Effect of host lizard anemia on host choice and feeding rate of larval western black-legged ticks (*Ixodes pacificus*)

William Pittman · Nicholas B. Pollock · Emily N. Taylor

Abstract Although ticks are known to exhibit preferences among host species, there is little evidence that ticks select hosts within a species based on physiological condition. It may be beneficial for ticks to choose hosts that are easier to feed upon if the ticks can perceive indicative chemical or other signals from the host. For example, if ticks can detect host hematocrit they may choose hosts with high hematocrit, facilitating a faster blood meal. It may similarly be adaptive for ticks to avoid anemic hosts because it may be difficult for them to obtain an adequate meal and feeding duration may be extended. We tested the hypothesis that larval western black-legged ticks (*Ixodes pacificus*) detect host hematocrit using external cues and choose healthy over anemic hosts, allowing them to feed more quickly. We presented groups of larval ticks with pairs of healthy and anemic male western fence lizards (*Sceloporus occidentalis*), allowed them to select a host, and measured the feeding duration of the ticks. We found that the ticks did not exhibit a statistically significant preference for healthy over anemic lizards, but that the ticks fed to repletion significantly faster on healthy hosts than on anemic hosts. Larval ticks may not be able to detect external cues indicating the health of the host, at least not in terms of their hematocrit. The extended feeding duration likely reflects the extra time needed for the ticks to concentrate the blood meal of their anemic hosts.

W. Pittman · N. B. Pollock · E. N. Taylor (✉)
Department of Biological Sciences, California Polytechnic State University, San Luis Obispo, CA 93407-0401, USA
e-mail: etaylor@calpoly.edu

Present Address:
W. Pittman
Albany Medical College, Albany, NY 12210, USA

Present Address:
N. B. Pollock
Department of Ecology, Evolution, and Natural Resources, Rutgers University, New Brunswick, NJ 08901-8551, USA

🖄 Springer

Introduction

Tick-host specificity, defined as a clear association between a tick species and a specific host vertebrate taxon, characterizes the vast majority of tick species (Hoogstraal and Aeschlimann 1982), as many as 700 of the approximately 800+ described tick species (Hoogstraal 1978). Specificity of tick and host results from a combination of biogeographical history, ecological specificity, and a history of co-evolutionary arms race, where the ticks' offenses and hosts' defenses become finely tuned to one another (Klompen et al. 1996; Jackson 2008; Soler et al. 2001). Clearly, host animal defenses vary within a taxon, with immune function varying by factors such as age (Cichoń et al. 2003; Greeley et al. 2001; Ujvari and Madsen 2006), sex (Klein 2000; Mondal and Rai 1999, 2002; Tschirren et al. 2003), nutritional status (Alonso-Alvarez and Tella 2001; Matarese 2000; Waagbø 1994), and season (Hussein et al. 1979; Møller et al. 2003; Nelson and Demas 1996). However, most studies find no evidence that ticks preferentially choose individuals within a given host taxon based on these variables (Dukes and Rodriguez 1976; Godfrey et al. 2011; James and Oliver 1990; Pollock et al. 2012b; Slowik and Lane 2009, but see Christe et al. 2000, 2003). From the perspective of a tick, it may be more beneficial to attach to the first host it encounters rather than wait for a "better" host to come by because the likelihood of encountering another host may be small.

However, the consequences to a tick for selecting a host with certain physiological characteristics may be dramatic. Ticks feeding upon hosts with strong immune function or with acquired resistance to components in tick saliva may experience increased feeding duration, reduced viability, reduced egg count, or be killed outright (Brossard and Wikel 2004; Champagne and Valenzuela 1996; Ribeiro 1989, 1995; Wikel 1996). In contrast, ticks feeding upon particularly unhealthy hosts may experience difficulty in obtaining an adequate blood meal, and the tick's parasitism could even kill the host and, therefore, likely the tick (Riek 1956). Since ticks must concentrate erythrocytes from their hosts in order to obtain an adequate blood meal, ticks feeding upon healthy hosts may feed more quickly to repletion than those feeding upon unhealthy, for example anemic, hosts. Also, the hematocrit (% erythrocytes by volume) of a host may be affected by circulating levels of immunosuppressive steroid hormones, such as corticosteroids and androgens, and may therefore indirectly link immune function to feeding success or duration. For example, testosterone is a strongly erythropoietic hormone (Glader et al. 1968; Pati and Thapliyal 1984), providing the mechanism responsible for higher hematocrit in males than in females and the positive relationship between testosterone levels and hematocrit (Coviello et al. 2008). Because testosterone is often strongly immunosuppressive, a tick feeding upon a host with high testosterone may experience the duel benefit of tapping into a high hematocrit blood supply with reduced immune defenses against its feeding, allowing the tick to feed to repletion quickly and with higher probability of success.

Despite the potential implications of host hematocrit on tick feeding success and duration, no study has examined whether ticks can detect anemia in hosts prior to attachment and potentially avoid feeding upon them. We conducted a controlled laboratory study examining this topic using larval western black-legged ticks (*Ixodes pacificus*) and adult male western fence lizards (*Sceloporus occidentalis*), a major host for juvenile *I. pacificus* in the western United States (Eisen et al. 2004). We hypothesized that juvenile

ticks detect host hematocrit using external cues and choose healthy over anemic hosts, allowing them to feed more quickly. If this is true, then ticks allowed to choose between healthy and anemic hosts will preferentially attach to the healthy hosts. Also, ticks feeding on anemic hosts will take longer to feed to repletion than ticks feeding on healthy hosts.

Material and Methods

Animal collection and maintenance

Twenty-two adult male lizards (*S. occidentalis*) were captured by hand-held noose at the Chimineas Ranch unit of the Carrizo Plain Ecological Reserve in eastern San Luis Obispo Co., California on October 3, 2010. In contrast to nearby coastal regions where *I. pacificus* loads on lizards can be very high (Lumbad et al. 2011), *I. pacificus* very rarely infests *S. occidentalis* at Chimineas, likely because this seasonally dry, inland site does not provide adequate humidity for *I. pacificus* development. Lizards were transported individually in cotton socks to the laboratory at the California Polytechnic State University, San Luis Obispo. Upon arrival, each lizard was measured for snout-vent length (SVL, ±0.5 mm), weighed (±0.5 g), and toe-clipped for identification. Lizards were maintained outdoors in 2.4 m diameter snapset kiddie pools (Intex Recreation, Long Beach, CA, USA) filled with 2 inches of sand and furnished with cinder blocks for basking and plastic plants for shade. Water was available ad libitum and crickets were offered daily.

Treatment

Lizards were divided randomly into one of two treatment groups, anemic (n = 11) or control (n = 11). Lizards in the anemic treatment group were bled from the postorbital sinus with heparinized microhematocrit tubes to induce anemia. Over the course of 2 days the volume of blood drawn ranged from 650 to 900 µl (lower volumes for slightly smaller lizards and higher volumes for larger lizards). An equal volume of the blood drawn from each lizard was replaced intracoelomically by injection with Reptile Ringer's solution. One microhematocrit tube from each anemic treatment lizard was spun in a microhematocrit centrifuge to determine initial hematocrit (% erythrocytes by volume). Initial hematocrit was not measured in control lizards in order to avoid drawing any blood and lowering hematocrit. Control lizards were probed with a syringe intracoelomically, but without injecting any solution. The following day, approximately 45 µl of blood was drawn in the same manner as above from each lizard in both treatment groups and centrifuged to determine the final hematocrit for all lizards. Lizards were considered anemic once they exhibited a 50 % decrease in hematocrit.

Tick infestation

Adult *I. pacificus* ticks were bred on bulls at the Cal Poly San Luis Obispo beef unit and larvae were harvested as in Pollock et al. (2012a). Fifty larvae were placed in each of eleven plastic microcentrifuge tubes. The day after inducing anemia in the anemic treatment group, each anemic lizard was size-matched and paired with a control lizard for infestation, making eleven pairs in total. The treatment groups did not differ in SVL (T = 0.52, P = 0.61) or body mass (T = −0.39, P = 0.70). Each pair of lizards was

placed in a 2.5 l beaker with one microcentrifuge tube of 50 tick larvae. To permit host basking, beakers were placed close to a 60 W incandescent lamp for approximately 12 h. Fine mesh was secured around the top of the beaker with rubber bands to prevent tick escape from the beakers. Infestation trials spanned 48 h during which beakers were periodically misted with distilled water to prevent desiccation of the larvae. Lizards were then removed, numbers of residual unattached ticks were recorded, and lizards were placed into individual 13 × 8 × 8 (cm) metal mesh cages elevated above tubs of water to collect ticks as they dropped off. Tubs were 30 × 16 × 8 (cm) and filled with 4 cm of water, such that any ticks dropping off the host lizards would fall into the tubs and float until they were retrieved daily by the investigators. The sides of the tubs were coated with Fluon, a slippery fluoropolymer resin (Bioquip, Rancho Dominguez, CA, USA), to prevent tick escape. Tubs were placed in environmental chambers (27 °C, 8:16 light:dark). Water was offered ad libitum and 2–3 crickets were offered per day. Replete tick numbers were quantified daily as ticks dropped off into the water for approximately 4 weeks, until all ticks were collected. At the termination of the experiment the total number of replete ticks and feeding duration (average time to engorgement and drop off) were calculated for each lizard.

Statistical analyses

Numbers of replete ticks were compared between anemic and control lizards using a paired *t* test. To examine the effects of body size on numbers of replete ticks, we conducted an analysis of covariance (ANCOVA) with log-transformed SVL as the covariate, comparing log-transformed replete tick loads between treatment groups. The homogeneity of slopes assumption for the ANCOVA was met. Tick feeding duration between treatment groups was compared using a two-sample *t* test. All *t* tests were two-tailed and all *P* values were considered significant at the $\alpha = 0.05$ level. Statistical analyses were performed using Minitab Statistical Software version 10 (State College, PA, USA).

Results

Control lizards had a mean hematocrit of 33.5 % at the time of infestation, which is in line with previous studies reporting hematocrit in *S. occidentalis* in California (Dunlap 1995, 2006). Removal of blood caused the anemic treatment lizards to drop from a mean initial hematocrit of 37.2 % to 14.8 % at the time of tick infestation, representing a 60 % decrease (Fig. 1). Anemic lizards exhibited no noticeable outward signs of poor health and ate well during the infestation period.

Although the replete tick loads on control lizards were greater than on anemic lizards, there was no significant difference in mean replete ticks between groups (control = 7.2 ± 1.1, anemic = 5.7 ± 1.2; two-tailed $T = 0.92$, $P = 0.37$; Fig. 2). Snout-vent length did not significantly affect replete tick loads (F = 1.40, $P = 0.25$). In contrast, ticks fed significantly slower on anemic lizards than on control lizards (mean duration: control = 17.6 ± 0.31 days, anemic = 18.8 ± 0.30 days; two-tailed $T = 2.71$, $P = 0.014$).

Discussion

Larval *I. pacificus* failed to display a statistically significant preference for healthy over anemic hosts, instead attaching to them at similar rates. This caused us to reject our

Fig. 1 Hematocrit (% erythrocytes by volume) of anemic (*filled circle*) and healthy control (*filled square*) male *Sceloporus occidentalis* before infestation with larval *Ixodes pacificus*. Lizards in each group were similar in mass but differed significantly in hematocrit
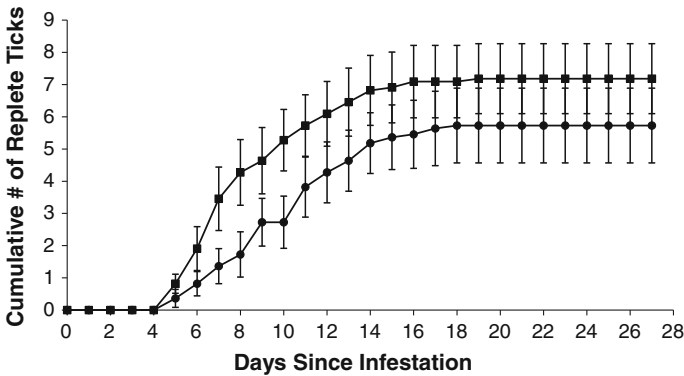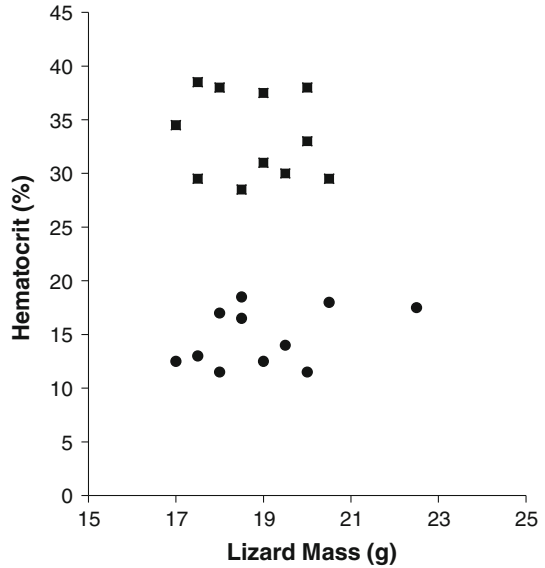
Fig. 2 Cumulative number of larval *Ixodes pacificus* feeding to repletion on anemic (*filled circle*) and healthy control (*filled square*) male *Sceloporus occidentalis* over time. There was no difference in the mean number of ticks that fed successfully on each group, but ticks fed faster on control lizards than on anemic lizards

hypothesis that juvenile ticks detect host hematocrit using external cues and choose healthy over anemic hosts. Rejection of the hypothesis is based on this single study only and should be confirmed. Our experimentally induced reduction in hematocrit was dramatic (60 % reduction), so if anemia induces any external cues indicating poor health—for example a change in chemical cues—then we would have expected significantly fewer ticks to attach to anemic lizards. Pollock et al. (2012b) found that ticks failed to select male lizard hosts over female lizard hosts using the same experimental design, despite the fact that male *S. occidentalis* in the wild host carry far higher tick burdens than females (Eisen et al. 2001; Lane and Loye 1989; Lumbad et al. 2011; Schall et al. 2000; Tälleklint-Eisen and Eisen 1999). Another study on hedgehogs demonstrated that ticks exhibited no clear preference between reproductive and non-reproductive individuals (Carrick and Bullough 1940).

Taken together, these studies suggest that ticks may be adapted to attach to any host that they encounter because the chances of encountering another better host are low. Randolph (1998, 2004) showed that host encounter rate and, thus, survival rate of ticks are both low regardless of life stage and are dependent on environmental temperature, humidity, day length, and host densities. Higher parasite burdens on males in the wild may instead result from sex differences in behavior (Ezenwa 2004; Klein 2000; Pollock et al. 2012a). For example, males may move more than females and/or through microhabitats with more questing ticks (Boyer et al. 2010; John-Alder et al. 2009; Olsson et al. 2000). It appears that juvenile ticks tend to exhibit host preferences mainly among different host species; for example among mammal, bird, and lizard hosts (James and Oliver 1990; Slowik and Lane 2009). There is little evidence that *I. pacificus* larvae choose hosts of variable physiological condition within a host species even when that condition may indicate immunosuppression; indeed ticks feeding on hosts with low testosterone concentrations suffered no observable negative effects relative to those feeding on hosts with high testosterone concentrations (Pollock et al. 2012b). Our study adds to the majority view in this growing body of literature: ticks do not actively choose hosts that may facilitate more successful feeding, in terms of sex, immune function, hematocrit, or other measures of host health.

Although host hematocrit did not significantly influence the host choice of larval *I. pacificus*, feeding duration was higher in the control group than in the anemic group. It is likely that the ticks in the control group were able to receive and concentrate an adequate blood meal from their healthy hosts sooner than the ticks in the anemic group. While feeding, ticks concentrate hemoglobin from blood cells and plasma proteins, including albumin, while excreting fluids and ions back into the host's circulatory and lymphatic systems (Bowman and Sauer 2004; Gregson 1967). Anemic hosts provide a lower concentration of cells, so ticks must feed for a longer duration in order to sufficiently concentrate cells. In the wild, hosts that are heavily burdened with ectoparasites are also anemic (Dunlap and Mathies 1993; Wanless et al. 1997). However, the host's anemia may result from the heavy parasite burden (Araujo et al. 1998; Jellison and Kohls 1938; Lehmann 1993), making the interpretation of cause and effect difficult. The effect of tick feeding on host hematocrit can only be directly observed in controlled laboratory studies (e.g. Glines and Samuel 1989; Rechav et al. 1980; Riek 1956); similarly, only in controlled studies such as ours can the direct effect of host hematocrit on tick feeding rates be observed. To our knowledge, ours is the first study to directly measure feeding duration of larval ticks in response to the experimentally manipulated variable of host hematocrit.

The average feeding duration of ticks on healthy lizards was 17.6 days; one extra day represented approximately a 7 % increase in feeding duration. It is unlikely that such a small increase in feeding duration would have a great impact on the fitness of the replete ticks. Depending on the site of tick attachment, hosts can sometimes scratch against objects in the environment to damage or dislodge ticks before they are replete (Arnold 1986; Cunha-Barros et al. 2003; Salvador et al. 1999). Extending feeding duration could increase the likelihood of this occurring; however, no ticks in this study dropped from their hosts until they were replete. In this study, we did not measure the mass of the replete ticks or their success in molting into nymphs; these measurements would help solidify whether feeding on anemic hosts presents any additional consequences beyond simply extending duration. Extended feeding duration observed on anemic hosts may affect transmission of tick-borne pathogens to the host, however. Longer feeding duration implies greater volume of injection of saliva and regurgitation of fluid into the host; this may increase the quantity of pathogens (e.g. viruses, filariae, borreliae, rickettsiae, and other pathogens, Aeschlimann 1991) transmitted from tick to host. This direct relationship with feeding duration and

pathogen transmission has been most often demonstrated with the Lyme disease bacteria, *Borrelia burdorferi* (des Vignes et al. 2001; Piesman et al. 1987). This hypothesis requires further study, however.

In summary, we found no support for the hypothesis that ticks can detect anemia in hosts prior to attachment, but found that ticks took an average of 1 day longer to feed on anemic hosts than on healthy hosts. This supports other studies that suggest that ticks are adapted to feed upon the first host they encounter, regardless of the host's condition (Dukes and Rodriguez 1976; Godfrey et al. 2011; James and Oliver 1990; Pollock et al. 2012b; Slowik and Lane 2009). Significant relationships between ectoparasite load and anemia reported in free-living animals likely represent an exsanguinating effect of parasites on the hematocrit of their hosts.

References

Aeschlimann A (1991) Ticks and disease: susceptible hosts, reservoir hosts and vectors. In: Toft CA, Aeschlimann A, Bolis L (eds) Parasite-host associations: resistance or conflict. Oxford University Press, Oxford, pp 148–156

Alonso-Alvarez C, Tella JL (2001) Effects of experimental food restriction and body-mass changes on the avian T-cell-mediated immune response. Can J Zool 79:101–105. doi:10.1139/z00-190

Araujo FR, Silva MP, Lopes AA, Ribeiro OC, Pires PP, Carvalho CM, Balbuena CB, Villas AA, Ramos JK (1998) Severe cat flea infestation of dairy calves in Brazil. Vet Parasitol 80:83–86. doi: 10.1016/S0304-4017(98)00181-2

Arnold EN (1986) Mite pockets of lizards, a possible means of reducing damage by ectoparasites. Biol J Linn Soc 29:1–21. doi:10.1111/j.1095-8312.1986.tb01767.x

Bowman AS, Sauer JR (2004) Tick salivary glands: function, physiology and future. Parasitology 129:S67–S81. doi:10.1017/S0031182004006468

Boyer N, Reale D, Marmet J, Pisanu B, Chapuis J (2010) Personality, space use and tick load in an introduced population of Siberian chipmunks *Tamias sibiricus*. J Anim Ecol 79:538–547. doi: 10.1111/j.1365-2656.2010.01659.x

Brossard M, Wikel SK (2004) Tick immunobiology. Parasitology 129:S161–S176. doi:10.1017/S003118 2004004834

Carrick R, Bullough WS (1940) The feeding of the tick, *Ixodes ricinus* L., in relation to the reproductive condition of the host. Parasitology 32:313–317

Champagne DE, Valenzuela JG (1996) Pharmacology of haematophagous arthropod saliva. In: Wikel SK (ed) The immunology of host-ectoparasitic arthropod relationships. Cab International, Wallingford, pp 85–106

Christe P, Arlettaz R, Vogel P (2000) Variation in intensity of a parasitic mite (*Spinturnix myoti*) in relation to the reproductive cycle and immunocompetence of its bat host (*Myotis myotis*). Ecol Lett 3:207–212. doi:10.1046/j.1461-0248.2000.00142.x

Christe P, Giorgi MS, Vogel P, Arlettaz R (2003) Differential species specific ectoparasitic mite intensities in two intimately coexisting sibling bat species: resource-mediated host attractiveness or parasite specialization? J Anim Ecol 72:866–872. doi:10.1046/j.1365-2656.2003.00759.x

Cichoń M, Sendecka J, Gustafsson L (2003) Age-related decline in humoral immune function in collared flycatchers. J Evol Biol 16:1205–1210. doi:10.1046/j.1420-9101.2003.00611.x

Coviello AD, Kaplan B, Lakshman KM, Chen T, Singh AB, Bhasin S (2008) Effects of graded doses of testosterone on erythropoiesis in healthy young and older men. J Clin Endocrinol Metab 93:914–919. doi:10.1210/jc.2007-1692

Cunha-Barros M, Van Sluys M, Vricibradic D, Galdino CAB, Hatano FH, Rocha CFD (2003) Patterns of infestation by chigger mites in four diurnal lizard species from a restinga habitat (Jurubatiba) of southeastern Brazil. Braz J Biol 63:393–399. doi:10.1590/S1519-69842003000300005

des Vignes F, Piesman J, Heffernan R, Schulze TL, Stafford KC III, Fish D (2001) Effect of tick removal on transmission of *Borrelia burgdorferi* and *Ehrlichia phagocytophila* by *Ixodes scapularis* nymphs. J Infect Dis 183:773–778

Dukes JC, Rodriguez JG (1976) A bioassay for host-seeking responses of tick nymphs (Ixodidae). J Kansas Entomol Soc 49:562–566

Dunlap KD (1995) External and internal influences on indices of physiological stress: II. Seasonal and size-related variations in blood composition in free-living lizards Sceloporus occidentalis. J Exp Zool 272:85–94. doi:10.1002/jez.1402720202

Dunlap KD (2006) Ontogeny and scaling of hematocrit and blood viscosity in western fence lizards, *Sceloporus occidentalis*. Copeia 2006:535–538

Dunlap KD, Mathies T (1993) Effects of nymphal ticks and their interaction with malaria on the physiology of male fence lizards. Copeia 1993:1045–1048

Eisen RJ, Eisen L, Lane RD (2001) Prevalence and abundance of *Ixodes pacificus* immatures (Acari: Ixodidae) infesting western fence lizards (*Sceloporus occidentalis*) in Northern California: temporal trends and environmental correlates. J Parasitol 87:1301–1307

Eisen L, Eisen RJ, Lane RS (2004) The roles of birds, lizards, and rodents as hosts for the western black-legged tick *Ixodes pacificus*. J Vector Ecol 29:295–308

Ezenwa VO (2004) Host social behavior and parasitic infection: a multifactorial approach. Behav Ecol 15:446–454. doi:10.1093/beheco/arh028

Glader BE, Rambach WA, Alt HL (1968) Observations on the effect of testosterone and hydrocortisone on erythropoiesis. Ann NY Acad Sci 149:383–388. doi:10.1111/j.1749-6632.1968.tb15172.x

Glines MV, Samuel WM (1989) Effect of *Dermacentor albipictus* (Acari: Ixodidae) on blood composition, weight gain and hair coat of moose, *Alces alces*. Exp Appl Acarol 6:197–213. doi:10.1007/BF01193980

Godfrey SS, Nelson NJ, Bull MC (2011) Microhabitat choice and host-seeking behavior of the tuatara tick, *Amblyomma sphenodonti* (Acari: Ixodidae). N Z J Ecol 35:52–60

Greeley EH, Ballam JM, Harrison JM, Kealy RD, Lawler DF, Segre M (2001) The influence of age and gender on the immune system: a longitudinal study in Labrador retriever dogs. Vet Immunol Immunopathol 82:57–71

Gregson JD (1967) Observations on the movement of fluids in the vicinity of the mouthparts of naturally feeding *Dermacentor andersoni* Stiles. Parasitology 57:1–8

Hoogstraal H (1978) Biology of ticks. In: Wilde JKH (ed) Tick-borne diseases and their vectors: proceedings of an international conference held in Edinburgh from the 27th September to the 1st October, 1976. Edinburgh University Press, Edinburgh, pp 3–14

Hoogstraal H, Aeschlimann A (1982) Tick-host specificity. Bull Soc Entomol Suisse 55:5–32

Hussein M, Badir N, El Ridi R, El Deeb S (1979) Effect of seasonal variation on immune system of the lizard, *Scincus scincus*. J Exp Zool 209:91–96

Jackson DE (2008) Chemical coevolution: host-parasite arms race runs hot and cold. Curr Biol 18:306–308. doi:10.1016/j.cub.2008.01.051

James AM, Oliver JH Jr (1990) Feeding and host preference of immature *Ixodes dammini*, *I. scapularis*, and *I. pacificus* (Acari: Ixodidae). J Med Entomol 27:324–330

Jellison WL, Kohls GM (1938) Tick-host anemia: a secondary anemia induced by *Dermacentor andersoni* Stiles. J Parasitol 24:143–154

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

Klein SL (2000) Hormones and mating system affect sex and species differences in immune function among vertebrates. Behav Process 51:149–166

Klompen JSH, Black WC IV, Keirans JE, Oliver JH Jr (1996) Evolution of ticks. Ann Rev Entomol 41:141–161. doi:10.1146/annurev.en.41.010196.001041

Lehmann T (1993) Ectoparasites: direct impact on host fitness. Parasitol Today 9:8–13. doi:10.1016/0169-4758(93)90153-7

Lumbad A, Vredevoe L, Taylor EN (2011) Season and sex of host affect intensities of ectoparasites in western fence lizards (*Sceloporus occidentalis*) on the central coast of California. Southwest Nat 56:369–377. doi:10.1894/F10-RW-01.1

Matarese G (2000) Leptin and the immune system: how nutritional status influences the immune response. Eur Cytokine Netw 11:7–14

Møller AP, Erritzøe J, Saino N (2003) Seasonal changes in immune response and parasite impact on hosts. Am Nat 161:657–671

Mondal S, Rai U (1999) Sexual dimorphism in phagocytic activity of wall lizard's splenic macrophages and its control by sex steroids. Gen Comp Endocrinol 116:291–298. doi:10.1006/gcen.1999.7370

Mondal S, Rai U (2002) In vitro effect of sex steroids on cytotoxic activity of splenic macrophages in wall lizard (*Hemidactylus flaviviridis*). Gen Comp Endocrinol 125:264–271. doi:10.1006/gcen.2001.7744

Nelson RJ, Demas GE (1996) Seasonal changes in immune function. Q Rev Biol 71:511–548

Olsson M, Wapstra E, Madsen T, Silverin B (2000) Testosterone, ticks and travels: a test of the immunocompetence-handicap hypothesis in free-ranging male sand lizards. Proc Roy Soc London B, Biol Sci 267:2339–2343

Pati AK, Thapliyal JP (1984) Erythropoietin, testosterone, and thyroxine in the erythropoietic response of the snake, *Xenochrophis piscator*. Gen Comp Endocrinol 53:370–374. doi:10.1016/0016-6480(84)90264-8

Piesman J, Mather TN, Sinsky RJ, Spielman A (1987) Duration of tick attachment and *Borrelia burdorferi* transmission. J Clin Microbiol 25:557–558

Pollock NB, Vredevoe LK, Taylor EN (2012a) The effect of exogenous testosterone on ectoparasite loads in free-ranging western fence lizards. J Exp Zool A Ecol Gen Physiol 317:447–454. doi:10.1002/jez.1737

Pollock NB, Vredevoe LK, Taylor EN (2012b) How do host sex and reproductive state affect host preference and feeding duration of ticks? Parasitol Res 111:897–907. doi:10.1007/s00436-012-2916-8

Randolph SE (1998) Ticks are not insects: consequences of contrasting vector biology for transmission potential. Parasitol Today 14:186–192. doi:10.1016/S0169-4758(98)01224-1

Randolph SE (2004) Tick ecology: processes and patterns behind the epidemiological risk posed by ixodid ticks as vectors. Parasitol 129:S37–S65. doi:10.1017/S0031182004004925

Rechav Y, Kuhn HG, Knight MM (1980) The effects of the tick *Amblyomma hebraeum* (Acari: Ixodidae) on blood composition and weight of rabbits. J Med Entomol 17:555–560

Ribeiro JMC (1989) Role of saliva in tick/host interactions. Exp Appl Acarol 7:15–20. doi:10.1007/BF01200449

Ribeiro JMC (1995) How ticks make a living. Parasitol Today 11:91–93. doi:10.1016/0169-4758(95)80162-6

Riek RF (1956) Studies on the reactions of animals to infestation with ticks. I. tick anaemia. Aust J Agric Res 7:209–214

Slowik TJ, Lane RS (2009) Feeding preferences of the immature stages of three western North American Ixodid ticks (Acari) for avian, reptilian, or rodent hosts. J Med Entomol 46:115–122. doi:10.1603/033.046.0115

Soler JJ, Martínez JG, Soler M, Møller AP (2001) Coevolutionary interactions in a host-parasite system. Ecol Lett 4:470–476. doi:10.1046/j.1461-0248.2001.00247.x

Tälleklint-Eisen L, Eisen RJ (1999) Abundance of ticks (Acari: Ixodidae) infesting the western fence lizard, *Sceloporus occidentalis*, in relation to environmental factors. Exp Appl Acarol 23:731–740. doi:10.1023/A:1006212323760

Tschirren B, Fitze PS, Richner H (2003) Sexual dimorphism in susceptibility to parasites and cell-mediated immunity in great tit nestlings. J Anim Ecol 72:839–845. doi:10.1046/j.1365-2656.2003.00755.x

Ujvari B, Madsen T (2006) Age, parasites, and condition affect humoral immune response in tropical pythons. Behav Ecol 17:20–24. doi:10.1093/beheco/ari091

Waagbø R (1994) The impact of nutritional factors on the immune system in Atlantic salmon, *Salmo salar* L.: a review. Aquat Res 25:175–197. doi:10.1111/j.1365-2109.1994.tb00573.x

Wanless S, Barton TR, Harris MP (1997) Blood hematocrit measurements of 4 species of north Atlantic seabirds in relation to levels of infestation by the tick *Ixodes uriae*. Colon Waterbirds 20:540–544

Wikel SK (1996) Host immunity to ticks. Ann Rev Entomol 41:1–22. doi:10.1146/annurev.en.41.010196.000245