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

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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 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. Higher prevalence of tick infections in 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 load

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 [1,2]. 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[3–6].

A complex interplay of factors determine ectoparasite (tick, mites, fleas, or lice) prevalence, including host species, sex, age, health, and habitat. Host sex can influence parasite load through hormonal variations that may affect immune responses and susceptibility to infection[7,8]. 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[9] with increasing exposure to pathogens, thus decreasing susceptibility to parasites[10]. 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[11,12]

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 an organism's immune function, thereby increasing vulnerability to parasitism[13,14]. In reptilian hosts, meta-analytic studies and experimental manipulations have supported the ICHH, where testosterone reduces immunocompetence and increases the incidence or severity of parasitism[15,16]. In lizards, locomotor performance is a sexually selected trait[17] that is strongly influenced by testosterone levels[18,19]. 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.

Most studies investigating the influence of tick parasitism on health and performance have been from experimental manipulation of tick prevalence on hosts[20,21] or through hormonal manipulations[12,22,23]. 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 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[23,24], and hormonal manipulations in wild males (exogenous testosterone-implants) have been shown to increase rates of tick infection[25]. 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 tick infections; (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*. During the Spring and Summer 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[23]. 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*[26]. 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 centre 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"[27]. 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. 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 analysed using Tracker Video Software (version 4.85; https://physlets.org/tracker/). Further details on video data collection can be found in Wild & Gienger[28]. 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. 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 proportion of ticks observed between males and females. Body condition index (BCI) was calculated from the residuals of an ordinary least squares linear regression of mass (g) on length (SVL)[29], 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 allometric effects of body size on performance[28]. 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%). This difference in tick infection between males and females was significantly different ($x^2 = 9$; df = 1; n = 92; p = 0.003). Due to the low infection frequency for females, they were not included in analysis for sprint performance. 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 with increasing body size. Specifically, there was a negative relationship between parasite prevalence and two estimates of locomotor performance (maximum sprint speed & 2-meter run speed) for male *Sceloporus undulatus.* Our results align with the Immunocompetence Handicap Hypothesis (ICHH) by demonstrating a higher prevalence of tick infections in male lizards relative to females, potentially due to the immunosuppressive effects of testosterone[15,16]. However, we demonstrate a functional trade-off in parasitized hosts, which may be a product of immune function differences between sexes and differences across age classes.

Male bias in parasite prevalence, mediated by sex differences in hormone levels, has been documented in other lizards[30–32]. The sex-specific differences in endocrine systems and behaviours[24,25,33] could provide a mechanism for the observed sex differences in tick prevalence. For example, male *S. undulatus* have higher testosterone levels[24], move considerably more often, move over longer distances [5,34], and have larger home ranges than females[33]. Consequently, high testosterone and increased activity could increase exposure to parasites seeking hosts[35].

Differences in endocrine systems between juvenile and adult lizards play a significant role in variation in traits throughout ontogeny[22,23,35], and not surprisingly, adults have higher testosterone than juveniles[24]. 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[23]. However, high testosterone also imposes fitness costs by lowering resistance to parasitism, inhibiting growth, and reducing survival rates [23,25,36]. 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[8]. 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*[20]). 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[37]. If blood makes up about 5-8% of a lizard's body mass[38], 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[39]. In an experimental study of Sleepy Lizards (*Tiliqua rugosa*), Main and Bull [20] 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 [40]. In contrast, adult *S. undulatus* are considerably smaller and are frequently killed by fast-moving thermophilic snakes and predatory birds[41]. Thus, smaller lizard species that experience high tick loads may be at higher risk of predation due to a reduction in locomotor performance.

Contrary to our findings, other studies have shown that ectoparasite infestation negatively affects or is associated with low body condition in reptiles[12,43,44]. It appears that ticks do not influence host energetic status, as evident by the lack of differences in body condition between uninfected and infected lizards. This aligns with previous findings, which suggested that ticks do not preferentially feed on healthier lizard hosts, but rather, the health of their hosts affects the speed at which ticks could feed[21]. 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. 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.

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. 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.
4. 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.
5. 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.
6. Moore J. Parasites and the Behavior of Animals. 1st ed. Oxford: Oxford University Press; 2002.
7. 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.
8. Moller AP, Christe P, Lux E. Parasitism, host immune function, and sexual selection. Source: The Quarterly Review of Biology. 1999;74(1):3–20.
9. Lochmiller RL, Deerenberg C. Trade-offs in evolutionary immunology: Just what is the cost of immunity? Oikos. 2000;88(1):87–98.
10. Boots M, Bowers RG. The evolution of resistance through costly acquired immunity. Proceedings of the Royal Society B: Biological Sciences. 2004;271(1540):715–23.
11. 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.
12. 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.
13. Hamilton WD, Zuk M. Heritable true fitness and bright birds: a role for parasites? Science (1979). 1982;218(22):384–7.
14. Folstad I, Karter AJ. Parasites, bright males, and the immunocompetence handicap. Am Nat. 1992;139(3):603–22.
15. Roberts ML, Buchanan KL, Evans MR. Testing the immunocompetence handicap hypothesis: A review of the evidence. Anim Behav. 2004 Aug;68(2):227–39.
16. 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 Nov 22;267(1459):2339–43.

17. Husak JF, Fox SF. Sexual selection on locomotor performance. Evol Ecol Res. 2008;10:213–28.
18. Mills SC, Hazard L, Lancaster L, Mappes T, Miles D, Oksanen TA, et al. Gonadotropin hormone modulation of testosterone, immune function, performance, and behavioral trade-offs among male morphs of the lizard *Uta stansburiana*. Am Nat. 2008;171(3):339–57.
19. Klukowski M, Jenkinson NM, Nelson CE. Effects of testosterone on locomotor performance and growth in field-active northern fence lizards, *Sceloporus undulatus hyacinthinu*s. Physiol Zool. 1998;71(5):506–14.
20. Main A, Bull MC. The impact of tick parasites on the behaviour of the lizard *Tiliqua rugosa*. Oecologia. 2000;122:574–81.
21. 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.
22. 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.
23. 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;49(4):393–407.
24. Cox RM, Skelly SL, Leo A, John HB. Testosterone regulates sexually dimorphic coloration in the Eastern Fence Lizard. Copeia. 2005;2005(3):597–608.
25. 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.
26. Angilletta J. Thermal and physiological constraints on energy assimilation in a widespread lizard (*Sceloporus undulatus*). Ecology. 2001;82(11):3044–56.
27. 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.
28. Wild KH, Gienger CM. Fire-disturbed landscapes induce phenotypic plasticity in lizard locomotor performance. J Zool. 2018;305(2):96–105.
29. Jakob EM, Marshall SD, Uetz GW. Estimating Fitness: A Comparison of Body Condition Indices. Oikos. 1996;77(1):61–7.
30. 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.
31. 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.

32. 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.
33. 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.
34. 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.
35. Miles DB, Sinervo B, Hazard LC, Svensson EI, Costa D. Relating endocrinology, physiology and behaviour using species with alternative mating strategies. Funct Ecol. 2007;21(4):653–65.
36. 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.
37. 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 Jul 1;7(5):880–92.
38. Prosser CL, Brown FA. Comparative animal physiology. 2nd ed. Amsterdam: W. B Saunders; 1961.
39. Lehmann T. Ectoparasites: direct impact on host fitness. Parasitology Today. 1993;9.
40. Bull CM, Freake MJ. Home-range fidelity in the Australian sleepy lizard, *Tiliqua rugosa*. Aust J Zool. 1999;47(2):125–32.
41. 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.

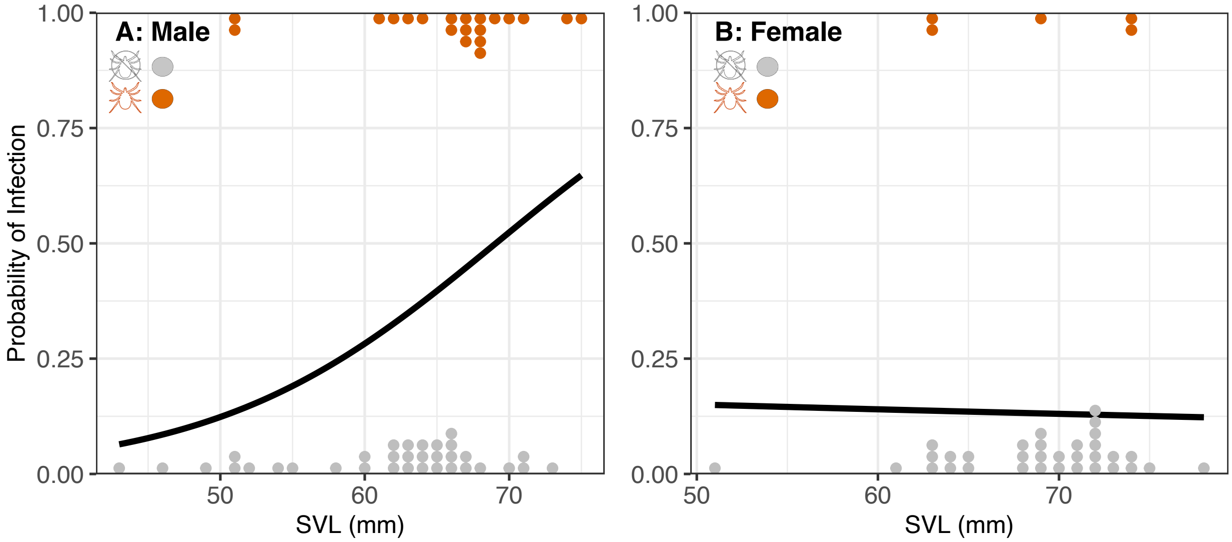

Figure 1. Relationship between body size (SVL) and probability of tick infection for male (A) and female (B) Eastern Fence Lizards. The line represents the probability function from logistic regression. Raw data points are shown with circles that distinguish if lizards were infected by ticks (yellow)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

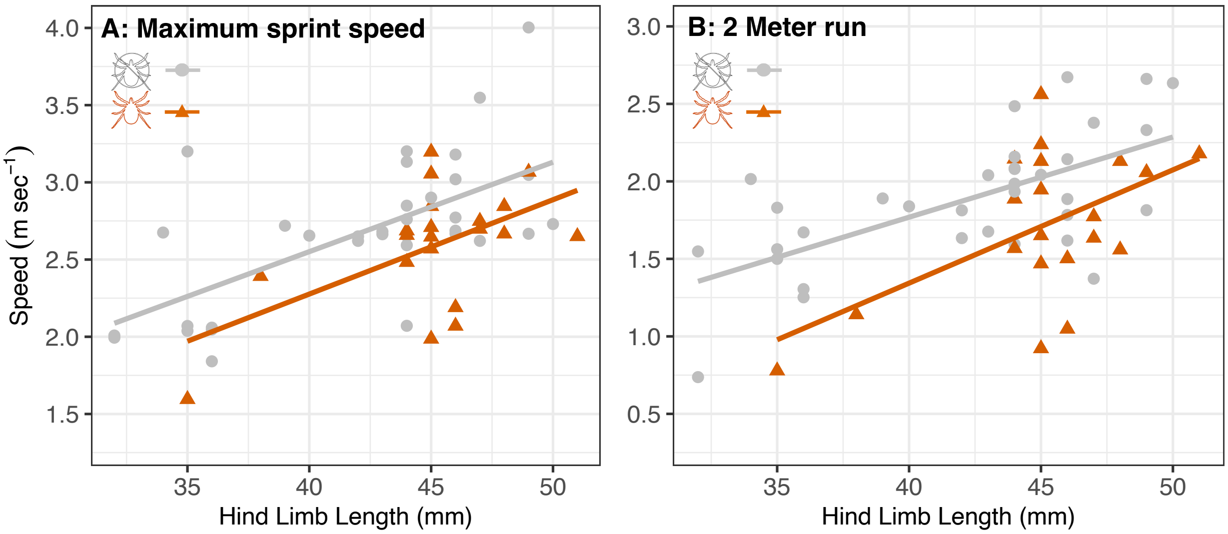

Figure 2. ANCOVA results of maximum sprint speed (a) and two-meter run speed (b) of male lizards. Hindlimb length (mm) was used as a covariate to remove the effect of body size on performance. The presence of ticks (yellow) significantly reduced maximum sprint speed ($p < 0.01$) and two-meter run speed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