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

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**Abstract (200 words):**

Host-parasite relationships are important components of ecological systems, influencing the evolution of both hosts and parasites. High levels of ectoparasitic tick infections can disrupt host homeostasis, causing adverse effects on host health and performance. In this study, we examined the interplay between tick parasitism and host characteristics (sex, body size) on body condition and locomotor performance in Eastern fence lizards (*Sceloporus undulatus*). We found a higher prevalence of tick infections in male lizards relative to females, with larger males being more likely to experience tick infection. Infected lizards appear to exhibit an energetic trade-off between increased immune function and reduced locomotor performance, which is consistent with the immunocompetence-handicap hypothesis (ICHH). Higher prevalence of tick infections in adult male lizards may be explained by age as well as the immunosuppressive effects of testosterone. However, tick infection did not appear to reduce overall body condition of the lizards. Our findings shed light on the interplay between ectoparasitic infection, host characteristics, and locomotor performance in natural conditions. Such insights are crucial for understanding host-parasite dynamics and managing ectoparasite prevalence in ecological contexts.

I added Garrido and Perez (2013), Ekner-Grzyb etal (2013), and Orton et al. (2019) to literature and Mendeley. These are directly relevant to sprinting/parasitism.

# 1| Introduction:

Host-parasite relationships have been a well-documented phenomenon across taxa and are a fundamental aspect of ecological systems that shape the evolutionary trajectories of both hosts and parasites 1,2. Parasites exploit resources from their host, and have the potential to disrupt host homeostasis, which can ultimately result in adverse effects on host health3influencing survival and reproduction4–6.

A complex interplay of factors, including host, sex, age, health, and habitat shapes ectoparasite prevalence. Host sex can influence parasite load, as hormonal variations may affect immune responses and susceptibility to infection7,8. Development can dictate physiological changes across different life stages and alter host vulnerability to parasites9,10. Body condition, reflecting the overall health and nutritional status of the host, can also be negatively impacted by parasitic infections11,12. Lastly, habitat can affect exposure to parasites and the host's ability to evade or cope with them11.

However, these relationships are more complex and often involve trade-offs1. For instance, a host's investment in growth or reproduction might compromise its immune function, increasing susceptibility to parasites6,13. More specifically, meta-analytic and experimental manipulations have supported the Immunocompetence-Handicap Hypothesis (ICHH), where testosterone reduces immunocompetence and increases incidence or severity of parasitism. Similarly, ectoparasites might face trade-offs between virulence and transmissibility14.

Most studies investigating the influence of tick parasitism on health and performance are derived from experimental manipulation of ticks on hosts15,16 or through hormonal manipulations12,17,18. Under natural conditions, there is limited information on how the host-parasite relationship varies with factors such as sex and age, and whether infection influences host physiological traits. Here, we investigate how tick infection varies across sex and body size, and test if locomotor performance is affected in Eastern Fence Lizards (*Sceloporus undulatus*). This species demonstrates sex differences in hormonal traits, including corticosterone and testosterone18,19, and hormonal manipulations (what kind? increased test?) have been shown to increase tick frequencies20. 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.

**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 *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 30 min. The incubator maintained (33°C ±1.0) which is the preferred temperature of *S. undulatus* (Angilletta, 2001). After 30 min, each lizard was placed on a race track (2.4 x 0.2m) and encouraged to run 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 entire race track. The camera recorded at a rate of 35 frames s-1. Lizards were raced three times, with trials separated by at least 30 min for recovery. The quality of each sprinting trial was classified as “poor” or “good”21. 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 25 cm interval of the trials, and maximum 2-meter run speed was the single fastest continuous 2 meter run 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 & Gienger22. Lizards were then marked with a unique toe clip and released back at their location of capture within 24 h 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 performance22.

**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 lower 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 reduction in 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 testosterone12,13. Furthermore, the significant reduction in both sprint 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 ICHH23.

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 parasites13. 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 17,18. More specifically, higher testosterone levels can be found in adults in comparison to juveniles19. Immunosuppression associated with differences in testosterone has been attributed to higher numbers of ticks found in lizards with higher levels of testosterone12.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 reproduction18,20,24. There is evidence across other taxa (birds, fishes, mammals, and insects) that immunocompetent males generally have higher success in mating and offspring production8. 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 lizards25–27. 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 behaviours19,20,28, which together, could provide a mechanism for the observed differences in tick prevalence between sex. For example, male *S. undulatus* have higher testosterone levels19 and larger home ranges than females28. 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 6,29. Consequently, this increased activity could increase exposure to parasites that are seeking hosts30. 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*15), 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. A female tick (*Amblyomma spp.*) takes about 7 to 12 days to become fully engorged, extracting up to (average?) 11 mg of blood31. If blood makes up about 5-8% of a lizard's body mass32, then a small-bodied lizard can lose considerable 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 performance33. In an experimental study, Main and Bull (2000) allowed ticks to attach and engorge on lizard hosts, and lizards with ticks had a significant reduction in sprint and endurance performance than lizards with no ticks15. Our results support the findings of Main & Bull15; however, *Tiliqua rugosa* are large-bodied lizards (~650g) and have relatively few predators as adults34 and rarely require sprinting to outrun predators. In contrast, adult *S. undulatus* are considerably smaller and are frequently preyed upon by thermophilic snakes and birds35. 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 reptiles12,36,37. 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 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 feed16. 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.

Literature cited

1. Anderson RM, May RM. Coevolution of hosts and parasites. Parasitology. 1982;85(2):411–26.

2. Minchella DJ, Scott ME. Parasitism: a cryptic determinant of animal community structure. Trends Ecol Evol. 1991;6(8):250–4.

3. Moore J. Parasites and the Behavior of Animals. 1st ed. Oxford: Oxford university press; 2002.

4. Lee KH, Whiting MJ, Leu ST. Are whole-organism performance and thermal preference linked to endo- and ectoparasites in a short-lived lizard? Ethology. 2023 ;129:432–3.

5. Sorci G, Clobert J, Michalakis Y. Cost of Reproduction and Cost of Parasitism in the Common Lizard, Lacerta vivipara. Oikos. 1996;76(1):121–30.

6. Gordon DM. Processes influencing the distribution of parasite numbers within host populations with special emphasis on parasite-induced host mortalities. Parasitology. 1982;85(2):373–98.

7. Knudsen R, Amundsen A, Klemetsen A. Parasite-induced host mortality: indirect evidence from a long-term study. Environ Biol Fishes. 2002;64:257–65.

8. Finnerty PB, Shine R, Brown GP. The costs of parasite infection: Effects of removing lungworms on performance, growth and survival of free-ranging cane toads. Funct Ecol. 2018;32(2):402–15.

9. Veiga JP, Salvador A, Merino S, Puerta M. Reproductive effort affects immune response and parasite infection in a lizard: a phenotypic manipulation using testosterone. Oikos. 1998;82(2):313–8.

10. Foo YZ, Nakagawa S, Rhodes G, Simmons LW. The effects of sex hormones on immune function: a meta-analysis. Biological Reviews. 2017;92(1):551–71.

11. Moller AP, Christe P, Lux E. Parasitism, host immune function, and sexual selection. Source: The Quarterly Review of Biology. 1999;74(1):3–20.

12. Hudson PJ, Dobson AP. Host-parasite processes and demographic consequences In: Host–parasite evolution. General principles and avian models. 7th ed. Clayton D, Moore J, editors. Host-parasite evolution: general principles and avian models. New York: Oxford University Press ; 1997. 128–154 p.

13. Hawlena H, Abramsky Z, Krasnov BR. Ectoparasites and age-dependent survival in a desert rodent. Oecologia. 2006;148(1):30–9.

14. Amo L, López P, Martín J. Habitat deterioration affects antipredatory behavior, body condition, and parasite load of female *Psammodromus algirus* lizards. Can J Zool. 2007;85(6):743–51.

15. Olsson M, Wapstra E, Madsen T, Silverin B. Testosterone, ticks and travels: A test of the immunocompetence-handicap hypothesis in free-ranging male sand lizards. Proceedings of the Royal Society B: Biological Sciences. 2000;267(1459):2339–43.

16. Roberts ML, Buchanan KL, Evans MR. Testing the immunocompetence handicap hypothesis: A review of the evidence. Anim Behav. 2004;68(2):227–39.

17. Choisy M, Brown SP, Lafferty KD, Thomas F. Evolution of trophic transmission in parasites: why add intermediate hosts? American Naturalist. 2003;162:172–81.

18. Main A, Bull MC. The impact of tick parasites on the behaviour of the lizard *Tiliqua rugosa*. Oecologia. 2000;122:574–81.

19. Pittman W, Pollock NB, Taylor EN. Effect of host lizard anemia on host choice and feeding rate of larval western black-legged ticks (*Ixodes pacificus*). Exp Appl Acarol. 2013;61(4):471–9.

20. Cox RM, Skelly SL, John-Alder HB. Testosterone inhibits growth in juvenile male eastern fence lizards (*Sceloporus undulatus*): implications for energy allocation and sexual size dimorphism. Physiological and Biochemical Zoology. 2005;78(4):531–45.

21. John-Alder HB, Cox RM, Haenel GJ, Smith LC. Hormones, performance and fitness: Natural history and endocrine experiments on a lizard (*Sceloporus undulatus*). Integr Comp Biol. 2009 Oct;49(4):393–407.

22. Cox RM, Skelly SL, Leo A, John HB. Testosterone regulates sexually dimorphic coloration in the Eastern Fence Lizard. Copeia. 2005;2005(3):597–608.

23. Klukowski M, Nelson CE. Ectoparasite loads in free-ranging northern fence lizards, *Sceloporus undulatus hyacinthinus*: Effects of testosterone and sex. Behav Ecol Sociobiol. 2001;49(4):289–95.

24. Van Berkum FH, Huey RB, Tsuji JS, Garland T. Repeatability of individual differences in locomotor performance and body size during early ontogeny of the lizard *Sceloporus occidentalis*. Funct Ecol. 1989;3(1):97–105.

25. Wild KH, Gienger CM. Fire-disturbed landscapes induce phenotypic plasticity in lizard locomotor performance. J Zool. 2018;305(2):96–105.

26. Alonso-Alvarez C, Bertrand S, Faivre B, Chastel O, Sorci G. Testosterone and oxidative stress: The oxidation handicap hypothesis. Proceedings of the Royal Society B: Biological Sciences. 2007;274(1611):819–25.

27. Salvador A, Veiga JP, Martin J, Lopez P, Abelenda M, Puerta M. The cost of producing a sexual signal: testosterone increases the susceptibility of male lizards to ectoparasitic infestation. Behavioral Ecology. 1996;7(2):145–50.

28. Alleklint-Eisen LT¨, Eisen RJ. Abundance of ticks (Acari: Ixodidae) infesting the western fence lizard, Sceloporus occidentalis, in relation to environmental factors. Exp Appl Acarol. 1999;23:731–40.

29. Václav R, Prokop P, Fekiač V. Expression of breeding coloration in European Green Lizards (*Lacerta viridis*): Variation with morphology and tick infestation. Can J Zool. 2007;85(12):1199–206.

30. Salkeld DJ, Schwarzkopf L. Epizootiology of blood parasites in an Australian lizard: A mark-recapture study of a natural population. Int J Parasitol. 2005;35(1):11–8.

31. Haenel GJ, Smith LC, John-Alder HB. Home-Range analysis in Sceloporus undulatus (Eastern Fence Lizard) spacing patterns and the context of territorial behavior. Copeia. 2003;26(1):99–112.

32. Belliure J, Smith L, Sorci G. Effect of testosterone on T cell-mediated immunity in two species of Mediterranean lacertid lizards. J Exp Zool A Comp Exp Biol. 2004;301(5):411–8.

33. Smolinský R, Hiadlovská Z, Martínková N. Ectoparasite load increase in reproductively active sand lizards. J Vertebr Biol. 2021;70(2).

34. Bullard R, Allen P, Chao CC, Douglas J, Das P, Morgan SE, et al. Structural characterization of tick cement cones collected from in vivo and artificial membrane blood-fed Lone Star ticks (*Amblyomma americanum*). Ticks Tick Borne Dis. 2016;7(5):880–92.

35. Prosser CL, Brown FA. Comparative animal physiology. 2nd ed. Amsterdam: W. B Saunders; 1961.

36. Lehmann T. Ectoparasites: direct impact on host fitness. Parasitology Today. 1993;9.

37. Bull CM, Freake MJ. Home-range fidelity in the Australian sleepy lizard, *Tiliqua rugosa*. Aust J Zool. 1999;47(2):125–32.

38. Crowley SR. Thermal sensitivity of sprint-running in the lizard Sceloporus undulatus: support for a conservative view of thermal physiology. Oecologia. 1985;66:219–25.

39. Dunlap KD, Mathies T. Effects of nymphal ticks and their interaction with malaria on the physiology of male fence lizards. Copea. 1993;28(4):1045–8.

40. Madsen T, Ujvari B, Olsson M. Old pythons stay fit; effects of haematozoan infections on life history traits of a large tropical predator. Oecologia. 2005 Jan;142(3):407–12.



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 (yellow) or lizards that were not (grey).

What about a second panel for females? If parasitism is a ‘male’ thing, then line should be straight-ish across for females (not a logistic function). But only 5 parasitized females?



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 = 0.02) in comparison to lizards with no ticks (grey).