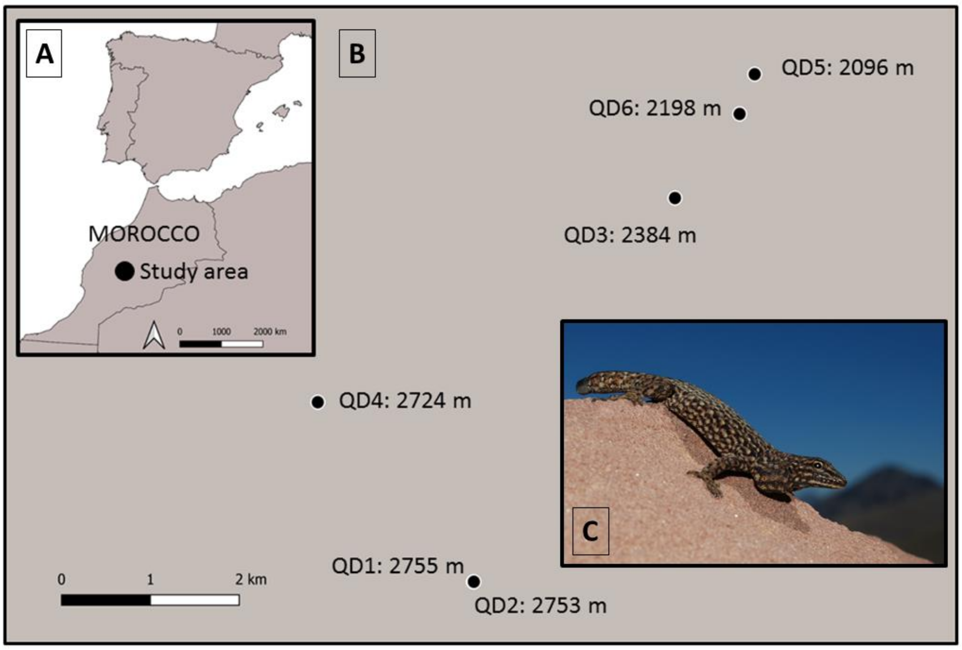

Figure 1 (A) Location of the study area in Morocco. (B) Spatial distribution of the six localities sampled, indicating their altitude above the sea level. Notice that QD1 and QD2 were so closed that the point was indistinguishable. (C) A photography of the Atlas day gecko.

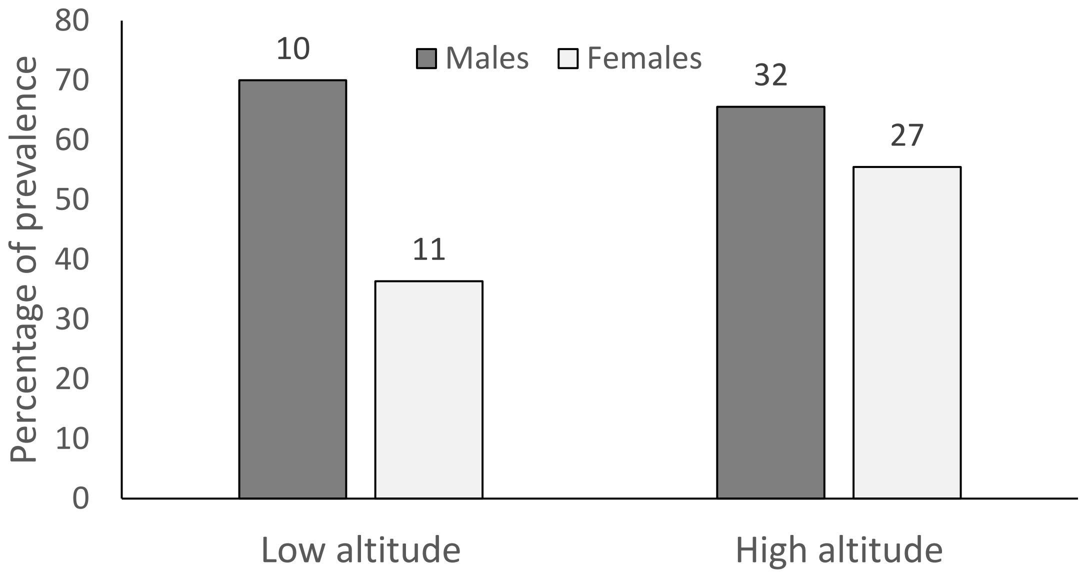

Figure 2 Prevalence (percentage of Atlas day geckos infested with mites) depending on elevation and sex (dark: males, white: females). The sample size is indicated over the bars.

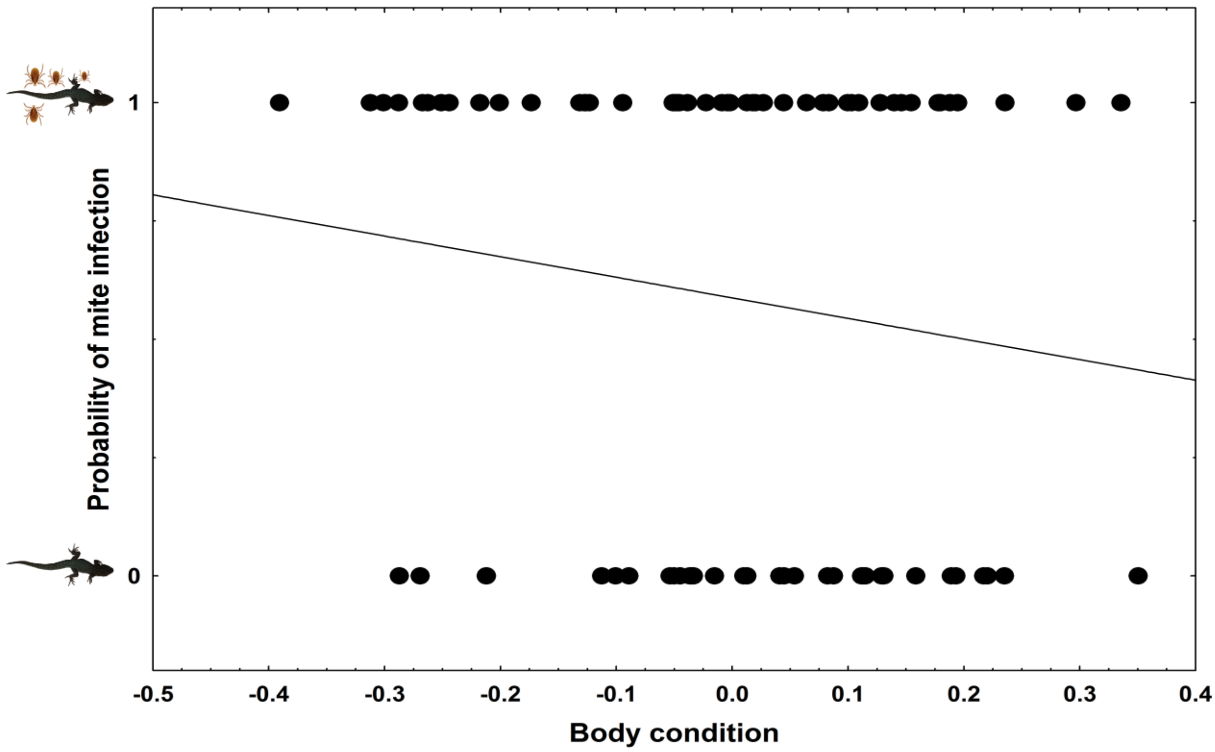

Figure 3 Relationship between the probability of mite infection and body condition: Atlas day geckos with lower values of body condition were more likely to be infested with mites.

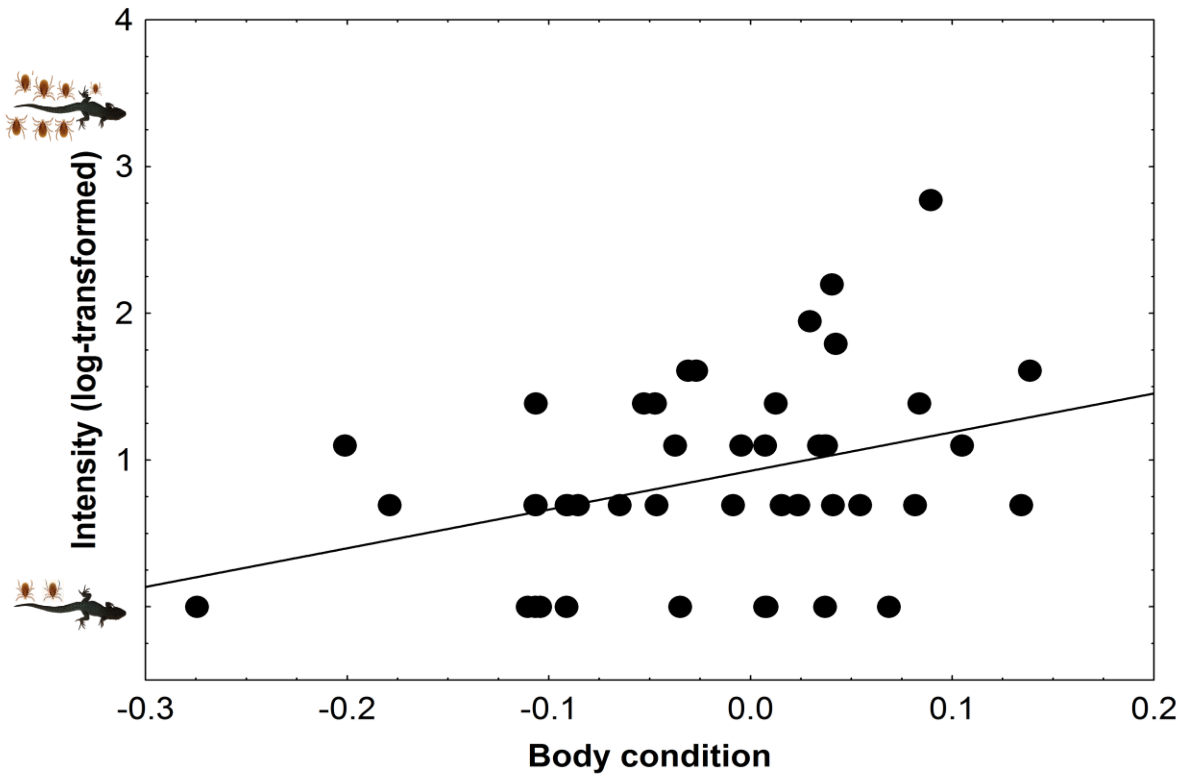

Figure 4 Relationship between intensity of mite infestation and Atlas day gecko's body condition.