Tick-tock, racing the clock: Parasitism is associated with decreased sprint performance in the Eastern Fence Lizard

Kristoffer H. Wild[1,2] & C.M. Gienger[2]

1. School of BioSciences, The University of Melbourne, Parkville, Victoria, Australia
2. Department of Biology and Center of Excellence for Field Biology, Austin Peay State University, USA

Abstract:
Host-parasite relationships are important components of ecological systems that influence the evolution of both hosts and parasites. High levels of ectoparasitic infections can disrupt host homeostasis, causing adverse effects on health and performance. However, the effects of natural ectoparasitic levels on host physiology are less understood, with most research designs implementing experimental or hormonal manipulations of hosts. In this study, we examined the interplay between tick parasitism and host characteristics on body condition and locomotor performance in Eastern fence lizards in natural settings. We found a higher frequency of tick infections in male lizards relative to females, with larger males being more likely to experience tick infection. Infected lizards had reduced locomotor performance. Together this appears to be an energetic trade-off between increased immune function and reduced locomotor performance, which is consistent with the immunocompetence-handicap hypothesis. Higher numbers of ticks on adult male lizards may be explained by age as well as the immunosuppressive effects of testosterone. Tick infection did not appear to reduce overall body condition of lizard hosts. Our findings shed light on the interplay between ectoparasitic infection, host characteristics, and locomotor performance under natural conditions. Such insights are crucial for understanding host-parasite dynamics and determining the trade-offs for hosts within ecological contexts.

Key words: immunocompetence-handicap hypothesis; sex; body size; locomotor performance; tick prevalence

1| Introduction:

Host-parasite relationships are a fundamental aspect of ecological systems and are shaped by the co-evolutionary trajectories of both hosts and parasites (Anderson & May, 1982; Minchella & Scott, 1991). Parasites exploit resources from their host and have the potential to disrupt behaviour and physiological function, which can ultimately compromise health, influencing survival and reproduction (Gordon, 1982; Veiga *et al.*, 1998; Moore, 2002; Finnerty, Shine, & Brown, 2018). Host responses to parasites can be nuanced and influenced by life history traits, such as reproductive strategies (Moore & Wilson, 2002) or hormonal fluctuations across different life stages (Foo *et al.*, 2017), which may dictate the degree of physiological investment in parasite defense mechanisms. While these interactions are often critical, they do not always translate into measurable impacts on host fitness (Paterson & Blouin-Demers, 2000; Conrad et al., 2023). This complexity of host-parasite dynamics highlights the need to consider a wide array of biological factors and ecological contexts to fully understand their impact on fitness consequences on hosts through time.

A complex interplay of factors determines ectoparasite (tick, mites, fleas, or lice) prevalence, including host species, sex, age, health, environment, and habitat. Host sex can influence parasite prevalence through hormonal variations that may affect immune responses and susceptibility to infection (Moller, Christe, & Lux, 1999; Foo *et al.*, 2017). Developmental processes can dictate host vulnerability across different life stages. For example, in organisms with longer lifespans, elements of the adaptive (acquired) immune system become more robust over time (Lochmiller & Deerenberg, 2000) with increasing exposure to pathogens, thus decreasing susceptibility to parasites (Boots & Bowers, 2004). Body condition, reflecting the host's overall health and nutritional status, can also be negatively impacted by parasitic infections as hosts use energy resources to fight infection rather than for other critical functions that benefit host fitness (Olsson *et al.*, 2000; Amo, López, & Martín, 2007). Other factors such as food availability or reproductive behaviours, can also modulate an individual's susceptibility to parasites, further complicating the dynamics of parasitism (Moore & Wilson, 2002). Finally extrinsic mechanisms such as habitat modification, fire, and rainfall can facilitate the abundance of parasites, and in some cases facilitate disease prevalence associated with ectoparasites (Berger *et al.*, 2014; Diuk-Wasser, Vanacker, & Fernandez, 2021; Gallagher *et al.*, 2022). Understanding the interactions between parasites and their effects on hosts within their natural environments can offer insights into the tradeoffs that drive host defenses and parasite strategies.

Trade-offs between immune function and growth/reproduction are central to the Immunocompetence-Handicap Hypothesis (ICHH), which postulates that the expression of sexually selected traits, driven by hormones, can negatively impact the host's immune function, thereby increasing vulnerability to parasitism (Hamilton & Zuk, 1982; Folstad & Karter, 1992). Current literature indeed presents mixed support for ICHH, where meta-analyses suggest that administration of exogenous testosterone correlates with an increase in parasitism (Roberts et al., 2004; Foo et al., 2017), but this relationship does not consistently emerge in studies with unmanipulated animals (Foo et al., 2017). However, meta-analytic work has shown that support for ICHHH in reptiles is species-specific (Roberts, Buchanan, & Evans, 2004). In reptilian hosts, experimental manipulations have shown support for the ICHH, where testosterone reduces immunocompetence and increases the incidence or severity of parasitism (Olsson *et al.*, 2000; Megía-Palma *et al.*, 2021). In lizards, locomotor performance is a sexually selected trait (Husak & Fox, 2008) that is strongly influenced by testosterone levels (Klukowski, Jenkinson, & Nelson, 1998; Mills *et al.*, 2008). Therefore, enhanced locomotor performance, driven in part by testosterone, may be accompanied by increased susceptibility to parasites such as ticks, resulting in a dynamic balance between sexual selection, performance, and survival. However trade-offs could occur with enhancement in locomotion, where increased mobility could increase the risk of parasite infestation with host mobility (Wieczorek *et al.*, 2020; Barrientos & Megía-Palma, 2021).

Most studies investigating the influence of tick parasitism on health and performance have been from experimental manipulation of tick load on hosts (Pittman, Pollock, & Taylor, 2013; Megía-Palma, Martínez, & Merino, 2018; Lanser, Vredevoe, & Kolluru, 2021) or through hormonal manipulations (Olsson *et al.*, 2000; Cox, Skelly, & John-Alder, 2005b; John-Alder *et al.*, 2009). Under natural settings, how host-parasite relationship varies with factors such as sex and age is understood (Amo *et al.*, 2007; Dudek *et al.*, 2016; Pollock & John-Alder, 2020), but there is limited information on how ectoparasites such as ticks can directly influence physiological traits for hosts *in situ* (but see Megía-Palma et al., 2020). Here, we investigate how tick infection varies across sex and body size, and test whether locomotor performance or body condition is affected by parasitism in Eastern Fence Lizards (*Sceloporus undulatus*). This species has pronounced sex and ontogenetic differences in hormonal profiles, including corticosterone and testosterone (Cox *et al.*, 2005a; John-Alder *et al.*, 2009), and hormonal manipulations in wild males (exogenous testosterone-implants) have been shown to increase rates of tick infection (Klukowski & Nelson, 2001). In this study, we tested four key predictions for how hosts are affected by naturally occurring tick infection: (1) that male and female lizards will show different prevalence of ticks; (2) that larger body size will be associated with a higher likelihood of tick infection; (3) that tick-infected lizards will exhibit reduced locomotor performance; and (4) that tick infection will influence the Body Condition Index (BCI) of the lizards. These data will help us understand the complex interplay between tick parasitism, host characteristics, and locomotor performance, thereby shedding light on the dynamics of host-parasite interactions in natural settings.

2| Methods

Field research was conducted at Land Between the Lakes National Recreation Area in Kentucky (United States), where *Dermacentor variabilis (*American Dog Tick) and *Amblyomma americanum* (Lone Star Tick) are common ectoparasites of *S. undulatus*. From May - September of 2014 and 2015, adult *S. undulatus* were captured by hand or by noosing. Morphological characteristics, including the enlarged base of the tail, femoral pores, and ventral colouration, were used to determine sex (John-Alder *et al.*, 2009). Snout-to-vent length (SVL), body mass, and hindlimb length were measured upon capture. Hindlimb length was defined as the greatest distance on the outstretched leg from the distal tip of the fourth toe to the point of insertion in the body wall. Lizards were measured to the nearest 0.1 mm for length and 0.25 g for mass. Capture locations were recorded with a handheld GPS (Garmin Fēnix® GPS). The number of ticks infecting each captured lizard was recorded in the field before each animal was placed in a cloth bag and transported to Hancock Biological Station (Murray, KY), where the ticks were recounted again before laboratory locomotor performance trials.

All locomotor performance trials were conducted within 24h of capture. Each lizard was placed individually into copper containers (repurposed autoclave pipette boxes; 4cm x 6cm x 25cm) and placed inside a lighted incubator (Percival I30-BLL) for 30 min. The incubator was maintained at 33°C (±1.0), the preferred temperature for *S. undulatus* (Angilletta, 2001). After 30min, each lizard was placed on a race track (2.4 x 0.2m) and encouraged to run by prodding with a soft-bristle paintbrush. Astroturf covered the race track floor, which was marked into 25cm segments. Each trial was recorded at a rate of 35 frames s^{-1} with a camera mounted 3m above the center of the race track. Lizards were raced three times, with trials separated by at least

30min for recovery. The quality of each sprinting trial was classified as "poor" or "good" (Van Berkum *et al.*, 1989). A poor trial was defined as a pause or reversal run by a lizard, and a good trial was defined as a continuous run by the lizard. A minimum of two good trials were required for an individual to be included in the analyses (Van Berkum *et al.*, 1989). Maximum sprint speed was defined as the single fastest 25cm interval of the trials, and maximum 2-meter run speed was the single fastest continuous 2-meter run of the trials. Videos were analyzed using Tracker Video Software (version 4.85; https://physlets.org/tracker/). Further details on video data collection can be found in Wild and Gienger (2018). Lizards were then marked with a unique toe clip and released back at their location of capture within 24h of initial capture.

All statistical analyses were conducted using the R environment, ver. 4.2.0 (www.r.-project.org), and significance was accepted at an α level of 0.05. We assessed the data for homogeneity of variances and normal distribution where relevant. If the data did not conform to these assumptions, we applied transformations to achieve approximate normality and variance homogeneity. For each sex, logistic regression was used to test if body size (SVL) predicted tick infection. Chi-square with Yates' correction was used to assess the independence of the prevalence of ticks observed between males and females while accounting for the total observations for each sex. Body condition index (BCI) was calculated from the residuals of an ordinary least squares linear regression of mass (g) on length (SVL) (Jakob, Marshall, & Uetz, 1996), and an Analysis of Variance was used to compare BCI measurements between uninfected lizards and infected lizards (≥ 1 tick). An Analysis of Covariance was used to compare individual performance measurements (maximum sprint speed and 2-meter run) between lizards infected and lizards uninfected with ticks. Hindlimb length was used as a covariate to remove the allometric effects of body size on performance (Wild & Gienger, 2018). Data, code, and additional resources are available at: https://github.com/kris-wild/Ticks_Wild_Gienger_2023.git.

3| Results

A total of 92 lizards were captured (females n = 38; males n = 54) during the 2014 and 2015 field seasons. There was a positive relationship between male body size, and the probability of tick infection ($F_{1,51}$ = 0.103, p = 0.045), where larger males had a higher probability of tick infection than smaller males (Fig. 1A). For females, there was no relationship between body size and the probability of tick infection ($F_{1,37}$ = -0.008, p = 0.928; Fig. 1B). The probability of tick infection was sex-specific, with the frequency of tick infection being more than two times higher in males (n = 20; 37%) than in females (n = 5; 13%). Sex differences in tick infection between males and females was significant (x^2 = 9; df = 1; n = 92; p = 0.003). Due to the low infection frequency for females, they were not included in analysis for sprint performance. A total of 54 male lizards were used in locomotor performance analysis. The infection rate for males ranged from one to seven ticks per individual. Maximum sprint speed was higher in uninfected lizards (LS mean = 2.741m/sec, 95%CI: 2.62 - 2.86) in comparison to infected lizards (LS mean = 2.48m/sec, 95%CI: 2.32 - 2.64; $F_{2,51}$ = 16.12; p = 0.016; Fig. 2a). Maximum 2-meter run speed was higher in uninfected lizards (LS mean = 1.942m/sec, 95%CI: 1.82 - 2.07) than in infected lizards (LS mean = 1.613m/sec, 95%CI: 1.45 - 1.78; $F_{2,51}$ = 15.01; p = 0.003; Fig. 2b). There were no differences in body condition indices between uninfected and infected lizards ($F_{2,51}$ = 0.025; p = 0.875).

4|Discussion

Our study clearly demonstrates that lizards infected with ticks had lower locomotor performance than noninfected lizards, and that tick prevalence differed between sexes and increased with body size for male lizards. Specifically, there was a negative relationship between prevalence and two estimates of locomotor performance (maximum sprint speed & 2-meter run speed) for male *Sceloporus undulatus.* Our findings are congruent with predictions of the Immunocompetence Handicap Hypothesis (ICHH), with male lizards exhibiting a higher tick infestation rate than females, which may be indicative of the immunosuppressive effects of testosterone (Olsson *et al.*, 2000; Roberts *et al.*, 2004). While we did not directly measure immune function or testosterone levels, our results are supported by a body of literature that establishes an effect hormone level, immune function, and tick load have in age or sex in this species (Klukowski & Nelson, 2001; Cox *et al.*, 2005b; John-Alder *et al.*, 2009). Other physiological parameters, such as reduction in hematocrit levels, could explain the negative effect of locomotor performance from tick infestation (Dunlap & Mathies, 1993; Lanser *et al.*, 2021). Together this suggests there may be a functional trade-off in parasitized hosts, which may be a product of immune function differences between sex and age, or direct physiological consequences from tick prevalence.

Male bias in parasite prevalence can be mediated by sex differences in hormone levels has been documented in other lizards (Alleklint-Eisen & Eisen, 1999; Salkeld & Schwarzkopf, 2005; Václav, Prokop, & Fekiač, 2007). The sex-specific differences in endocrine systems and behaviours for *S. undulatus* (Klukowski & Nelson, 2001; Haenel, Smith, & John-Alder, 2003; Cox *et al.*, 2005a) could provide a mechanism for our observed sex differences in tick prevalence. For example, male *S. undulatus* have higher testosterone levels (Cox *et al.*, 2005a), move considerably more often, move over longer distances (Veiga *et al.*, 1998; Belliure, Smith, & Sorci, 2004), and have larger home ranges than females (Haenel *et al.*, 2003). Consequently, a combination of high testosterone and increased activity could increase exposure to parasites seeking hosts.

Differences in endocrine systems between juvenile and adult lizards play a significant role in variation in traits throughout ontogeny (Cox *et al.*, 2005b; Miles *et al.*, 2007; John-Alder *et al.*, 2009), and not surprisingly, adult *S. undulatus* have higher testosterone than juveniles (Cox *et al.*, 2005a). Studies using exogenous implants have shown positive effects of testosterone on male fitness by enhancing endurance, stimulating reproductive activity, expanding home-range areas to include more females, and ultimately giving higher reproductive success (John-Alder *et al.*, 2009). However, high testosterone also imposes fitness costs by lowering resistance to parasitism, inhibiting growth, and reducing survival rates (Salvador *et al.*, 1996; Klukowski & Nelson, 2001; John-Alder *et al.*, 2009). Evidence across other taxa - birds, fishes, mammals, and insects - supports that immunocompetent males generally have higher success in mating and offspring production than immunocompromised males (Moller *et al.*, 1999). Together our data indicate that trade-offs exist in male performance, where the effects of high testosterone levels potentially lead to increased sprint speed but also increased susceptibility to parasitic infection.

Indeed, the impact of ticks on whole-animal performance is an underexplored area in ecological studies (*but see* Main & Bull, 2000). We have shown that, even in small numbers, ticks may alter physiological function, resulting in lower performance. Parasitized lizards in this study ranged from one to seven ticks, with an average of three ticks on each infected lizard. A female tick (*Amblyomma spp.*) takes about 7 to 12 days to become fully engorged, extracting an average of 11mg of blood (Bullard *et al.*, 2016). If blood makes up about 5-8% of a lizard's body mass (Prosser & Brown, 1961), then an average-sized lizard in our study (9.5g) could potentially lose 1-2% of blood for each engorged tick. This blood loss can have significant physiological consequences, including anemia, where a reduction of oxygen-carrying capacity could explain the lower levels of locomotor performance, such as sprint speed (Lehmann, 1993). Additionally, a reduction in hematocrit levels associated with tick prevalence could provide as a mechanism for poor locomotor performance (Dunlap & Mathies, 1993; Lanser *et al.*, 2021). In an experimental study of Sleepy Lizards (*Tiliqua rugosa*), Main and Bull (2000) allowed ticks to attach and engorge on lizard hosts, and those with ticks had a significant reduction in sprint and endurance performance than lizards with no ticks. Our results similarly reflect those findings, however, *Tiliqua rugosa* are large-bodied lizards (~650g) with relatively few predators as adults and rarely require sprinting to escape predators (Bull & Freake, 1999). In contrast, adult *S. undulatus* are considerably smaller and are frequently killed by fast-moving thermophilic snakes and predatory birds (Crowley, 1985). Furthermore, lizards infested with ticks have been shown to select cooler temperatures, which could be a strategy to conserve energy to overcome the tick infestation (Megía-Palma *et al.*, 2020). Together, smaller lizard species that experience high tick loads may be at higher risk of predation due to a reduction in locomotor performance or may have to adjust other behaviours to avoid parasitism risk.

Contrary to our findings, other studies have shown that ectoparasite infestation negatively affects or is associated with low body condition in reptiles (Dunlap & Mathies, 1993; Olsson *et al.*, 2000; Madsen, Ujvari, & Olsson, 2005). It appears that ticks do not markedly reduce host health, as evident by the lack of differences in body condition between uninfected and infected lizards. Conrad et al. (2023) found that mite parasitism did not significantly affect growth or body condition in *S. undulatus,* suggesting that some hosts may employ effective compensatory strategies to deal with parasitic infection. Our data show that other factors, such as the sex and size of lizard hosts, may play a more significant role than relative condition in tick infection rates. Other factors such as seasonality of parasitism and how parasitism may vary by sex would be fruitful area to investigate. A recent investigation into mite parasitism of *S. undulatus* across different seasons found that mite loads vary seasonally, with the highest loads in the warmer months, and are influenced by environmental mite abundance (Pollock & John-Alder, 2020). More specifically adult females experienced higher mite loads than males during early summer, while yearling males had higher mite loads than females later in the season (Pollock & John-Alder, 2020). Such complex interactions should be considered in future studies when investigating how larger ectoparasites, such as ticks, vary seasonally between sex and age. Although tick infection appears to affect sprint speed, it did not appear to be a factor in the overall body condition of the host, indicating a potential trade-off between physical performance and susceptibility to parasitism.

Data Availability:

Data, code and additional resources are available on GitHub : https://github.com/kris-wild/Ticks_Wild_Gienger_2023.git

Acknowledgements:

Support was provided by the Center of Excellence for Field Biology and Department of Biology at APSU. We thank the US Forest Service and Land Between the Lakes National Recreation Area for access to study sites. Logistical support and research facilities were provided by Hancock Biological Station (Murray State University). We thank Bryan Gaither for assistance in constructing research equipment. For help in both the laboratory and field, we thank James Flaherty, Amanda Mosher, Brooke Bedal, Savannah Price, Dustin Owen, Andy Mueller and Mallory Strawn-Wild. Finally, this work would not have been possible without the help of Kentucky Gentleman and Lizardpalooza 2014-15. Research was conducted under approved APSU IACUC protocol #14.005.

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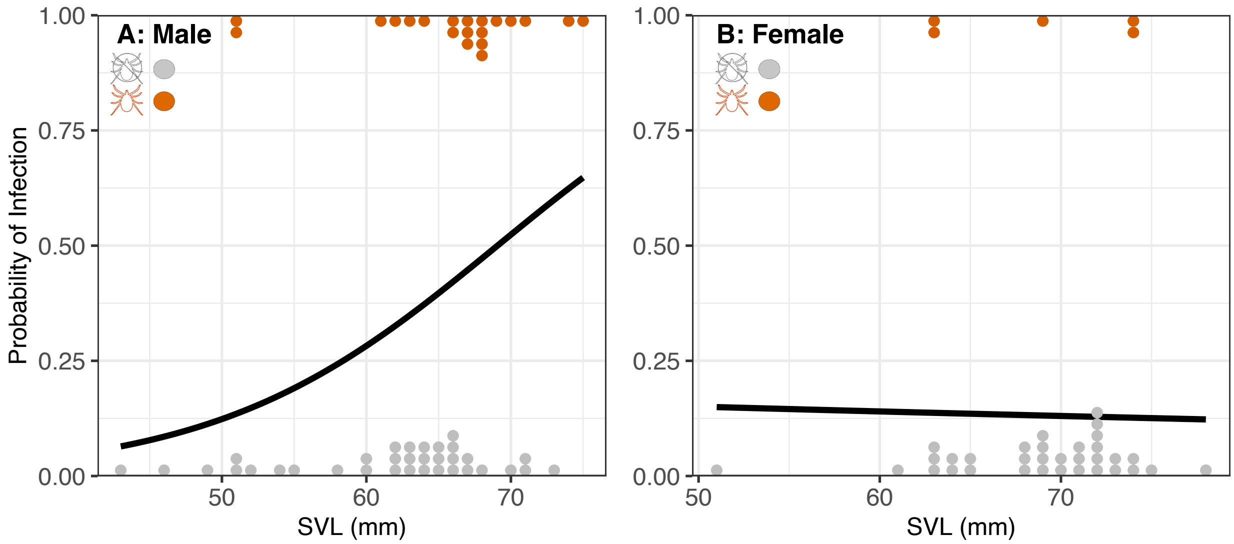

Figure 1. Relationship between body size (SVL) and probability of tick infection for male (A) and female (B) Eastern Fence Lizards. The line represents the probability function from logistic regression. Raw data points are shown with circles that distinguish if lizards were infected by ticks (orange) or lizards that were not (grey).

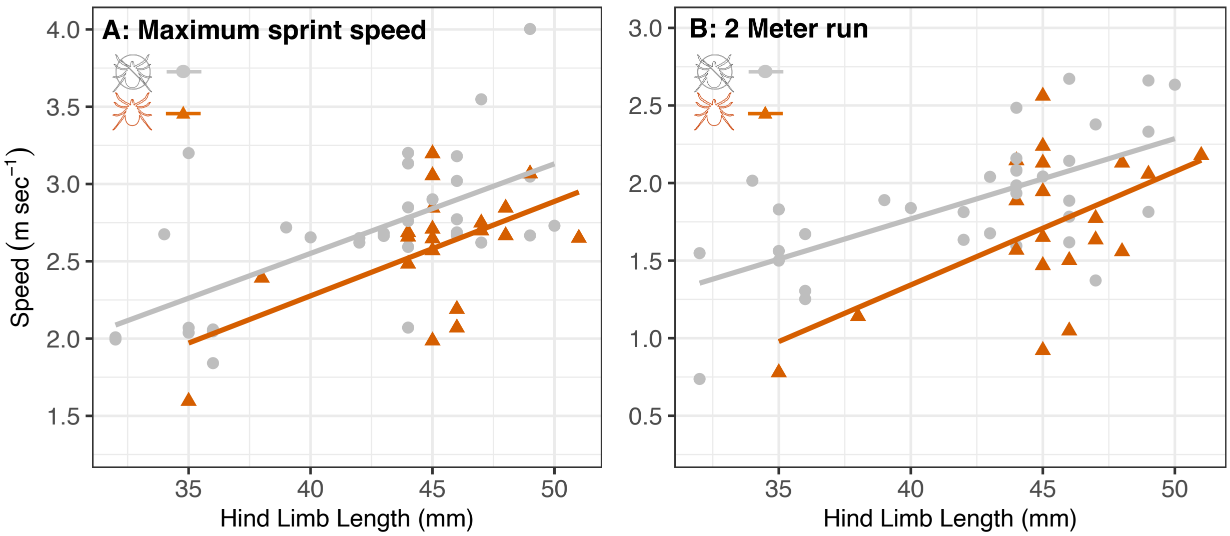

Figure 2. ANCOVA results of maximum sprint speed (a) and two-meter run speed (b) of male lizards. Hindlimb length (mm) was used as a covariate to remove the effect of body size on performance. The presence of ticks (yellow) significantly reduced maximum sprint speed ($p < 0.01$) and two-meter run speed ($p = 0.003$) in comparison to lizards with no ticks (grey).