**Tick infection is sex-specific and is associated with low locomotor performance in the eastern fence lizard**

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**Abstract (200 words):**

Host-parasite relationships are vital components of ecological systems, influencing the evolution of both hosts and parasites. Ectoparasitic tick infections can disrupt host homeostasis, leading to varying effects on host health and performance. In this study, we examined the interplay between tick infection and host characteristics (sex, body size) in Eastern fence lizards (*Sceloporus undulatus*) to understand the effects on body condition and locomotor performance. We found a higher prevalence of tick infections in male lizards, with larger males were more susceptible to tick infection. Infected lizards exhibited reduced locomotor performance compared to uninfected ones, likely due to the energy trade-off between immune function and dealing with parasitic stress. However, tick infection did not impact the overall health condition of the lizards. Our findings shed light on the intricate relationships between ectoparasitic infection, host characteristics, and locomotor performance in natural conditions. Together, we suggest that higher prevalence of tick infections in adult male lizards may be explained by the immunosuppressive effects of testosterone. Such insights are crucial for understanding host-parasite dynamics and managing ectoparasite prevalence in ecological contexts.

# 1| Introduction:

Host-parasite relationships have been a well-documented phenomenon across taxa, and relationships are a fundamental aspect of ecological systems that are responsible in shaping the evolutionary trajectories of both hosts and parasites 1,2. In brief, parasites exploit resources from their host, and during this exchange, parasites disrupt the host's homeostasis, which can ultimately result in negative effects on the host's health3. A spectrum of host responses to parasites does exist, where infection can have little to no effect on host health or where infection can result in deleterious effects to host health4–7. Currently, there is limited work clearly linking how natural levels of ectoparasitic infection impact hosts regarding sex, age, body condition, and behaviours. Depending on the context, these interactions can have profound impacts on host fitness, influencing survival and reproduction6,8,9.

Ectoparasite prevalence, a critical aspect of host-parasite dynamics, is shaped by a complex interplay of factors, including host sex, age, health, and habitat. Host sex can influence parasite load, as hormonal variations may affect immune responses and susceptibility to infection10,11. Life stage is another determinant, as physiological changes across different stages can alter host vulnerability to parasites12,13. Body condition, reflecting the overall health and nutritional status of the host, can also be negatively impacted by parasitic infections14,15. Lastly, habitat can affect exposure to parasites and the host's ability to evade or cope with them14. However, these relationships are not straightforward and often involve trade-offs1. For instance, a host's investment in growth or reproduction might compromise its immune function, increasing susceptibility to parasites9,16. More specifically, meta-analytic and experimental manipulations have indicated support for the immunocompetence-handicap hypothesis (ICHH), where testosterone reduces immunocompetence and increases parasitism across reptile species15,16. Similarly, ectoparasites might face trade-offs between virulence and transmissibility17. Understanding these intricate relationships and trade-offs is crucial for predicting and managing ectoparasite prevalence in various ecological contexts.

Most studies investigating the influence of ticks on health and performance are derived from experimental manipulation of ticks on hosts18,19 or through hormonal manipulations15,20,21. Under natural conditions there is limited information on how host-parasite relationship varies across different factors, such as sex, age, and if infection influences host physiological traits. Here, we investigate how tick infection varies across sex, body size, and test if locomotor performance is affected in eastern fence lizard (*Sceloporus undulatus)*. This species demonstrates sex differences in hormonal traits, corticosterone and testosterone21,22 and hormonal manipulations have been shown to increase tick frequencies23. Suggesting that the Immunocompetence Handicap Hypothesis (ICHH) may be at play, where testosterone reduces immunocompetence and increases parasitism. This study aims to quantify the complex interplay between host characteristics, such as sex and body size, and test if tick infection affects host body condition and locomotor performance. Together, these data will provide valuable insights into host-parasite dynamics under natural conditions.

**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*.During the Spring and Summer of 2014 and 2015, adult male and female *S. undulatus* were captured by hand or by noosing. Morphological characteristics including enlarged base of the tail, femoral pores, and ventral colouration, were used to determine sex. Upon capture, snout-to-vent length (SVL), body mass, and hindlimb length were measured for all individuals. 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) which was then placed inside a lighted incubator (Percival I30-BLL) for 30min. The incubator maintained (33°C ±1.0) which is the preferred temperature of *S. undulatus* (Angilletta, 2001). After 30min, each lizard was encouraged to run on a race track (2.4 x 0.2m) by prodding with a soft-bristle paintbrush. The race track floor was covered by Astroturf that was marked into 25cm segments. Each trial was recorded with a camera that was mounted 3m above the center of the race track to ensure visibility of the whole race track. The camera recorded at a rate of 35 frames s-1. 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”24. Where 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 needed for an individual to be included in analyses. Maximum sprint speed was defined as the single fastest 25cm interval of the trials, and maximum 2-meter run speed (2 meter run) was the single fastest continuous 2 meter run speed of the trials. Videos were analysed using Tracker Video Software (version 4.85; www.cabrillo.edu/tracker). Further details on video data collection can be found in Wild & Gienger25. Lizards were then marked with a unique toe clip and released back at their location of capture within 24h of initial capture.

All statistical analysis were conducted using the R environment, ver. 4.2.0 ([www.r.-project.org](http://www.r.-project.org)), and significance was accepted at an α level of 0.05. Chi-square with Yates’ correction was used to assess the independence of the proportion of ticks observed between males and females. A logistic regression was used to test if body size (SVL) predicted the number of ticks found on an individual. Body condition index (BCI) was calculated from the residuals of an ordinary least squares linear regression of mass (g) on length (SVL), and an Analysis of Variance was used to compare BCI measurements between uninfected lizards and infected lizards (1 ≥ ticks). An Analysis of Covariance was used to compare individual performance measurements (maximum sprint speed and 2-meter run) between lizards infected (1 ≥ ticks) and lizards uninfected with ticks. Hindlimb length was used as a covariate to remove the potential effects of body size on performance25.

**3| Results**

A total of 92 lizards were captured (females n= 38; males 54) during the 2014 and 2015 field seasons. The frequency of tick infections was highly sex-specific, with the frequency of tick infection being over 2 times higher in males (n = 20; 37%) than in females (n = 5; 13%). Females were therefore precluded from further statistical analysis because the difference in tick infections was significantly different between sex (x = 9; df = 1; n = 92; p = 0.003). The infection rate for males ranged from one to seven ticks per individual. There was a positive relationship between male body size and the number of ticks (F = 0.103, p = 0.045), where larger males had a higher probability of tick infection than smaller males (Fig. 1). Maximum sprint speed was significantly higher in uninfected lizards (LS mean = 2.741m/sec) in comparison to infected lizards (LS mean = 2.48m/sec; F = 16.12; p = 0.016; Fig. 2a). Maximum 2-meter run speed was significantly higher in uninfected lizards (LS mean = 1.942m/sec) than in infected lizards (LS mean = 1.613m/sec; F = 15.01; p = 0.003; Fig. 2b). There were no differences in body condition indices between uninfected and infected lizards (F = 0.025; p = 0.875).

**4|Discussion**

Our study demonstrates that ectoparasite (tick) prevalence differed between sex and body size, and lizards infected with ticks had different locomotor performance than noninfected lizards. Specifically, there was a negative relationship between parasite prevalence and two estimates for locomotor performance (maximum sprint speed & 2-meter run speed) for male *Sceloporus undulatus.* Together these clear differences in infection probability between sex and performance may be driven by behavioural and/or physiological differences between male and female lizards. Our results of this study align with the Immunocompetence Handicap Hypothesis (ICHH) by demonstrating a higher prevalence of tick infections in male lizards, potentially due to the immunosuppressive effects of testosterone15,16. Furthermore, the significant reduction in both performance metrics in infected lizards, regardless of their body condition, could be a consequence of the energy trade-off between maintaining immune function and dealing with the physiological stress of parasitic infection, another key aspect of the ICHH26.

The positive correlation between male body size and tick infection rate could be explained by the ICHH, where larger males with higher testosterone levels, may have compromised immune systems, making them more susceptible to parasites16. Physiological differences linked to endocrine systems between juvenile and adult male *S. undulatus* lizards play a significant role in variation in their life-history traits 20,21. More specifically, higher testosterone levels can be found in adults in comparison to juveniles22. Immunosuppression associated with differences in testosterone has been shown to attribute to higher intensities of ticks found in lizards with higher levels of testosterone15.Moreover, in comparison to individuals with low testosterone, lizards with elevated testosterone have been shown to have lower growth, higher mortality rates, higher energetic costs, and higher costs associated with reproduction21,23,27. There is evidence across other taxa (birds, fishes, mammals, and insects) that immunocompetent males generally have higher success in mating and offspring production11. Collectively, these findings suggest the existence of trade-offs in male *S. undulatus*, particularly between behavioural traits that enhance life-history productivity and the increased risk of parasitism. There is evidence that this balance is primarily influenced by the testosterone levels in these lizards, highlighting the intricate relationship between endocrine systems, immune function, and life-history traits.

Male bias in parasite prevalence or parasite abundance has been documented in other lizards28–30. The results of our study show that ticks are more commonly found on male lizards compared to females. Male and female *S. undulatus* have different endocrine systems and behaviours22,23,31, which together, could provide a mechanism for the observed differences in tick prevalence between sex. For example, male *S. undulatus* have higher testosterone levels22 and larger home ranges than females31. High testosterone in males may directly suppress the immune response, indirectly influence the host's energy expenditure, or stimulate males to move more frequently or over longer distances 9,32. Consequently, this increased activity could heighten exposure to parasites that are seeking hosts33. Additional research is needed to determine the impact of hormonal and behavioural variations on the susceptibility to tick infections in lizards and to determine if these effects vary between the sex.

Indeed, the impact of ticks on individual performance metrics in host animals is an underexplored area in ecological studies (*but see*18), yet in reasonable numbers, it is conceivable that ticks can alter physiological aspects that would result in a reduction in performance. Parasitized lizards in this study ranged from one to seven ticks, with an average of three ticks on each infected lizard. An engorged female tick (*Amblyomma spp.*) takes about 7 to 12 days to engorge up to 11mg34. If blood makes up about 5-8% of a lizard's body mass35, then a small-bodied lizard can lose a large amount of blood for each engorging female. 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, such as anemia, where a reduction of oxygen-carrying capacity of the blood could explain the overall lower levels of locomotor performance36. In an experimental study where ticks were allowed to attach and engorge on lizard hosts, lizards with ticks had a significant reduction in sprint and endurance performance than lizards with no ticks18. To our knowledge, this is the only experimental manipulation study to show a negative correlation between individual sprint and endurance performance that is associated with tick prevalence. Our results support the findings of Main & Bull18; however, *Tiliqua rugosa* are large-bodied lizards (~650g) and have relatively few predators as adults37. In contrast, adult *S. undulatus* are considerably smaller and are frequently preyed upon by thermophilic snakes and birds38. Thus, individuals with high tick loads and lower locomotor performance may be more at risk of predation.

Contrary to our findings, other studies have shown that ectoparasite infestation negatively affected body condition in reptiles15,39,40. Considering the findings from our study, it appears that ticks do not selectively infect hosts based on their health status. This is evident by the lack of significant differences in body condition indices between uninfected and infected lizards, even though infected lizards exhibited slower sprint and run speeds. This aligns with the findings of previous work, which suggested that ticks do not preferentially feed on healthier hosts, but the health of their hosts can affect the speed at which ticks could feed19. Experimentally testing how the duration or the frequency of tick infection influences physiological traits will provide promising insights into the consequences of such effects. Finally, the results from our study further suggest that factors such as the sex and size of the lizards may play a more significant role in tick infection rates. Therefore, while tick infection does have an impact on the lizards' speed, it does not appear to be related to the lizards' overall health condition.

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Figure 1. Relationship between the probability of tick infection and body size (SVL) for male lizards. The line represents the probability function from logistic regression, and light grey bands represent 95CI of model fit. Raw data points are shown with circles that distinguish if lizards were infected by ticks (yellow) 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 size on performance. The presence of ticks (yellow) significantly reduced maximum sprint speed (p < 0.01) and two-meter run speed (p = 0.02) in comparison to lizards with no ticks (grey).