



Red imported fire ant (*Solenopsis invicta*) aggression influences the behavior of three hard tick species

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Received: 13 June 2019 / Accepted: 13 September 2019 / Published online: 24 September 2019
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Abstract

Few studies have documented the indirect effects of predators on tick behavior. We conducted behavioral assays in the laboratory to quantify the effects of a highly abundant predator, the red imported fire ant (*Solenopsis invicta*), on three species of ticks endemic to the southern USA: the lone star tick (*Amblyomma americanum*), the Gulf Coast tick (*A. maculatum*), and the Cayenne tick (*A. mixtum*). We documented ant aggression toward ticks (biting, carrying, and stinging) and determined the effects of ants on tick activity. Ticks were significantly less active in the presence of fire ants, and tick activity was negatively associated with ant aggression, but in many cases the effects of fire ants on ticks varied by tick species, stage, and engorgement status. For example, fire ants took half as long (~62 s) to become aggressive toward unfed *A. americanum* adults compared with unfed *A. maculatum*, and only ~8 s to become aggressive toward engorged *A. maculatum* nymphs. Correspondingly, the activity of unfed *A. americanum* adults and engorged *A. maculatum* nymphs was reduced by 67 and 93%, respectively, in the presence of fire ants. This reduction in tick activity translated to less questing by unfed ticks and less time spent walking by engorged nymphs. Our results suggest that fire ants may have important non-consumptive effects on ticks and demonstrate the importance of measuring the indirect effects of predators on tick behavior.

Keywords Predation · Indirect effects · Questing · Ixodidae · Ticks

Electronic supplementary material The online version of this article (<https://doi.org/10.1007/s10493-019-00419-8>) contains supplementary material, which is available to authorized users.

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Introduction

Ticks are important vectors of many pathogens that impact human and animal health and are, consequently, among the most costly ectoparasites in the world (Zingg et al. 2018). It is critical to understand the factors that affect tick abundance and behavior in order to develop effective management practices that reduce the economic and health impacts of tick-borne pathogens (Mac et al. 2019). Factors such as climate, habitat, and host populations are known to influence tick abundance and disease risk (Crowl et al. 2008; Gage et al. 2008; Randolph 2004). Other extrinsic variables such as predation also affect ticks and their propensity to spread pathogens (Burtis and Pflueger 2017; Fischhoff et al. 2018; Keesing et al. 2009; Levi et al. 2016; Mwangi et al. 1991; Samish and Rehacek 1999; Samish and Alekseev 2001). Predators can directly reduce tick abundance by consuming them (Burtis and Pflueger 2017; Keesing et al. 2009; Levi et al. 2016; Samish and Alekseev 2001), consequently reducing pathogen transmission. For example, Virginia opossums consumed 96.5% of tick larvae that attempted to feed on them (Keesing et al. 2009), making opossums a potential dilution host in the spread of Lyme disease (Levi et al. 2016). In addition to directly reducing tick abundance, predators can also have important non-consumptive (indirect) effects by altering tick foraging or feeding behaviors (Fischhoff et al. 2018). For example, the blacklegged tick (*Ixodes scapularis*) quested 50% less often in the presence of spiders (Fischhoff et al. 2018). The indirect effects of predators on prey are critical in other ecological systems, and often have cascading impacts on the entire community (Hawlena and Pérez Mellado 2009; Schmitz et al. 1997; Trussell et al. 2002). Grasshoppers, for example, decreased foraging to the point of starvation in the presence of ‘non-lethal’ spiders (with glued chelicerae to prevent consumption), which reduced grasshopper abundance by 20% and increased plant biomass by almost 30% (Schmitz et al. 1997). Few studies have documented the indirect effects of predators on ticks (Fischhoff et al. 2018), but by altering the amount of time ticks spend questing, predators may also influence transmission of tick-borne pathogens.

Ants are thought to be among the most effective tick predators (Barré et al. 1991; Samish and Alekseev 2001; Samish and Rehacek 1999), but their effects on tick species in North America are relatively unknown. The red imported fire ant (*Solenopsis invicta*; hereafter, fire ant) may play an under-appreciated role in tick predation and alteration of tick behavior in North America. Fire ants are an invasive species that are extremely abundant throughout their invaded range in the southern USA (Porter et al. 1997; Vinson 1997). In some areas of Texas, the number of fire ant mounds per hectare has been estimated to range from 50–75 with upwards of 200,000–300,000 ant workers per mound (Vinson 1997). Fire ants are voracious generalist predators, with workers regularly bringing back more than 40 different prey items to a colony within a single hour (Rashid et al. 2013). Fire ants almost certainly encounter ticks in the field. Areas with fire ants have been associated with reduced tick abundance in several studies (Burns and Melancon 1977; Castellanos et al. 2016; Fleetwood et al. 1984). The lone star tick (*Amblyomma americanum*), for example, was 27 times less abundant in habitats with fire ants compared to habitats without fire ants (Burns and Melancon 1977). The reason for this reduction in tick abundance is presumed to be predation by fire ants, but the exact mechanism is unknown. Although fire ants are associated with a lower abundance of *A. americanum*, their association with other tick species and stages likely vary. For example, the Gulf Coast tick (*A. maculatum*) is often abundant at fire ant-infested sites in Texas (Castellanos et al. 2016; Teel et al. 1998) and is sympatric in the ant’s native range in South America (Teel et al. 2010). In studies with

other ant and tick species, ant predation was significantly affected by tick species, stage, and engorgement status (Barré et al. 1991; Dawes-Gromadzki and Bull 1997; Samish and Rehacek 1999). For example, the tropical fire ant (*Solenopsis geminata*), a close relative of the red imported fire ant, was found to feed only on engorged ticks (Barré et al. 1991). Given the role of some tick species in transmitting a suite of tick-borne pathogens to wildlife and humans, it is important to examine the effects of fire ants on tick vectors.

The lone star tick (*A. americanum*), the Gulf Coast tick (*A. maculatum*), and the Cayenne tick (*A. mixtum*) are three species in Texas that affect the health and wellbeing of humans, livestock, and wildlife (Beati et al. 2013; Mitchell et al. 2016; Nieto et al. 2018; Paddock and Childs 2003; Teel et al. 2010). These three species comprise 64% of the ticks that were removed from humans and were sent to the Texas Department of State Health Services for pathogen testing from 2008–2014 (Mitchell et al. 2016). Fire ants are among the most abundant arthropod predators in Texas (Vinson 1997), so they are potentially an important predator of these three co-occurring tick species. It is critical to understand the interactions between fire ants and ticks of different species and life stages to determine how fire ants might impact ticks in the field. We conducted laboratory experiments documenting the interactions between fire ants and the three tick species mentioned above (*A. americanum*, *A. maculatum*, and *A. mixtum*). We tested the effects of tick stage (adult and nymph) and nymphal engorgement status (engorged and unfed) on the behavior of fire ants and ticks. We hypothesized that fire ants would be least aggressive toward *A. maculatum* ticks because *A. maculatum* is often abundant in sites with fire ants (Castellanos et al. 2016; Teel et al. 1998) and is sympatric with fire ants in their native range in South America (Teel et al. 2010). We also hypothesized that fire ants would be most aggressive toward engorged nymphs based on past research with other ant species (Barré et al. 1991; Samish and Alekseev 2001). We predicted that fire ant aggression would correspond with tick behavior, with differential impacts of fire ants across all treatments. Thus, we predicted that *A. maculatum* behavior would be least affected by fire ants compared with the other two species, and that engorged nymph behavior would be most affected by fire ant presence.

Materials and methods

We collected 10 fire ant colonies from College Station, Texas, USA (Texas A&M Field Laboratory, Burleson Co., TX; 30°33'14"N, 96°25'41"W; permission granted by Texas A&M AgriLife Research). Colonies were extracted from the soil using drip flotation (Banks et al. 1981), and each field colony was divided into three standardized experimental colonies of 1.5 g of workers (~2500 ants) and 0.5 g of brood (~200 larvae & pupae) to serve as colony replicates (Bockoven et al. 2015). Experimental colonies were maintained in individual foraging arenas (38×55×6 cm plastic box) lined with Fluon® (Insect-a-slip Insect Barrier, BioQuip Products, Rancho Dominguez, CA, USA) with an artificial nesting tray (15 cm diameter black-lidded petri dish with dampened plaster) and 'questing rods' consisting of three vertical, 15 cm sticks in plaster. We also painted a sticky barrier (Tanglefoot®, Contech Enterprises, Victoria, BC, Canada) along the upper edge of each container.

All colonies were maintained in standardized laboratory conditions throughout the experiment (12:12 h light/dark cycle, 24–32 °C temperature, 40–70% relative humidity). Colonies were given tubes of water and artificial nectar *ad libitum* and fed four

adult crickets (*Acheta domesticus*) three times per week (Wilder and Eubanks 2010). We allowed all experimental colonies to acclimatize to laboratory conditions for at least 1 week but no more than 4 weeks prior to introducing ticks.

Ticks used in experiments were obtained from colonies maintained at the Tick Research Laboratory, Texas A&M AgriLife Research (College Station, TX). Colonies were maintained under a 14:10 h light/dark cycle, at 22–28 °C and 80–85% relative humidity using young cockerels (*Gallus gallus*) as bloodmeal hosts according to procedures approved by the Institutional Animal Care and Use Committee of Texas A&M University (AUP no. 2014–255).

Behavioral assays

We conducted behavioral assays to examine the behavior of fire ants and ticks when together. We used 12 experimental ant colonies (four field colonies were each divided into three experimental colonies) plus 12 controls without ants to document tick behavior in the absence of ants. Control foraging arenas were constructed to be identical to those with ants (i.e., one nesting tray and three questing rods). We introduced a single tick into each experimental and control foraging arena and waited 30 s to allow ticks to acclimatize. After 30 s, we recorded tick behavior (described below) in each foraging arena every 10 s for 5 min, resulting in 30 total observations per foraging arena. In the foraging arenas with ants, we also recorded ant behavior during the same observation periods. Our preliminary results indicated that this amount of time was sufficient for quantifying ant and tick behaviors and is similar to the sampling procedures in a previous study of tick behavior in the presence of a predator (Fischhoff et al. 2018).

Tick behavior was recorded as still, questing, walking, or climbing (Table 1), and the location of the tick (ground or questing rod) was also recorded. Ticks were recorded as questing when they were not walking and their first pair of legs was held outstretched. If ants grabbed the tick with their mandibles, carried and/or dragged the tick, or stung the tick, we scored this as aggressive behavior (Table 2). After 5 min, the tick was removed from the experiment. We conducted four separate assays: one for unfed adults of all species (N = 15 for each species), one for unfed nymphs of all species (N = 15 for each species), one for bloodfed nymphs of *A. americanum* (N = 15), and one for bloodfed nymphs of *A. maculatum* (N = 15). Assays of bloodfed *A. mixtum* nymphs were not performed because we did not have enough bloodfed *A. mixtum* ticks to include in the study.

Table 1 Description of tick behaviors that were recorded in each foraging arena every 10 s for 5 min

Samples	Type	Description
Still	Not active	Still (on horizontal or vertical surface); includes not moving, grooming, and curled up/playing dead
Walking	Active	Walking horizontally around foraging arena
Climbing	Active	Climbing vertical questing rods
Questing	Active	Questing (horizontal or vertical surface)

Table 2 Description of ant behaviors that were recorded in each foraging arena every 10 s for 5 min

Ant behavior	Type	Description
None	None	No ant in vicinity of tick
Ignore	Neutral	Walking over or past tick
Antennate	Neutral	Examining tick with antennae
Bite	Aggressive	Grabbing tick with mandibles
Carry	Aggressive	Biting and carrying or dragging tick
Sting	Aggressive	Biting and stinging tick

Data analysis

All analyses were conducted using statistical software R v3.4.1 (R Core Team 2017). Because we did not use any engorged adults, we conducted two separate analyses: one for unfed tick adults and nymphs, and the other for engorged and unfed nymphs.

We calculated the time to aggression by fire ants as the time from when ants initially encountered the tick (i.e., walked past or antennated the tick) to the time when ants were first recorded as aggressive toward the tick. Response variables for our analyses included the time to aggression, the total number of times ticks were scored as active (walking/questioning), the total number of times ticks were questing, and the total number of times ticks were walking. These variables were over-dispersed and contained a high number of zeros; therefore, we constructed zero-inflated Poisson regression models using the function *zero-infl* in the statistical package *pscl* (v1.5.2; Zeileis et al. 2008). For ant behavior, we tested the effects of tick species, tick stage, nymphal engorgement status, and the interaction among these variables. For tick behavior, we tested the effects of tick species, tick stage, nymphal engorgement status, ant presence, and the interaction among these variables. Type II analysis of deviance tables were generated to determine the significance of each predictor variable using the *car* package (v3.0-2; Fox and Weisberg 2018), and Tukey's honestly significant difference (HSD) test was used as a post-hoc test ($\alpha = 0.05$) with the *emmeans* statistical package (v1.1.2; Lenth 2018). All plots were generated using the statistical package *ggplot2* (v3.1.0; Wickham 2016).

Results

Fire ant aggression differed significantly by tick species ($\chi^2 = 20.054$, $df = 2$, $P < 0.001$), but there was also a significant interaction between tick species and unfed tick stage ($\chi^2 = 15.548$, $df = 2$, $P < 0.001$). Fire ants took approximately half as long to display aggressive behaviors toward unfed *A. americanum* adults (62.5 ± 29.4 s) compared with unfed *A. mixtum* nymphs (135.8 ± 40.4 s) and unfed *A. maculatum* ticks of both stages (adults: 154.2 ± 38.3 s; nymphs: 140.0 ± 39.9 s; Fig. 1a). Likewise, fire ants were highly aggressive toward engorged nymphs ($\chi^2 = 59.710$, $df = 1$, $P < 0.001$), taking an average of 30 s to attack engorged nymphs, but the level of aggression depended on tick species ($\chi^2 = 62.273$, $df = 1$, $P < 0.001$; Fig. 1b). Fire ants took the least amount of time to become aggressive toward engorged *A. maculatum* nymphs (8.9 ± 1.7 s) and the longest amount of time to become aggressive toward unfed *A. maculatum* nymphs (139.8 ± 39.4 s). Each type of

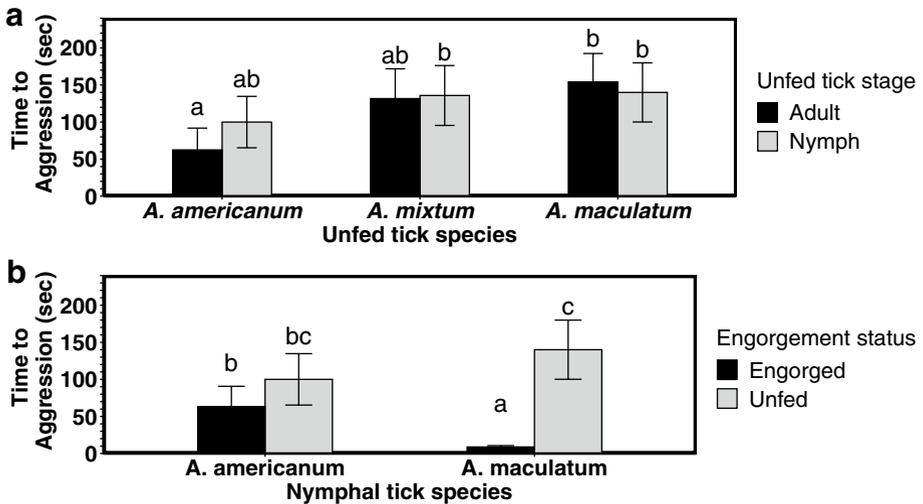


Fig. 1 Mean (\pm SE) time to aggression by fire ants, calculated as the time difference from the initial discovery of ticks by ants to the first aggressive behavior (biting, carrying, or stinging) by ants. Means within a panel capped with different letters are significantly different (Tukey's HSD: $P < 0.05$). **a** Time to ant aggression compared between unfed tick species (*A. americanum*, *A. mixtum*, and *A. maculatum*). **b** Time to ant aggression compared between tick species and nymphal engorgement status (engorged or unfed)

aggressive behavior (biting, carrying, and stinging), along with the proportion of time within the 5-minute observation period that fire ants were aggressive toward ticks, are presented in Online Resource 1 of the supplementary materials.

Overall, ticks were much less active in the presence of fire ants. Unfed tick activity was reduced by approximately 50% in the presence of fire ants ($\chi^2 = 99.7884$, $df = 1$, $P < 0.001$). The effect of fire ants on unfed tick activity, however, varied by species ($\chi^2 = 10.9498$, $df = 2$, $P = 0.004$; Fig. 2a), with unfed *A. americanum* tick activity most strongly affected by fire ants. Unfed *A. americanum* ticks were active $74 \pm 8\%$ of the time when ants were absent and only $24 \pm 6\%$ of the time when ants were present (Fig. 2a). The effects of fire ants on unfed tick activity did not differ significantly by life stage ($\chi^2 = 2.9497$, $df = 1$, $P = 0.09$). There was, however, a significant interaction between tick species, nymphal engorgement status, and ant presence ($\chi^2 = 35.5254$, $df = 1$, $P < 0.001$; Fig. 2b). Engorged *A. maculatum* nymphs were least active in the presence of ants ($6 \pm 2\%$ of the time with ants, $94 \pm 2\%$ without ants) compared with engorged *A. americanum* nymphs ($36 \pm 10\%$ with ants, $94 \pm 3\%$ without ants).

Unfed tick questing was strongly reduced in the presence of fire ants ($\chi^2 = 20.9474$, $df = 1$, $P < 0.001$), with unfed ticks questing on average 54% less often in the presence of ants compared with no ant controls. This reduction differed, however, by tick species ($\chi^2 = 14.6319$, $df = 2$, $P < 0.001$; Fig. 3). For example, unfed *A. americanum* ticks were most strongly affected by ant presence, questing $28 \pm 5\%$ of the time in the absence of ants and only $3 \pm 1\%$ in the presence of ants. The questing by unfed *A. mixtum* and *A. maculatum* ticks was also reduced in the presence of ants, but to a lesser degree (*A. mixtum*: $18 \pm 8\%$ with ants, $35 \pm 13\%$ without ants; *A. maculatum*: $14 \pm 5\%$ with ants, $42 \pm 8\%$ without ants). Unfed nymphal questing was more strongly reduced in the presence of ants compared with unfed adults ($\chi^2 = 5.1996$, $df = 1$, $P = 0.023$), but this effect did not differ by tick species ($\chi^2 = 2.1977$, $df = 2$, $P = 0.33$). Unfed nymphal questing was also more

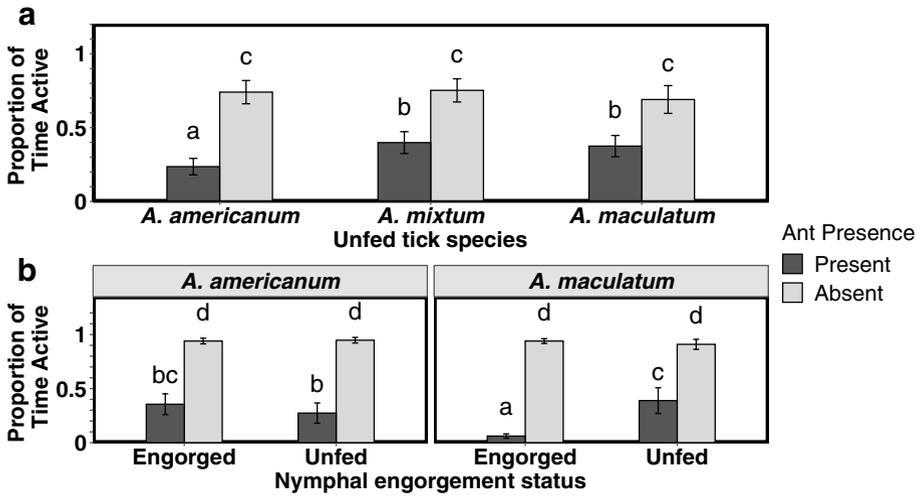


Fig. 2 Mean (\pm SE) proportion of the time that ticks were recorded as active (walking, climbing, and/ or questing; out of 30 total observations over 5 min) in the presence or absence of ants. Means within **a** or **b** capped with different letters are significantly different (Tukey’s HSD: $P < 0.05$). **a** Activity in unfed ticks compared between tick species. **b** Activity in nymphal ticks compared between tick species and engorgement status

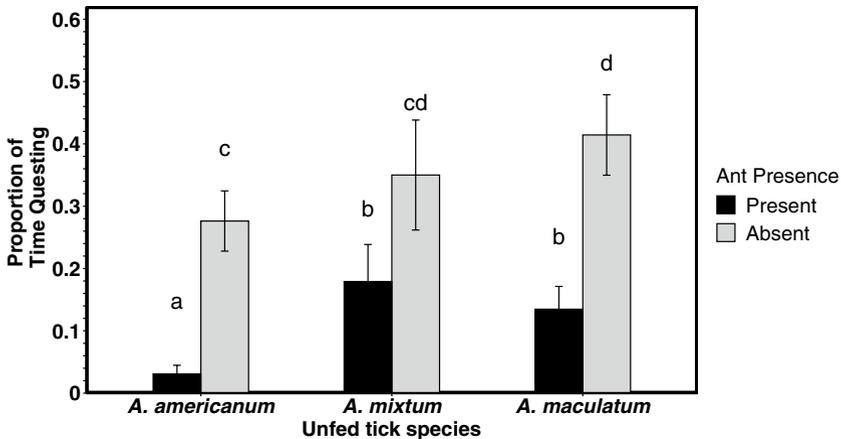


Fig. 3 Mean (\pm SE) proportion of the time that unfed tick species were recorded as questing (out of 30 total observations over 5 min) in the presence or absence of ants. There was no significant interaction between tick species and tick stage, so results from unfed adults and unfed nymphs are averaged together. Means capped with different letters are significantly different (Tukey’s HSD: $P < 0.05$)

strongly reduced in the presence of ants compared with engorged nymphs ($\chi^2 = 25.4185$, $df = 1$, $P < 0.001$). Unfed nymphs quested $41 \pm 4\%$ of the time when ants were absent and only $5 \pm 2\%$ when ants were present. By contrast, engorged nymphs quested very little in both treatments ($1 \pm 1\%$ in presence of ants, $0.5 \pm 0.5\%$ in absence of ants).

Engorged nymphs spent significantly more time walking than unfed nymphs ($\chi^2 = 14.1325$, $df = 1$, $P < 0.001$). Walking by engorged nymphs was strongly reduced in the

presence of ants compared with walking by unfed nymphs ($\chi^2 = 45.1457$, $df = 1$, $P < 0.001$). Engorged nymphs, for example, walked more than 70% less often in the presence of fire ants than when ants were absent ($17 \pm 5\%$ in presence of ants, $68 \pm 10\%$ in absence of ants). The effect of ant presence on walking by engorged nymphs differed, however, by tick species ($\chi^2 = 14.5922$, $df = 1$, $P < 0.001$; Fig. 4). Walking in engorged *A. maculatum* nymphs was most strongly affected by ant presence, as engorged *A. maculatum* nymphs spent $60 \pm 11\%$ walking in the absence of ants and only $6 \pm 2\%$ walking in the presence of ants. The proportion of time out of the 5-minute observation period that ticks were recorded as active, including each type of active behavior (questing, walking, or climbing), are presented in Online Resource 2 of the supplementary materials.

Discussion

Under laboratory conditions, we found that ticks were significantly less active in the presence of ants (Fig. 2). This reduction of tick activity in the presence of fire ants translated to less questing by unfed ticks (Fig. 3) and less time spent walking by engorged nymphs (Fig. 4). Importantly, fire ant aggression corresponded with tick activity; tick activity was more strongly reduced when fire ants became aggressive more quickly. Tick host-seeking behavior is influenced by abiotic factors such as temperature and relative humidity (Crowl et al. 2008; Randolph 2004; Teel et al. 2010), but the non-consumptive (biotic) effects of predators on tick activity and questing have rarely been documented (Fischhoff et al. 2018). As far as we know, Fischhoff et al. (2018) is the only other study to document the non-consumptive effects of a predator on tick questing. The presence of spiders strongly reduced questing of *Ixodes scapularis* nymphs by over 50%, but spiders killed only ~16% of ticks (Fischhoff et al. 2018). Studies examining only the direct effects of predators on ticks are likely missing important indirect effects of predators on tick behavior.

As we predicted, fire ants had a stronger effect on *A. americanum* behavior compared with *A. maculatum* or *A. mixtum*. Fire ants were very aggressive toward unfed *A.*

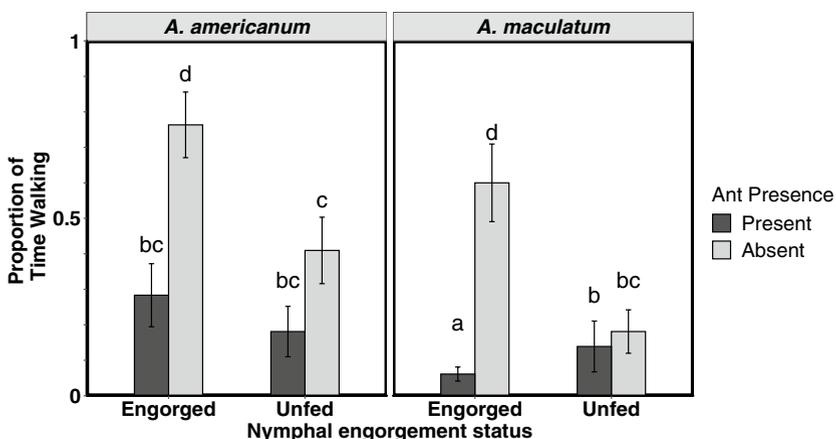


Fig. 4 Mean (\pm SE) proportion of the time that engorged and unfed nymphal ticks were recorded as walking (out of 30 total observations over 5 min) in the presence or absence of ants. Means capped with different letters are significantly different (Tukey's HSD: $P < 0.05$)

americanum ticks (Fig. 1a), which corresponded with a larger reduction in overall activity (Fig. 2a) and questing (Fig. 3) by unfed *A. americanum* in the presence of ants compared with all other unfed ticks. Fleetwood et al. (1984) found that fire ants directly predate engorged *A. americanum* ticks in field mesocosms, but our results indicate that fire ants may also influence *A. americanum* questing behavior. By contrast, fire ants took twice as long to become aggressive toward unfed *A. mixtum* nymphs and unfed *A. maculatum* ticks of both stages. Our results reflect observations from the field that report a lower abundance of *A. americanum* but a higher abundance of *A. maculatum* ticks in fire ant-infested sites (Burns and Melancon 1977; Castellanos et al. 2016; Fleetwood et al. 1984; Teel et al. 1998). Teel et al. (1998) speculated that *A. maculatum* are less exposed to encounters with fire ants because they are most seasonally active when temperatures reduce ant activity, which allows *A. maculatum* to reach high abundances regardless of fire ant presence. Our results suggest that even when fire ants encounter unfed *A. maculatum* ticks, they are less aggressive than when they encounter other species or stages, especially compared with the unfed adults of *A. americanum*. The association between fire ants and *A. mixtum* ticks in the field has not been studied, but we predict that *A. mixtum* abundance might also be unaffected by fire ant presence based on the similarities in our results for both *A. mixtum* and *A. maculatum* ticks.

Interestingly, fire ants were highly aggressive toward the engorged state of *A. maculatum*, attacking them more than 128 s faster than unfed *A. maculatum* of both stages and stinging them the most often of all other ticks studied ($36 \pm 6\%$ of the total observation time; Online Resource 1). Correspondingly, engorged *A. maculatum* nymphs were substantially less active in the presence of fire ants, walking 90% less often than when ants were absent. Increased aggression toward engorged ticks has been documented with other predators (Barré et al. 1991; Burtis and Pflueger 2017; Samish and Alekseev 2001). Engorged ticks likely carry products obtained from the host that could make them more attractive to fire ants and other predators, including skin secretions and bacteria that provide enhanced chemical cues. Additional research into why fire ant behavior differs by tick species and how this influences tick survival will be important for understanding the impacts of fire ants on ticks.

We show the importance of examining the indirect effects of a predator on ticks. Fire ants strongly reduced tick questing. Tick questing behavior has been identified as a potential mechanism influencing risk of tick-borne disease exposure in humans. Geographic differences in the questing height of *I. scapularis* populations, for example, may be associated with variation in the prevalence of Lyme disease in the United States (Arsnoe et al. 2019). The ultimate effects of predators on tick-borne diseases have not been documented, but in other pathosystems, the indirect effects of predators on vectors can strongly influence pathogen transmission (Finke 2012; Jeger et al. 2011; Long and Finke 2015). For example, the presence of a single arthropod predator on wheat altered the behavior of aphids and reduced plant infection by an aphid-vectoring plant virus by over 60% (Long and Finke 2015). It will be critical for future studies to examine 1) how fire ant and tick behaviors translate to the field where the differential phenology of ants and ticks could be considered, and 2) if the indirect effects of predators on ticks correlate with disease dynamics in the field. Combining the effects of both biotic and abiotic conditions on tick behavior and abundance will help to develop a more predictive framework for tick-borne disease risk.

Acknowledgements We thank Otto F. Strey, Tick Research Laboratory, who reared all of the ticks used in this experiment. We also thank Eric Bockoven for helping maintain fire ant colonies and collect data. This work was funded by a grant from the Management of Invasive Ants in Texas Program through Texas A&M

AgriLife Research. This is publication 1611 of the Biodiversity Research and Teaching Collections at Texas A&M University.

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